Impacts of clear-cut harvesting on carabid beetle (Coleoptera: Carabidae) assemblages of aspen dominated forests in central Alberta

by

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Abstract

Disturbances, both natural and those related to human activity, reset succession in boreal ecosystems, and affect forest biodiversity. The link between forest harvesting and biodiversity is of considerable conservation concern. In this thesis, I investigate the impacts of clear-cut harvesting on carabid beetle assemblages, dominant predators in ground dwelling communities, and explore alternative approaches to assess their recovery patterns along a regeneration chronosequence of aspen (*Populus tremuloides*) dominated forest stands in west central Alberta, Canada. Specifically, I show how forest age, or time since last harvest, can only partially characterize impacts on carabid assemblages, and how in addition of small scale habitat characteristics in statistical models can improve description of the recovery patterns. I also explore the use of alternative biodiversity indexes to assess the impacts of harvesting activities. I use indices that account for the functional complexity of carabid assemblages, and for the array of life traits expressed, specifically functional richness.

My results show that, although time after harvest is important in explaining carabid beetle assemblage recovery, the use of small scale habitat variables increases the explanation for the effect of post-harvesting on recovery of carabid beetle assemblages. This improves our understanding of clear cut harvest impacts and post harvest regeneration for carabid beetle assemblages. In addition, measures of functional traits show a clear reduction in functional diversity in carabid beetles after clear-cut harvesting.

Overall, this thesis provides new information about carabid assemblages in aspen dominated forests of the eastern slopes of the Rockies and develops wider approach for research on carabid beetle diversity in forests. I have also tried to highlight the potential usefulness of functional diversity in integrated biodiversity studies aimed at understanding the impact of forest harvest.

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Chapter 1- Introduction

The Taiga, including boreal forests of North America, is the largest terrestrial biome, constituting approximately 33% of the total forested area of the world (State of the World's Forests, FAO, 2014). Boreal ecosystems are central in providing goods and services at both local and global scales (FAO, 2014). Historically, these ecosystems have been subjected to a number of sources of disturbance (Pickett et al., 1985; Bonan et al., 1989; Attiwill, 1994; Chen et al., 2002) that change their structural heterogeneity, modify successional trajectories and influence biodiversity (Pickett et al., 1985; Kuuluvainen, 1994; Bergeron et al., 1998). Specifically, unmanaged boreal areas are commonly subjected to wildfires, pest outbreaks, pathogens, storms and floods (Esseen et al., 1997; Engelmark et al., 1999), while commercially managed areas are increasingly subjected to harvesting at various levels of intensity (Esseen et al., 1997; Bergeron et al., 2012; The State of Canada's Forests, 2015).

The increased use of boreal forests as a source of raw material for industrial use has made harvesting one of the primary sources of disturbance for boreal ecosystems (Esseen et al., 1997; Bergeron et al., 2012). Understanding how disturbances may change the dynamics of boreal forests, and how this affects biodiversity, is a central theme of sustainable forest management (SFM) (Canadian Council of Forestry Ministers, 2005). SFM policies aimed to foster a level of forest use that ensures their natural regeneration, protect their diversity, and promote their ability of sustain ecological and economic functions (FAO, 2014).

The impacts of harvesting on boreal biodiversity are of particularly interest in Canada, with respect to the national move to sustainable forest management (The State of Canada's

Forests, 2015). Boreal ecosystems provide habitats for highly valued biodiversity, and are important both for regulation of atmospheric CO_2 levels and as a source of raw material for the Canadian forest industry. Forested areas managed for industrial production in Canada are primarily the more productive forests located in the southern part of the country (Bickerstaff et al., 1981; Band 2000). These areas are subjected to a variety of harvesting protocols. Among these, some form of clear-cut harvesting is still considered the most commonly applied prescription in Canada (The State of Canada's Forests, 2015).

Clear-cut harvests have well known and huge impacts on forest ecosystems, changing habitat structure and affecting the diversity of taxa adapted for life in forests. Clear-cut involves the complete removal of the tree cover and, in most cases, subsequent application of post-harvest management protocols. These may involve removal of woody debris, often followed by soil scarification and the use of chemicals (herbicides and pesticides) thought to encourage recovery of commercially desirable forest elements. These activities alter the resources and ecological niches available for animals and plants using forest habitats (Keenan, 1993), and as a result influence forest biodiversity, affecting species richness, community composition and relative abundances of species (Spence et al., 2001; Venier et al., 2014).

An important part of developing efficient and effective forest management policies and protocols is effectively monitoring and quantifying harvest impacts (CCFM, 2005). The majority of studies on boreal forests use an approach based on regeneration chronosequence and common biodiversity indicators (species richness, abundances) to explore these impacts and to assess biodiversity and use it as a measure of ecosystem recovery (Niemelä et al., 1993, 2007; Niemelä, 1997 Koivula et al., 1999; Magura et al., 2005; Cobb et al., 2007 Vanbergen et al., 2010). For particular groups of species, these indicators and approaches could limit our understanding of the magnitude of impact and the subsequent regeneration process of the boreal ecosystem. Thus, in this thesis I explore alternative approaches to quantify harvest-related impacts on the biodiversity of litter dwelling communities. These include the use of small scale habitat descriptors, which may improve characterization of the impact of current harvest protocols and recovery of assemblages (Chapter 2), and the use of alternative biodiversity indicators, which account for the functional structure of the assemblages (Chapter 3).

1.1. Carabid beetles as model taxon for study of forest recovery

Various taxa have been used to represent biodiversity in assessing impacts of forest disturbance. Among these, carabid beetles (Coleoptera: Carabidae) have been used specifically to test correlations between biodiversity and forest management prescriptions in forest areas subjected to clear-cut harvesting (Niemelä et al., 1993; Niemelä, 1997; Rainio, 2003). Carabids are an excellent group for such assessments because: 1) their natural history and taxonomy are reasonably well known (Lindroth, 1961-1969); 2) they are considered good indicators of local habitat conditions (Rainio et al., 2003; Thiele, 1977); and 3) there is a direct correlation between changes in forest characteristics, attributable to harvest practices, and carabid beetle diversity (Niemelä et al., 1993, 2007; Pearce et al., 2006). Furthermore, changes in forest structure after harvest have been strongly associated with changes in carabid beetle assemblages; specifically, there is a well-documented shift in species composition from species adapted to mature forests towards species adapted to open habitats (Niemelä et al., 1993; Magura et al., 2005). These correlations make carabid beetles a suitable study model for ecological research about the dynamics of northern forests.

1.2. Thesis rationale and chapters structure

In this thesis, I intend to demonstrate that current methods of measuring carabid beetle diversity can be improved to better interpret their recovery after clear-cut harvests. The thesis is organized in 4 chapters: the present Introduction chapter (Chapter 1), two data chapters based on original data (Chapter 2 and Chapter 3) and centered on the study of carabid beetle assemblages in aspen stands of west central Alberta, and a final chapter to provide a general discussion and my overall conclusions (Chapter 4).

In chapter 2, I consider the ability of macro-scale variables to explain recovery patterns of carabid beetle assemblages along a forest regeneration chronosequence for aspen stands in western Alberta. I demonstrate that a combination of small scale-scale variables, which describe changes of habitat characteristics at the litter level, are more strongly associated with recovery patterns than the overall stand structure (canopy closure and stand age). In chapter 3, I explore the impact of forest harvest on functional diversity of carabid beetles, and consider how such information can provide useful description of the recovery process along the forest regeneration chronosequence. Finally, in Chapter 4 (General Discussion and Conclusions) I summarize my findings, and suggest possible directions for new research about recovery of forest carabid beetle assemblages after harvest.

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Chapter 2- Variation in habitat structure and post-harvest recovery of carabid beetle (Coleoptera: Carabidae) assemblages

2.1. Introduction

Northern forests are shaped by a variety of disturbances (Pickett et al., 1985; Bonan et al., 1989; Attiwill, 1994; Chen et al., 2002) that change their structural heterogeneity, modify successional trajectories and influence their biodiversity (Pickett et al., 1985; Kuuluvainen, 1994; Bergeron et al., 1998). Historically, wildfire has been the most common natural disturbance and initiator of secondary succession in the Canadian boreal zone, followed by, in order of total area impacted, insect outbreaks, pathogens and, in more minor proportion, by storms and floods (Engelmark et al., 1999, The State of Canada's Forests, 2015). However, with increased use of forests as sources of raw material for industrial production, harvesting has become a major forest disturbance and initiator of secondary succession in Canada (Bergeron et al., 2012; Venier et al., 2014). Understanding the impact of harvesting on forest biodiversity is a central theme of ecological studies of northern forest ecosystems (Spence, 2001), and such considerations are central to development of sustainable forest management policies and protocols (SFM) (FAO, 2014; The State of Canada's Forests, 2015).

Removal of tree cover and the subsequent application of post-harvest treatments (*i.e.*, removal of wood debris, soil scarification, the use of herbicides and pesticides), as are included in many clear-cut prescriptions, alter the resources and ecological niches available for animals and plants (Keenan et al., 1993). These changes in habitat structure influence forest biodiversity through effects on species richness, composition and relative abundances (Spence, 2001; Venier et al., 2014), and over time such changes may influence the ecological function and stability of forest ecosystems. Because of these relationships, biodiversity is one of the six key indicators of sustainable forest management adopted by the Canadian Council of Forest Ministers (CCFM, 2005).

Under the umbrella of sustainable forest management, particular taxa are commonly used as indicators to investigate the impacts of harvesting on biodiversity and assess the subsequent recovery in forest communities. Among these taxa, carabid beetles (Coleoptera: Carabidae) are an excellent target group for ecological studies of northern forests (Pearce et al., 2006). Changes in forest structure after harvest are associated commonly with changes in carabid beetle assemblages, specifically shifts in species composition from species adapted to more stable mature forests toward species adapted to open and more disturbed habitats (Niemelä et al., 1993; Koivula, 1999; Koivula, 2002a; Koivula et al., 2002b; Magura, 2005).

It has been common practice in management of boreal ecosystems to use plant community structure to quantify the degree of post-harvest forest recovery (Bergeron et al., 1998, 2012; Niemelä et al., 1993, 2007). Recovery of plant communities follows successional trajectories that lead over time to climax communities with a certain level of similarity with old-growth forest, which depend on geographic position, tree species composition and time since the last harvest (Luken, 1990). However, recovery of other forest-dwelling taxa likely occurs on different timelines, driven by different mechanisms. For example, post-harvest recovery of carabid assemblages is influenced by resource availability (Koivula et al., 1999; Vanbergen et al., 2010) and by overall habitat structure

(Niemelä et al., 1993; Koivula et al., 1999; Magura et al., 2005), with small-scale habitat structure (variation within a forest patch), often referred to as ‘microhabitat’, playing a significant role (Thiele, 1977; Koivula, 1999; Rainio, 2003; Niemelä, 2007). Thus, I argue that small scale habitat features, only marginally correlated with stand age, could more strongly influence post-harvest recovery of animal taxa like carabids than does forest successional stage (Yemshanov et al., 2003; Taylor et al., 2013).

Small scale structure influences on insect distributions have long been a central entomological topic, and the importance of small scale habitat conditions for carabid beetles has been partially explored in relation to post disturbance recovery of assemblages (Niemelä et al., 1993; Koivula et al., 1999; Koivula, 2002a; Koivula et al., 2002b; Magura et al., 2005). A more in-depth description of microhabitat variation along the forest recovery chronosequence could foster a more complete interpretation of how stand structure affects carabid beetles and assemblages of other epigaeic invertebrates. Such understanding could illuminate aspects of forest structure that should be considered when assessing post-harvest recovery in biodiversity studies and contribute to developing conservation plans more sensitive to biodiversity in the context of sustainable forest management (SFM).

In this chapter, I demonstrate that small scale habitat structure better predicts recovery of carabid assemblages than does the characterization of stands in terms of tree cover alone. My objective is to investigate whether forest age on its own is a good predictor of post-harvest recovery for carabid beetles, based on species richness, species composition and species abundances. Specifically, I will answer the following questions: (1) is forest age an effective indicator of post-harvest recovery for carabid beetle assemblages? (2) Do forest structural characteristics at small scale affect carabid beetle recovery? (3) Does the addition of small scale characteristics in predictive models improve understanding of carabid beetle assemblage recovery?

2.2. Methods

The analyses presented in this chapter are based on data collected from the Lower-Upper Foothill transition zone (EcoRegions Working Group, 1989) in forests near the town of Hinton (53.4114° N, 117.5639° W), in west central Alberta, Canada (Appendix A). The area is commercially managed for forest products by West Fraser Timber Co. Ltd., which has commonly applied clear-cut harvesting with a rotation period (time interval between two consecutive harvesting to allow forest structure to recover) of 80 years (Udell et al., 2013).

The forest stands selected for field work are dominated by trembling aspen (*Populus tremuloides*), with a variable percentage of interspersed spruces (white spruce, *Picea glauca*, or black spruce, *Picea mariana*), and a more minor component of lodgepole pine (*Pinus contorta*). Stands were selected along a post-harvest regeneration chronosequence, ranging from recently harvested stands to mature forests used as controls, representing 5 age categories: recent clear-cut (from 2 to 4 years after harvest), 20 (± 4), 40 (± 2), 60 (± 3) years post-harvest, and mature never-harvested stands (80 years or older). Stand age was determined using West Fraser Timber Co. Ltd. GIS® data (personal communication). For each age category, four replicate sites were identified in the field, for a total of 20 forest stands.

A total of 120 pitfall traps were used to collect information about composition and relative abundance of carabids. Each pitfall trap consisted of a 1L plastic cup, placed in the ground with the upper rim at the ground level, to serve as a sleeve to minimize disturbance of edge at collection, with a smaller 250 ml plastic cup nested inside (Spence et al., 1994). The inner cup was partially filled with a 70% solution of ethylene glycol, which served as killing agent and preservative. Traps were covered with a 10x10 cm PVC roof, held in place with metal wire (Appendix B).

Six traps were positioned in each stand at a minimum distance of 20 m from each other in two roughly parallel lines of three traps each. This distance appears to be sufficient to minimize autocorrelation of catches among pitfall traps in similar habitats (Digweed et al., 1995). Trapping covered approximately the frost-free period, between May and the end of August 2014, which includes the period of highest activity of most adult carabid species in these forests. Specimens were collected and the preservative was replenished at two-week intervals, providing a total of 7 collections.

All adult carabids were identified to the species level following Lindroth (1961-1969) and named according to Bousquet (2013). To minimize effects of trap disturbance on species abundances, catches were standardized to 100 days of trapping effort (length of the trapping period). In other words, total number of individuals, captured by each trap, was first divided by the number of days the trap was functional and undisturbed, and then multiplied by 100.

2.2.1. Data about small scale variables

Small scale variables that described forest structure around each trap were measured during summer of 2014, as described in detail below. These variables were selected to describe canopy structure around each trap, litter structure and soil characteristics using ground layer plants and small scale climate using data loggers. Variables selected include total number of standing trees, both living and dead, tree species composition, canopy cover, ground cover (% of herbaceous plants) and herbaceous vegetation composition (most abundant herbaceous species). Data about temperature and light intensity were collected over summer 2014 using HOBO® data loggers for a subset of 38 pitfall traps, chosen to represent all age classes. A complete list of the habitat variables used in the analyses and the relative codes are listed in Table 2-1.

2.2.2. Tree species composition and canopy cover

I characterized tree species composition around each trap in terms of the dominant tree species (the tree species with the highest number of individuals, among all trees with DBH >5 cm), inside a 100 m^2 (10x10m) square centered on the trap. All living trees were counted and recorded according to species, and the species with most individuals was considered as dominant. Recently clear-cut plots, lacking any canopy cover, were classified as having no dominant tree species. A similar count method and the same area were used to tally number of dead trees (standing dead trees and stumps, at least 1.3 m in height), without distinction or selection for different tree species.

Canopy cover (%) was estimated in mid-July 2014, at the time of maximum foliage coverage for deciduous species, using a concave spherical densitometer modified according to Strickler (1959). A graphical description of the method is presented in Figure 2-1: for each pitfall trap, the number of nodes covered by the foliage projection inside the V-sections of the densitometer was considered as the canopy cover; this measure was repeated for the four cardinal directions, and the sum of the four measurements considered as the canopy cover for the trap.

2.2.3. Herbaceous species and ground cover

I also characterized herbaceous species composition in terms of the species that covered the majority of the area in a circular plot (radius of 5 m, ~78.5 m^2) centered on each pitfall trap. Given species-specific requirements for herbaceous plants, species composition can be related to soil moisture, drainage and soil nutrients content, as well as small scale-climate around the trap (temperature, moisture).

Percent ground cover was estimated as the projection on the ground of green leaves and live branches of understory plants below breast height (1.3 m from the ground). Photographs of 1x1m squares, centered on each pitfall trap (Fig. 2-2), were taken in late June and in mid-August 2014. The percentage of ground covered was calculated using the image analyses software ImageJ® (Abramoff et al., 2004). The software estimates the percentage of "green" and "non-green" coverage based on pixel analysis. The distinction between the two pixel categories is based on a threshold value, selected to incorporate green leaves and branches, but to exclude bare ground, litter or debris. The result is a percentage of pixels identified as cover, which was then converted into the percentage of the 1x1m square covered by green leaves (Fig. 2-2). Values obtained from each set of pictures were then averaged to obtain mean cover the summer (*Covav*), and used to calculate the ground cover variation (*Covvar*) as the difference in percentage cover between June and August.

2.2.4. Temperature and light intensity

Temperature (°C) and light intensity were measured for a subset of 38 pitfall traps during summer 2014 (May to August), using HOBO data loggers (HOBO® Pendant). The traps monitored were selected among all the traps to represent all age categories along the forest recovery chronosequence. The data loggers were placed on a plastic support about 10 cm above the ground, mounted on a wooden pole close to the rim of each selected pitfall trap. The data obtained were used to calculate average summer temperature (*AvT*), minimum (*MinT*) and maximum (*MaxT*) temperature, and average light intensity (*AvL*).

2.2.5. Data analyses

All analyses presented were performed using the package *vegan*, part of the *R* software package for statistical analyses (v. 3.1.2, R Core Team, 2014).

2.2.5.1. Rarefied Species Richness

Rarefied species richness was calculated following Chao et al. (2012), and compared among stand age classes. Use of rarefaction allows comparisons of species richness among samples (in this case, from different age classes), regardless of variability in capture rates and levels of disturbance.

2.2.5.2. Additive partition of biodiversity

Additive partition of biodiversity (Crist et al., 2003), based on rarefied species richness (Chao et al., 2012), indicates the proportional contribution of α diversity (taken to be that revealed at the lowest sampling level, *i.e.*, individual pitfall traps), and β diversity partitioned among increasingly higher hierarchical sampling levels (among traps, trap lines, plots) to total γ diversity (species richness of the whole data set). This analytical approach considers patterns of spatial variation at several levels, and regards high β diversity values, calculated between hierarchical levels, as an indication of variation in species composition at different spatial scales (Crist et al., 2003). Specifically, the hierarchical levels considered are: traps, among traps inside each forest stand, among traps in forest stands of the same age, and among traps in forest stands of different ages. If time since harvest is a sufficient indicator of carabid beetle recovery, then β diversity among different age classes should contribute more to total γ diversity than β diversity calculated among stands inside each age class.

Two different additive partitions were calculated: the first used carabid beetle captures with no distinction among age classes, but divided in three categories, based on species relative abundance (total species richness, species richness considering only common species, and species richness considering only less abundant species); the second considers total species richness, regardless of any division in the analyses between age classes. These partitions were intended to show the different contributions of subsequent hierarchical sampling levels to total diversity of carabid species, and to illustrate how diversity changes along the regeneration chronosequence.

2.2.5.3. Redundancy Analysis (RDA)

Given my hypothesis that information in addition to stand age can improve prediction of carabid assemblages, I expected that an RDA that classifies assemblages based on forest stand age would explain less variance in beetle assemblages than those incorporating other combinations of variables. Thus, I ran four separate RDAs, to model the captures from each of the 120 pitfall traps using different combinations of potential explanatory variables. Before ordination, the pooled captures for each trap were Hellinger transformed (Legendre, 2001) so that Euclidean-based distance metrics could be used without violating the linearity assumption of such methods (Legendre et al., 2001). Two different matrices were used for each RDA presented: one including the abundances of each species in each trap, and one including the environmental variables that describe small scale structure, selected for each specific RDA, associated with each trap.

2.3. Results

Total beetle abundance was higher for plots in the three oldest age classes (40 and 60 years after harvest, and mature stands) than in the two youngest groups of stands (clear-cut and 20 years old) (Fig. 2-4). In contrast, rarefied species richness was lowest in younger stands, and increased along the regeneration chronosequence (Fig. 2-5).

2.3.1. Additive partition of biodiversity

The first additive partition, based on specimens from all traps, forest stands and age classes (left stacked bar, Fig. 2-6), shows that α diversity at the trap level and β diversity among traps inside each forest stand contribute most to γ diversity for common species, while β diversity among age classes is more important for rare species. β diversity among stands makes a higher proportional contribution to γ diversity of carabid assemblages in these landscapes than does variation among age classes. The center-stacked bar in Fig. 2-6 shows the same analysis for data restricted to common species (present in most forest stands and with higher abundances). The main component influencing γ diversity of common species is α diversity at the trap level, *i.e.*, for these species there is little spatial variation on these landscapes.

The opposite can be said for rare species, for which variation is partitioned in the right stacked-bar of Fig. 2-6. Here, β diversity between forest stands of different age classes shows higher influence on γ diversity. This pattern is driven mainly by species that are primarily adapted to open habitats and recent clear-cuts (mainly the genera *Amara*, *Notiophilus*, *Agonum* and *Harpalus*). Thus, presence of open habitats, suitable for these species, affect their abundance more than small scale habitat variation within forest stands.

An additive partition based on all traps, separated by age class (Fig 2-7), shows that as stand age increases, species composition changes. Species adapted to open areas and influenced by spatial distribution and structural characteristics of younger stands, are replaced by forest specialists, adapted to areas with closed canopy. For forest specialists β diversity among traps becomes increasingly more influential for γ diversity, suggesting that the differences in small scale habitat characteristics among each trap have an impact on species composition. Overall, the results of the additive partition show that variation in species richness in older stands is primarily driven by α diversity at the trap level ($\alpha 1$) and β diversity among traps ($\beta 1$), while in younger stands total γ diversity is mostly influenced by β diversity among forest stands ($\beta 3$).

2.3.2. Redundancy Analysis (RDA)

RDA ordinations depict the variation in overall carabid abundance and species composition among traps, and clarify the significance and relative contribution of each explanatory variable included in these analyses toward explaining variation in carabid assemblages (Tables 2-1 and 2-2). Variables selection among the pool of variables collected in the field was performed for each RDA using Variance Inflation Factor (VIF, Gross, 2003). The significance of each explanatory variables was assessed using an ANOVA test with 1000 permutations. Total data variability explained by the combination of variables reported in the results is the adjusted r-squared (R^2). In each RDA, ellipses represent the 95% confidence interval around the centroid of each group of traps for each age class.

Time since harvest, or "*Age*", was the only explanatory variable in RDA1 (Fig. 2-8). This ordination shows larger spread among traps in younger stands (red and blue points, clear-cut and 20 years old), indicating that assemblages of recent clear-cuts were more variable. Lower variability was detected among traps and among groups of traps from more mature stands (40, 60 and 80 years old). This model, including only stand age, explained about 22% of the variability in these assemblages, as represented by these samples.

Subsequent RDAs incorporate alternative groups of variables (Table 2-1) to further assess the effect of small scale habitat characteristics on carabid assemblages and the ability of these alternative data to explain variation in assemblages.

The first of these RDAs, RDA2, includes the influence of average ground cover (*Covav*) and its variation over the summer (*Covvar*), main herbaceous species (*Mainsp*), total number of living (*TotAlive*) and dead (*D*) trees, and canopy cover (*Cancov*) (Fig 2-9). The use of these alternative combinations variables produced a model explaining approximately 29% of the variation in the data; identity of the main herbaceous species (*Mainsp*) significantly affected the variation in carabid species composition and abundances, while variation of ground cover (*Covvar*) and number of dead standing trees (*D*) had only marginally significant effects. Euclidean distances among points associated with traps and groups of traps identified by age class are similar to the ones showed in RDA1, suggesting that the patterns depicted are the same, although the total variability explained is increased.

RDA3 (Fig. 2-10), restricted to data from traps positioned in older stands (40 and 60 years after harvest, and mature stands), further illustrates the effectiveness of small scale variables in interpreting assemblages recovery in stands that are approaching rotation age. This ordination explains approximately 36% of the variation in the data for these older stands. Average ground cover (C*ovav*), main herbaceous species (*Mainsp*) and the number of dead standing trees (*D*) significantly affected carabid beetle assemblages. The RDA3 ordination underscores that variation in forest structure at the ground level (herbaceous species composition, amount of bare ground and volume of decaying biomass) drives variability on species composition for carabid beetle assemblages in older stands.

RDA4 (Fig. 2-11) shows the effects of temperature and light intensity on trap catches, given the influence of the covariates used in the previous RDAs, but restricted to the subset of 38 traps for which small scale climatic data were available. The ordination explains about 45% of the variation in the data. Average temperature (*AvT*) and minimum temperature (*MinT*) were significantly associated with structure of carabid assemblages, while ground cover variables (C*ovav*, *Covvar*) had only a marginally significant effect. Although explaining more of the overall variability, RDA4 is mostly likely highly sensitive to differences in small scale climate between open areas and mature forest.

2.4. Discussion

The foregoing analyses show that information about habitat structure measured at relatively small scales can increase understanding of carabid assemblage recovery after forest harvest. For carabid beetle assemblages, a clear and well-known recovery pattern for species richness and overall abundance can be depicted on the basis of forest age alone (Niemelä et al., 1993; Koivula, 2002a, Koivula et al., 2002b) (Fig. 2-4 and 2-5). This pattern commonly shows higher species richness but lower abundances in recently clear-cut stands. In western Canada, this mainly reflects a shift in species composition from assemblages that are dominated by species of the genera *Harpalus* and *Agonum* in clear-cuts toward more abundant assemblages dominated by species of the genera *Pterostichus* and *Calathus* in older stands.

Forest age, however, is less effective for predicting recovery in relation to variation in species composition and relative species abundances. The importance of small scale forest structure for carabid assemblages has been explored in previous studies (Koivula et al., 1999; Magura et al., 2005; Pearce et al., 2006), but has been rarely framed in the context of understanding how small scale habitat variability is related to recovery of assemblages after harvest. When forests reach later successional stages, overall canopy cover and tree species composition appear to become less important in driving assemblage structure than is habitat structure at scales smaller than the stand level (Niemelä et al., 1993; Koivula, 1999 et al.; Koivula, 2002a; Koivula et al., 2002b; Magura, 2005). This is reflected in the above analyses of γ diversity of forests stands of different age (Fig. 2-7). Species richness in forests that have reached different levels of recovery toward their original habitat structure (*i.e.*, 40 and 60 years post-harvest stands) reflects mainly the number of species captured in each trap (α1), and differences in species richness among traps (β1) in each stand. Thus, changes in species richness can be related to both habitat structure and the amount of resources available, as influenced very locally by forest structure at the stand and trap levels.

Results of the four RDAs presented above (Figs. 2-8 through 2-11) support the claim that small scale habitat structure is an effective predictor of carabid assemblage structure. Clearly, including small scale variables increases the explanatory power of these ordinations, especially with respect to recovery of assemblages to their state in never harvested forest. In general, RDAs detected patterns of variation among traps and age classes consistent with our understanding of factors associated with habitat use for forest carabids (Niemelä et al., 2007).

The first RDA (Fig. 2-8) shows that in an overall analysis of beetle assemblages in relation to time since stand origin, use of stand "*Age*" alone explains about 25% of the variation observed. It is likely, however, that the variability explained is mainly attributable to differences in species composition between assemblages in younger stands (clear-cut and 20 years old), dominated by open habitat specialists, and assemblages in older stands that have, to different degree, recovered structures more similar to that of mature forest (Niemelä et al., 1993).

Including additional explanatory variables (Figs. 2-9 to 2-11) increases the amount of variation explained, improving description of assemblage recovery. The results show that forest structural characteristics at the ground level, such as percentage of ground covered by herbaceous plants and their species composition, and abiotic factors, such as temperature, strongly affect carabid assemblages. These variables are apparently associated with recovery of assemblages after disturbance in ways not simply associated with time since disturbance.

Small scale habitat characteristics are central to habitat requirements of both adult (Koivula et al., 1999; Koivula, 2002a; Koivula et al., 2002b) and larval (Thiele, 1997) carabids, and may not be strongly related to characteristics of canopy layer vegetation. Herbaceous plant composition can be influenced by soil physical characteristics, like the depth of the organic layer, soil moisture, drainage and soil profile. Variation in all of these factors in relation to forest disturbance associated with harvesting can influence the post-harvest recovery process for carabid beetle assemblages. For similar reasons, abiotic factors like temperature fluctuation can also affect magnitude of assemblage recovery. The structure of carabid assemblages in mature forest unaffected by harvesting depends on local variation in small scale habitat characteristics, important for individual species (Niemelä et al., 1993; Koivula et al., 1999). Harvest can delay natural development of forest stands, by homogenizing habitat structure of the starting point of the regeneration succession (Niemelä et al., 1993; Engelmark et al., 1998). This means that a stand that has reached the “old-growth” stage, in relation to its age and canopy structure, may not necessarily have all habitat characteristics required to support the fauna of an unharvested stand.

2.4.1. Final considerations

Management of forest resources is likely to be more effective with better understanding of the disturbance dynamics that shape and influence forest ecosystems. In this chapter, I demonstrate that recovery of ground beetles may be only partially related to the age of the forest per se, and that it depends strongly on small scale habitat characteristics. Because conservation of biodiversity is one of the six criteria of sustainable forest management in Canada (SFM; CCFM, 2005), faunal recovery to pre-harvest states is a significant aspect of setting stand rotation times. The information presented in this thesis about carabids, which serve as an effective model for other taxa (Niemelä et al., 1993; Rainio et al., 2003), suggest that including fine scale forest structure characteristics in assessments of stand recovery may improve our ability to predict faunal recovery in post-harvested forests. At least, information about carabids may be usefully predict recovery of other epigaeic taxa, e.g., spiders (Arachnida: Aranea) or rove beetles (Coleoptera: Staphylinidae), commonly included in studies on forest biodiversity.

Connections between ground beetle assemblages and small scale habitat characteristics, as presented in this chapter, could be used in two different but complementary ways. On the one hand, habitat structure could be used in studies on forest biodiversity as additional variables that can improve effectiveness of monitoring efforts, to better assess the aspects of stand structure important to maintain ground beetles and, more widely, litter dwelling communities diversity. Such information about carabid beetles could be used, on the other hand, to infer and execute harvest in a way that allows for a more natural overall forest structure regeneration, and to quantify the effects of different harvesting strategies or post-harvest management protocols on forest diversity.

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Table 2-1: Variable used in the RDAs and their descriptions

Variable name	Description
Age	Forest age (time since last harvesting)
Covav	Average ground cover (% of green leaves)
Covvar	Variation of ground cover over the summer
Mainsp	Main herbaceous species (highest % covered)
Mtree	Main tree species
Cancov	Canopy cover percentage
TotAlive	Total number of alive trees around the trap
D	Number of standing dead trees
AvT	Average temperature over the summer
MaxT	Maximum temperature
MinT	Minimum temperature
AvL	Average light intensity over the summer

Table 2-2: Significance of explanatory variables (α= 0.05) for each RDA

Variable	RDA1	RDA2	RDA3	RDA4
Age	0.001*	-	-	-
Covav	-	0.053.	0.001*	0.023.
Covvar	-	0.007*	0.25	0.031.
Mainsp	-	0.0002*	0.0002*	0.087
Mtree	-	-	0.7	-
Cancov	-	0.0002*	0.25	-
TotAlive	-	0.0002*	0.16	-
D	-	0.006*	0.004*	-
AvT	-	-	-	0.001*
MaxT	-	-	-	0.05.
MinT	-	-	-	0.001*
AvL	-	-	-	0.21

Significance levels: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’

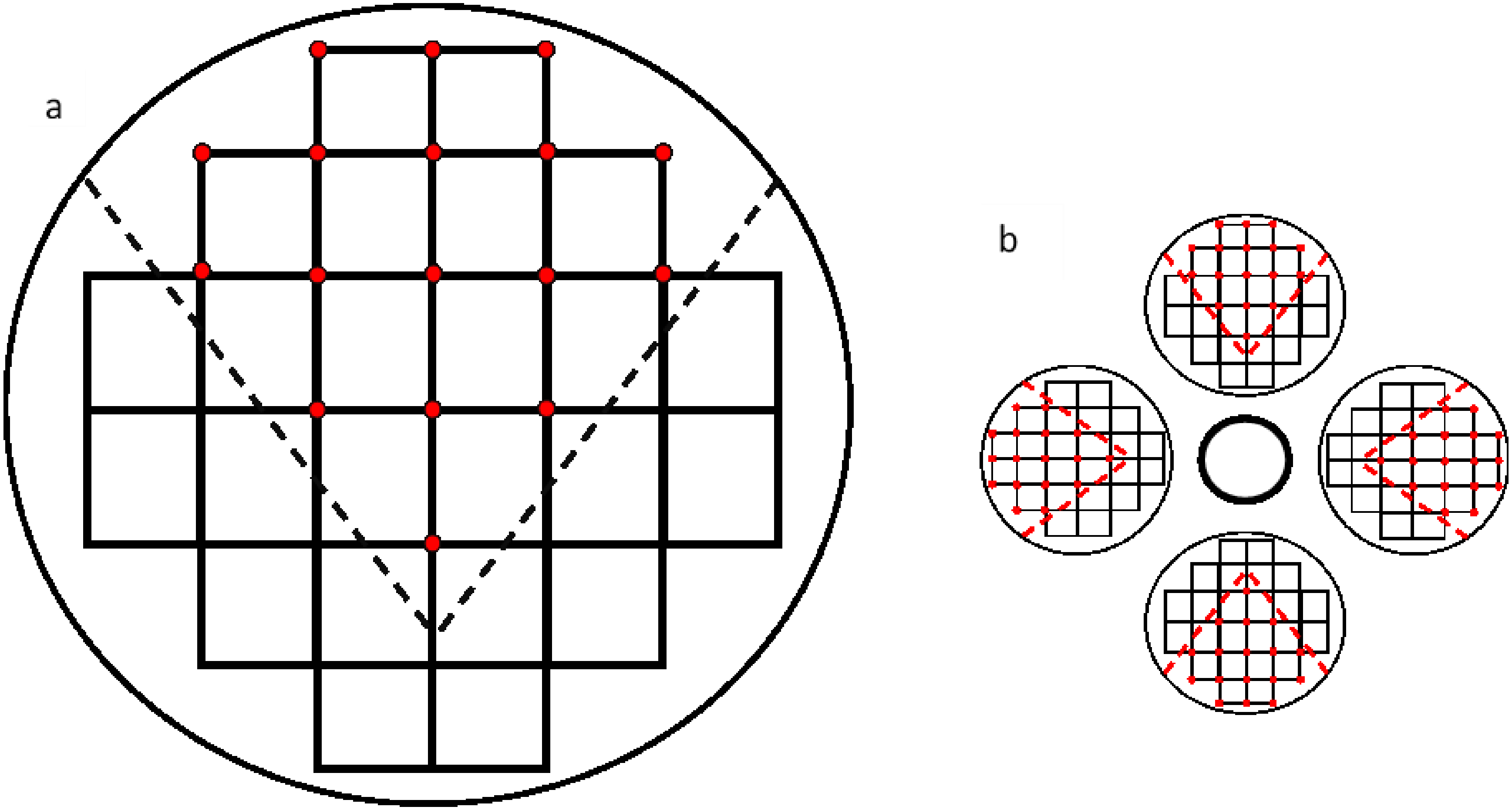

Fig 2-1: Modified method for canopy cover detection (Strickler, 1959) using a concave densitometer (a). The 17 dots (red circles) at the line intersections inside the V-shaped section (dashed line) are the ones considered when calculating canopy cover. Each point covered by the projection of the canopy is counted. The same operation is repeated four times, each time pointing the densiometer at a different main cardinal direction (N, S, E and W) around the trap (b). To calculate the percentage covered, the total number of point covered is then multiplied by 1.5 (Strickler, 1959).

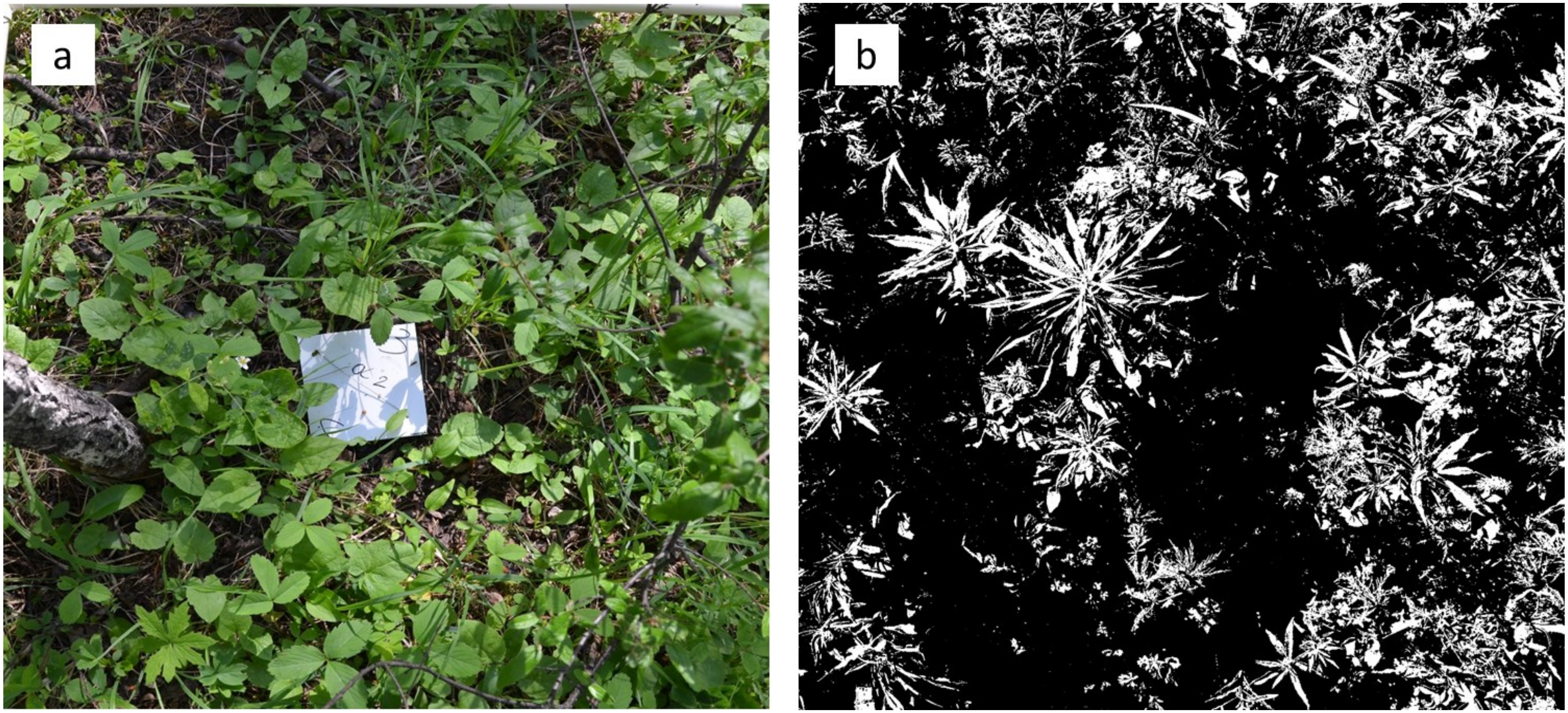

Fig 2-2: The procedure used to calculate ground cover percentage. A picture of a 1x1m square, centered on each pitfall trap (a) was taken at the end of June and in mid-August. The pictures were analyzed using the software ImageJ®, transforming the image in a black and white pixel mask (b), where white pixels represent green areas (leaves, grass), and black pixels represent bare ground or areas not covered by vegetation. The mask is then used to calculate the percentage of the area covered.

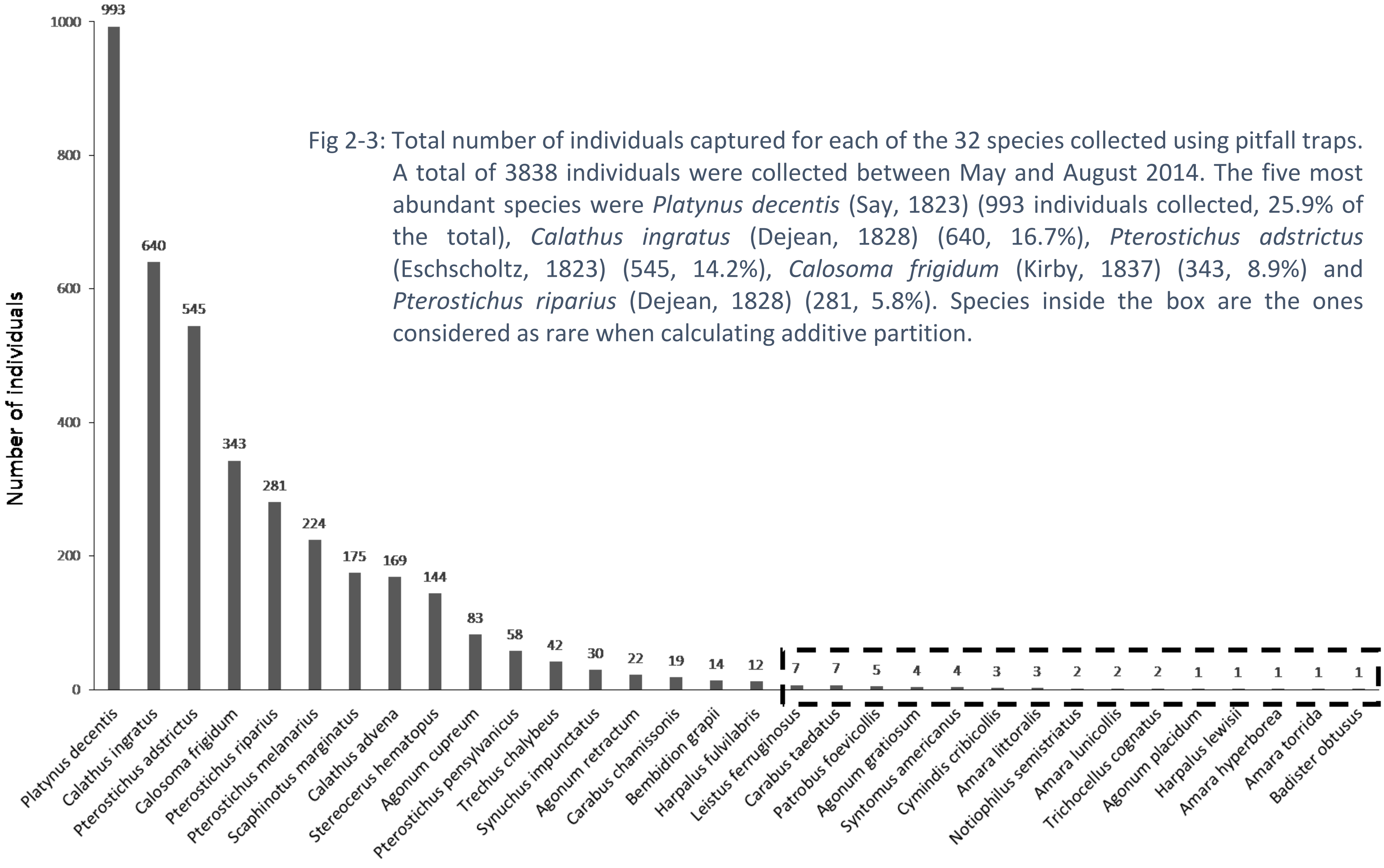

Fig 2-3: Total number of individuals captured for each of the 32 species collected using pitfall traps. A total of 3838 individuals were collected between May and August 2014. The five most abundant species were *Platynus decentis* (Say, 1823) (993 individuals collected, 25.9% of the total), *Calathus ingratus* (Dejean, 1828) (640, 16.7%), *Pterostichus adstrictus* (Eschscholtz, 1823) (545, 14.2%), *Calosoma frigidum* (Kirby, 1837) (343, 8.9%) and *Pterostichus riparius* (Dejean, 1828) (281, 5.8%). Species inside the box are the ones considered as rare when calculating additive partition.

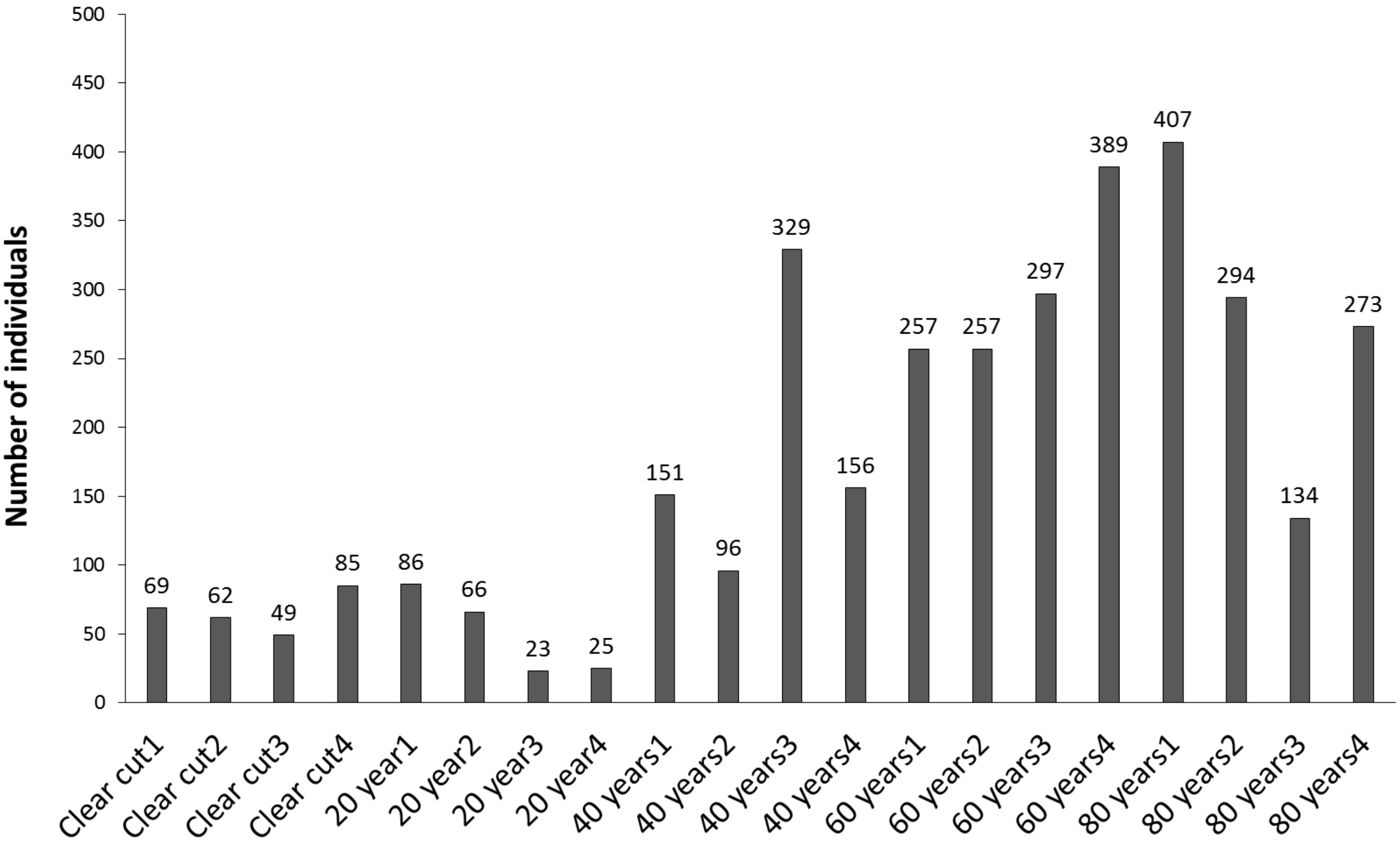

Fig 2-4: Total carabid captures for each site divided by age class. Overall captures are higher in older forest stands.

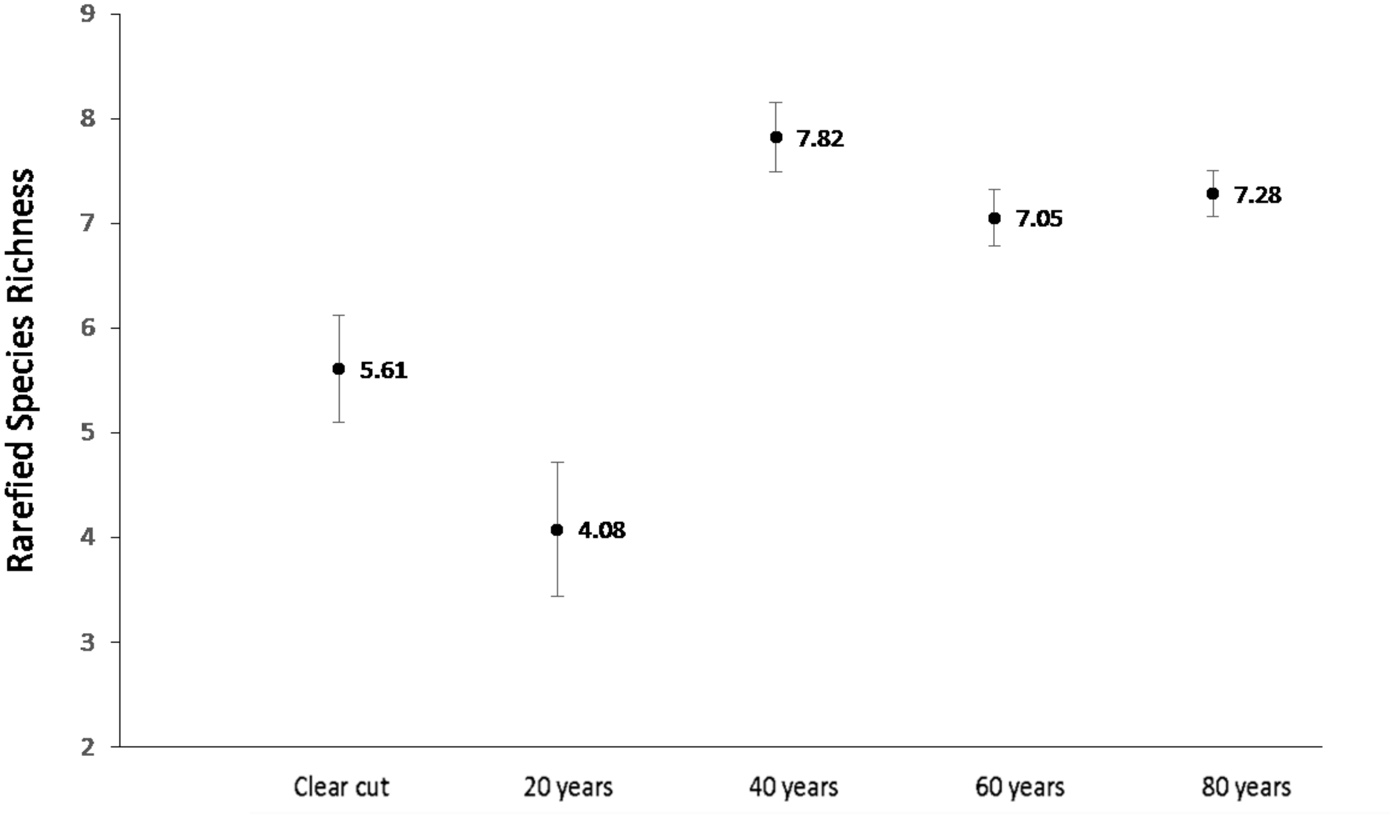

Fig 2-5: Rarefied species richness for each age class. Species richness increases along the regeneration chronosequence. Older forest stands (40, 60 and 80 years old) do not differ significantly. Error bars: 95% confidence interval.

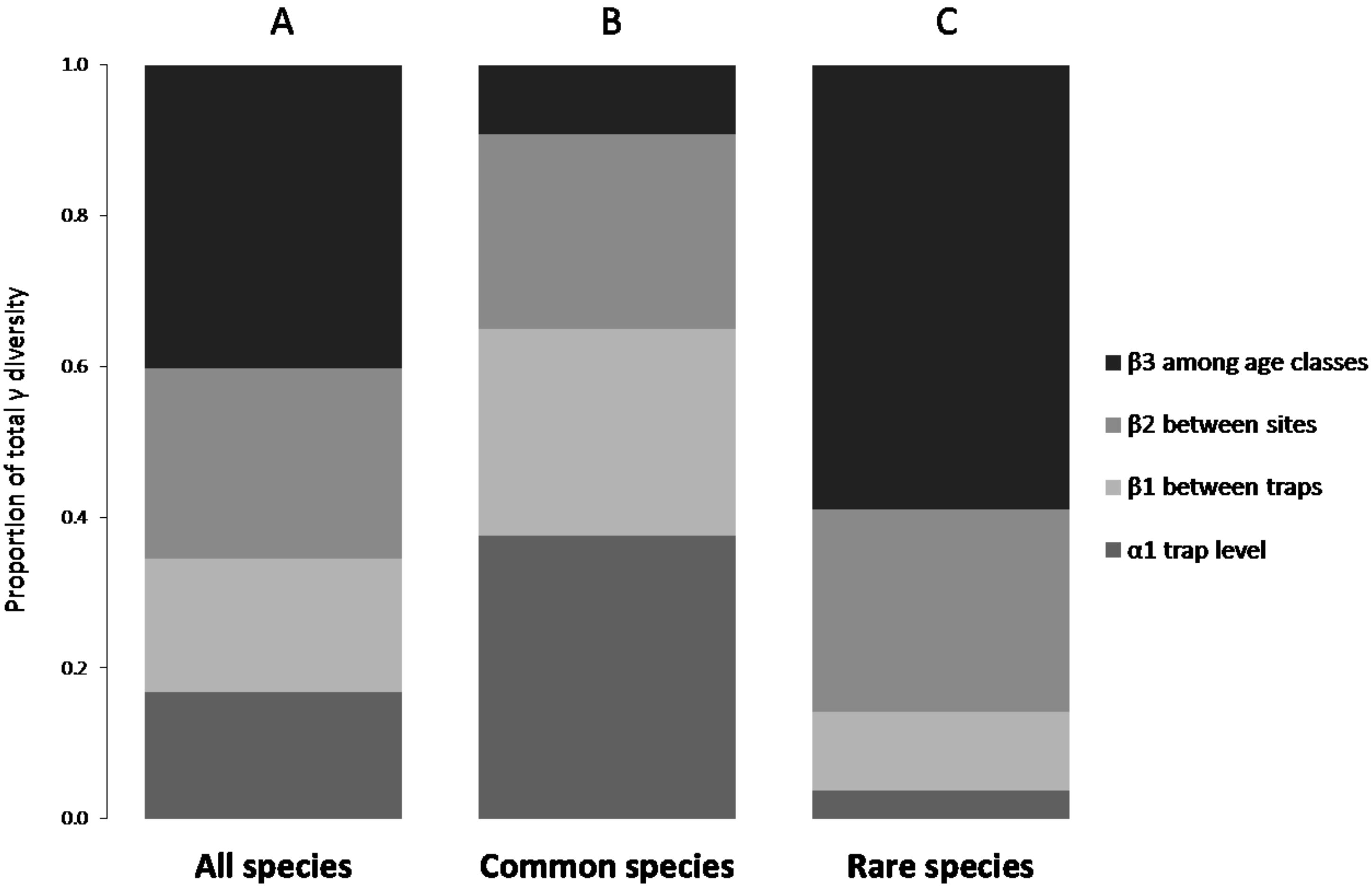

Fig 2-6: Additive partition (Crist, 2003). Values for the first stack column on the left (A) were calculated including all the species, for the central one (B) using only common species (abundant species found in almost every site), and for the one on the left (C) using only rare species (species with low abundances, with a sparse distribution among sites). α diversity at the trap level (α1) contributes more to γ diversity of common species, indicating that the variation in species richness can be related to microscale variability, while β diversity between age classes (β3) is more influential for rare species.

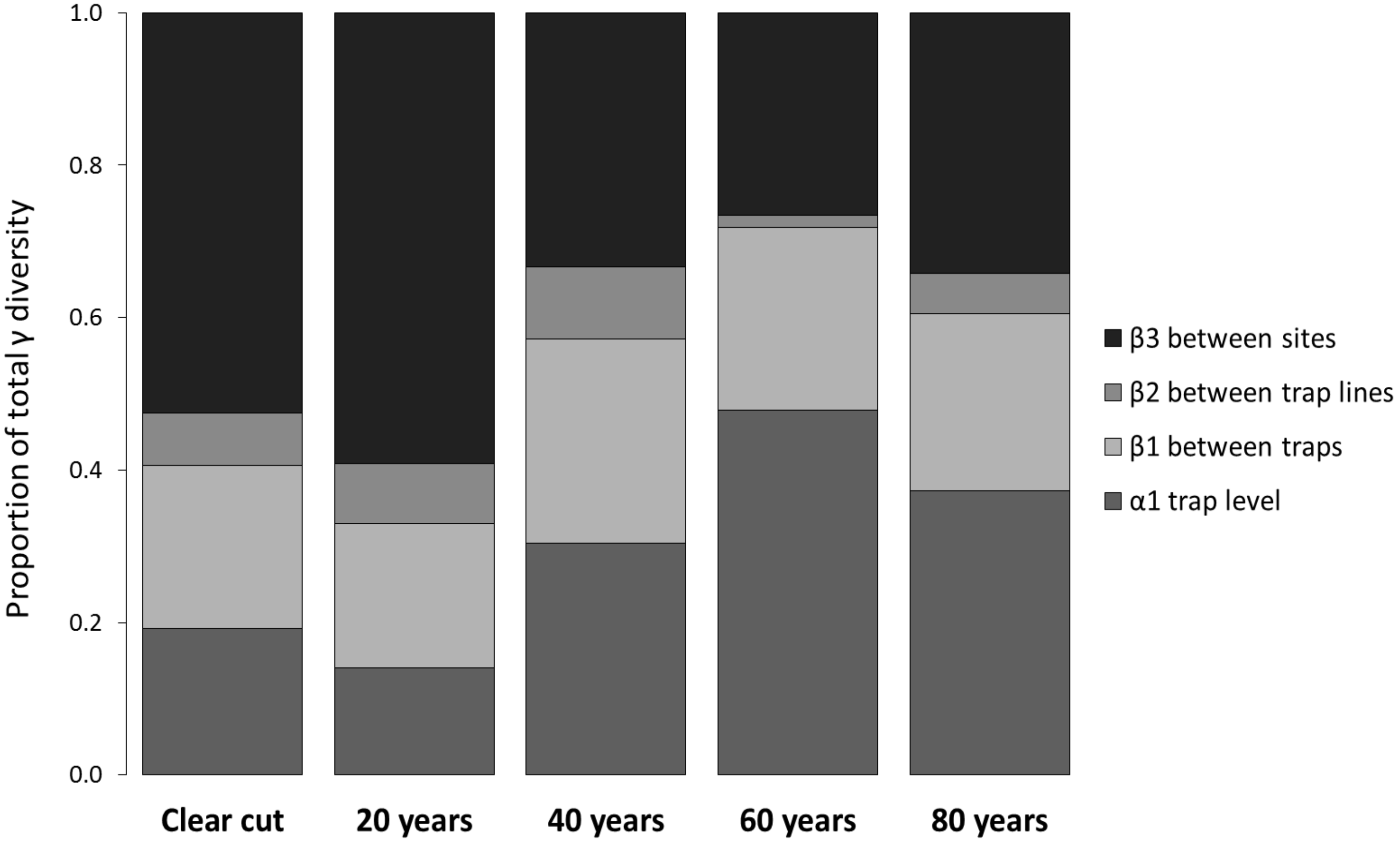

Fig 2-7: Additive partition (Crist, 2003), divided by age class. The contribution of α and β diversity to total γ diversity changes among different age classes. As forest stands become older, contribution of α diversity at the trap level and β diversity between traps increases, suggesting a more important spatial pattern of species richness variation at small scale.

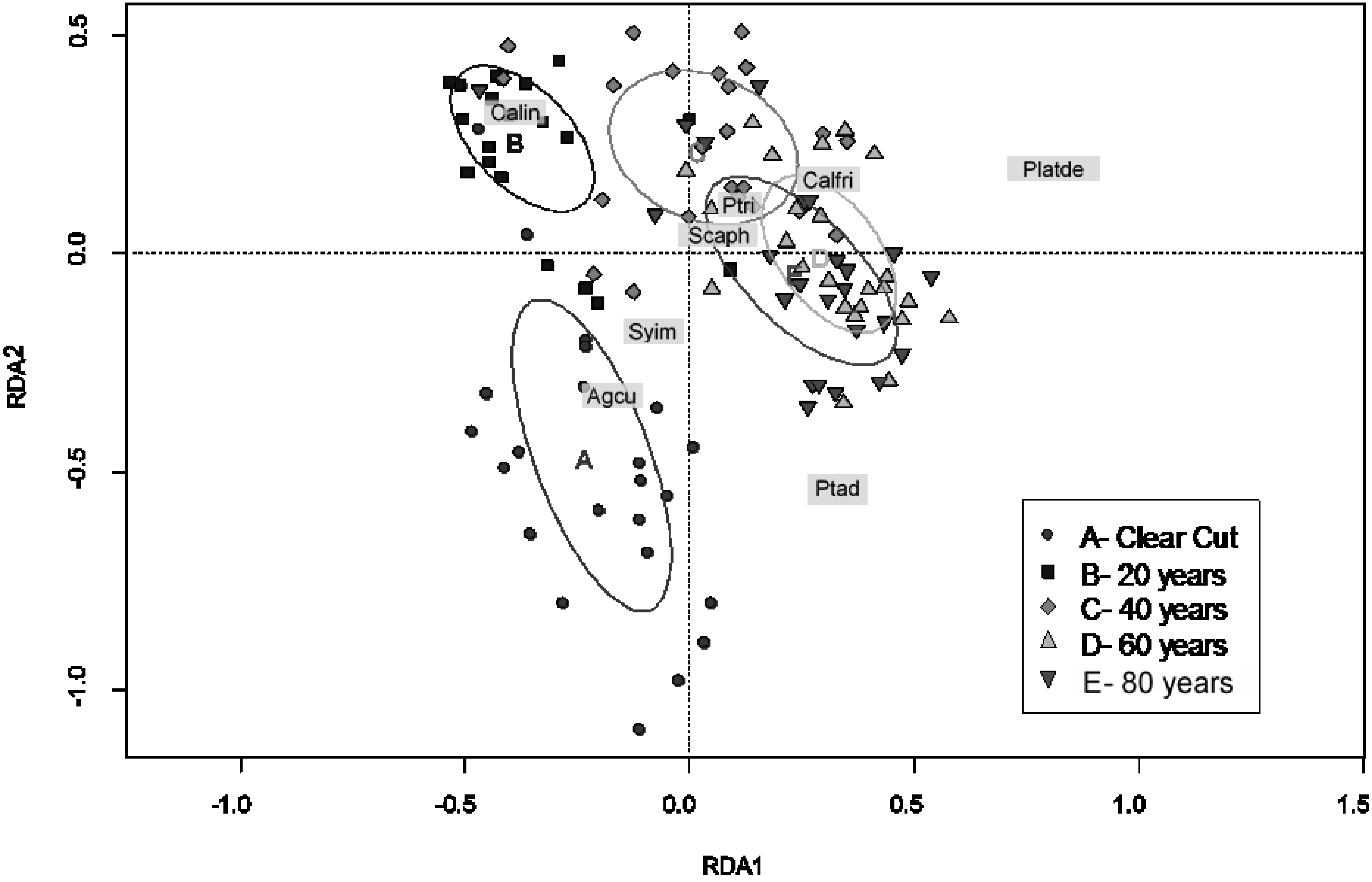

Fig 2-8: RDA1, with only Age as explanatory variable. 25% of data variability can be explained by forest age. F= 9.65, p-value= 0.001. Species codes: Agcup- *Agonum cupreum*; Calfri- *Calosoma frigidum*; Calin- *Calathus ingratus*; Platde- *Platynus decentis*; Ptad- *Pterostichus adstrictus*; Pttrip- *Pterostichus riparius*; Scaph- *Scaphinotus marginatus*; Syim- *Synuchus impunctatus*.

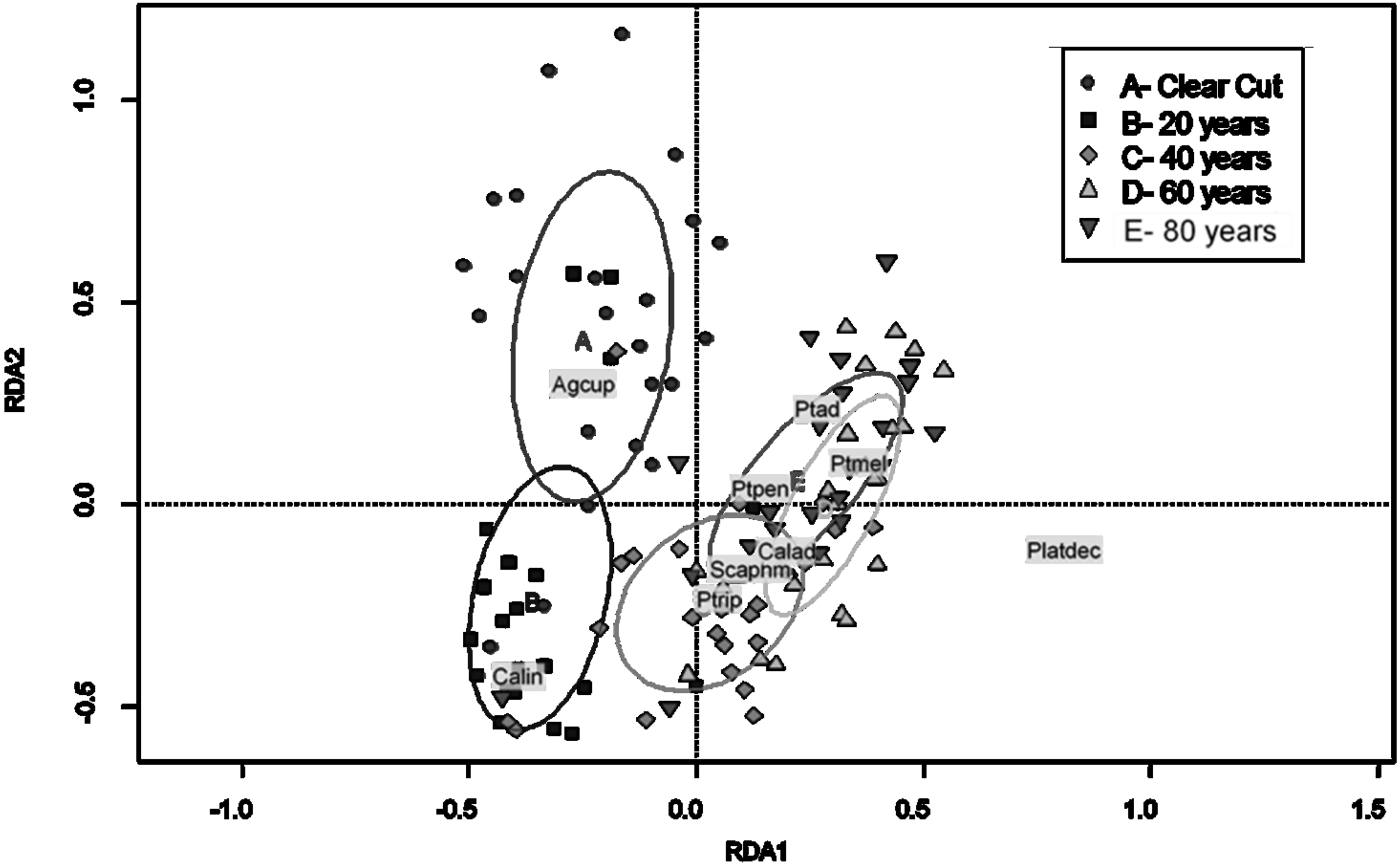

Fig 2-9: RDA2, based on carabid beetle captures in all 120 pitfall traps. For this RDA, a combination of microhabitat characteristics is used as explanatory variables (Table 2.1). About 45% of data variability can be explained by the selected combination of variables. F= 2.17, p-value= 0.001. Species codes: Agcup- *Agonum cupreum*; Calad- *Calathus adstrictus*; Calin- *Calathus ingratus*; Calfri- *Calosoma frigidum*; Platde- *Platynus decentis*; Ptad- *Pterostichus adstrictus*; Ptpen- *Pterostichus pensylvanicus*; Ptmel- *Pterostichus melanarius*; Pttrip- *Pterostichus riparius*; Scaph- *Scaphinotus marginatus*.

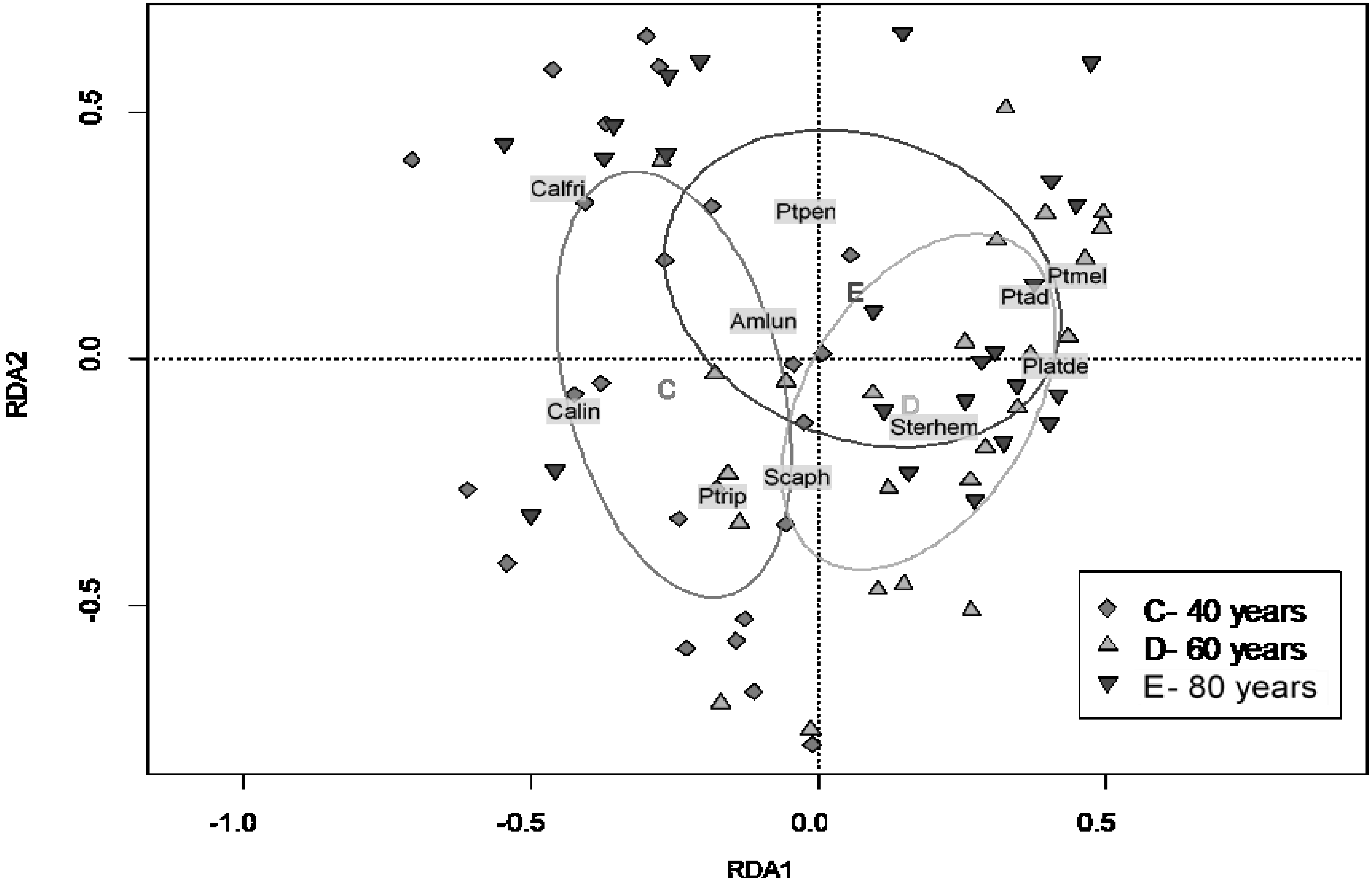

Fig 2-10: RDA3, including traps placed in older age classes (40, 60 and 80 years). 45% of data variability explained. F= 2, p-value= 0.001. Species codes: Amlu- *Amara lunicollis*; Calin- *Calathus ingratus*; Calfri- *Calosoma frigidum*; Platde- *Platynus decentis*; Ptad- *Pterostichus adstrictus*; Ptpen- *Pterostichus pensylvanicus*; Ptmel- *Pterostichus melanarius*; Pttrip- *Pterostichus riparius*; Scaph- *Scaphinotus marginatus*; Sterhem- *Stereocerus hematopus*.

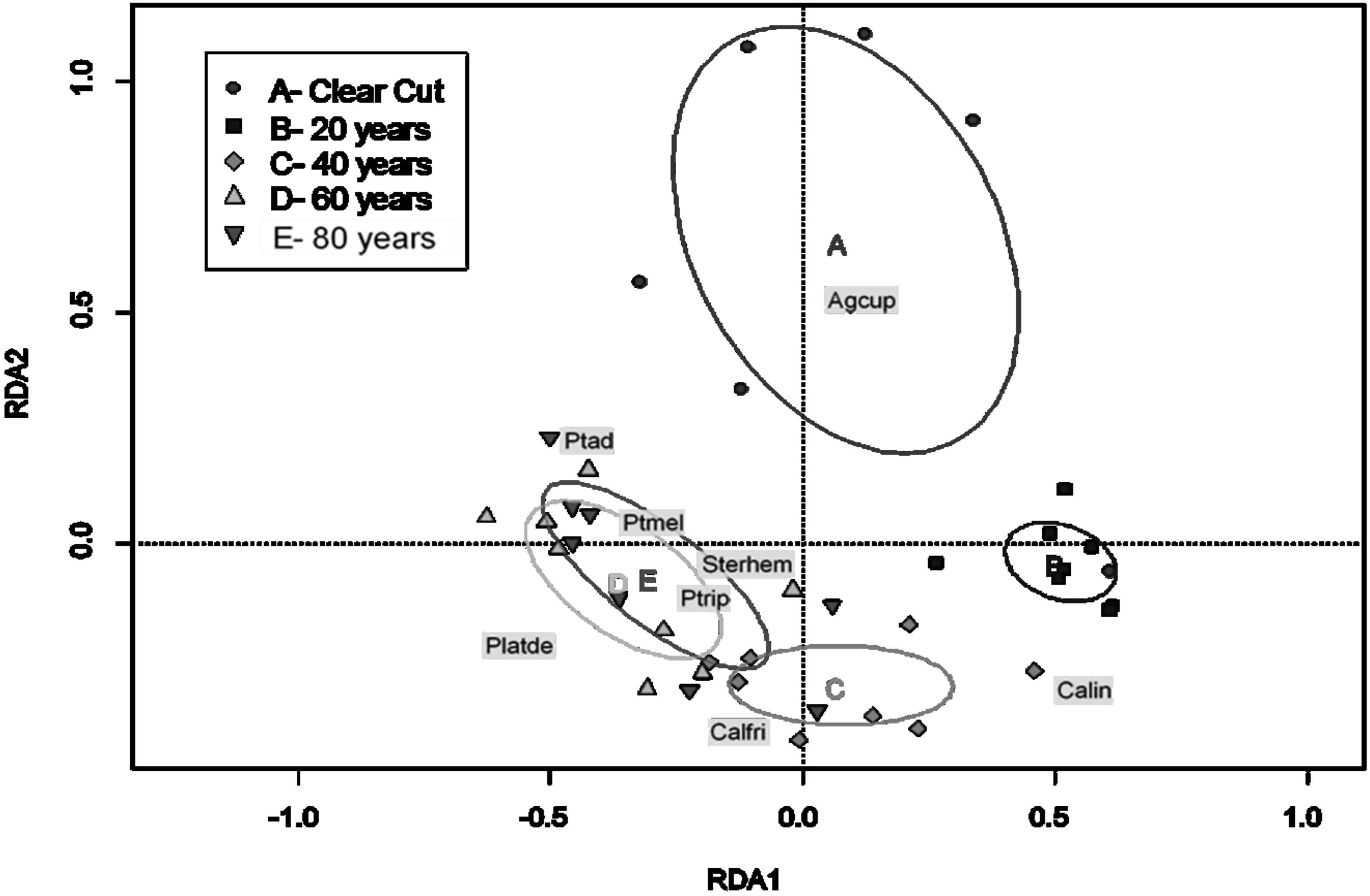

Fig 2-11: RDA 4, based on data collected using a subset of 38 pitfall traps. For this RDA, temperature and light intensity values are used as explanatory variables in addition to the data used in previous RDAs. About 70% of data variability can be explained using this combination of explanatory variables. F= 1.77, p-value= 0.001. Species codes: Agcup- *Agonum cupreum*; Calin- *Calathus ingratus*; Calfri- *Calosoma frigidum*; Platde- *Platynus decentis*; Ptad- *Pterostichus adstrictus*; Ptmel- *Pterostichus melanarius*; Pttrip- *Pterostichus riparius*; Sterhem- *Stereocerus hematopus*.

Chapter 3- Effects of clear-cut harvesting on functional diversity of carabid beetles (Coleoptera: Carabidae)

3.1. Introduction

Effects of disturbance on natural ecosystems are a central issue in discussions about conservation of biodiversity (Fox et al., 2008; Lepczyk et al., 2008; Pimm 2008). This is particularly true for northern forests, where a system shaped by natural disturbances is increasingly subject to anthropogenic disturbance associated with timber extraction (Attiwill, 1994; Bergeron et al., 1998; Spence, 2001). The magnitude of such impacts, and more generally their effects on biodiversity, is commonly assessed using measures such as species richness (*i.e.*, number of species recovered in samples), species abundances, and species composition of communities (Whittaker, 1972; Noss, 1990; Lande, 1996). In such studies, the degree of correspondence of these measures between disturbed and reference systems is generally taken as a measure of disturbance or site recovery (Niemelä et al., 1993; Pearce et al., 2006).

In recent years, there has been much interest in use of diversity measures that account for the functional complexity of communities to evaluate the ecological effect of disturbance on natural ecosystems (Aubin et al., 2013). Measures such as functional diversity (Laliberté et al., 2010) are commonly used in ecological studies (Schleuter et al., 2010), and thought to be directly connected with important aspects of ecosystem function and regulation (Bilde et al., 2004; Duflot et al., 2014). Functional diversity represents the range of traits, such as body size, behavior, trophic role or reproductive strategies that are represented in a community (Tilman et al., 1997; Diaz et al., 2001). Much empirical evidence suggests that high functional diversity corresponds to high community resilience (Bilde et al., 2004; Aubin et al., 2013). Functional diversity is influenced by habitat structure, and thus, changes in environmental conditions can alter type and frequencies of functional traits expressed in the biota of an ecosystem (Frenette-Dussault et al., 2013; Duflot et al., 2014). By characterizing functional diversity under non-natural disturbance regimes, it is possible to determine how shifts in habitat structure, related to forest harvest, for example, can influence ecosystem function.

In this chapter, I investigate how changes in forest structure, following clear-cut harvest, influences functional diversity of carabid beetle assemblages in relation to results for this taxon from other systems (Ribera et al., 2001; Bilde et al., 2004; Aubin, 2013). I will test the following two hypotheses: (1) two of the main components of functional diversity, Functional Richness and Functional Divergence (Laliberté et al., 2010), decrease after clear-cut harvest, and gradually recover over time in parallel with recovery of forest structure, as has been detected in other systems (Bilde et al., 2004; Aubin et al., 2013); (2) post-harvest habitat structure acts as a filter for species functional traits, altering their relative frequency and selecting for specific trait combinations in areas subjected to harvest.

3.2. Material and methods

3.2.1. Study area

The analyses presented in this chapter are based on data collected using pitfall traps in the forested area surrounding the town of Hinton (53.4114° N, 117.5639° W), in the Lower-Upper Foothills transition zone (EcoRegions Working Group, 1989) of west central

Alberta, Canada (Appendix A). A total of 20 aspen (*Populus tremuloides*) dominated forest stands were sampled along a post-harvest regeneration chronosequence, ranging from recently harvested stands to mature forests, with mature never-cut stands used as controls. Four replicate sites were identified in the field for each of 5 age categories: recent clear-cut, 20 (± 4), 40 (± 2), 60 (± 3) years post-harvest, and mature forest stands (80 years or older). Stand age was assessed using West Fraser Timber Co. Ltd. GIS® data (personal communication).

Each of the 120 pitfall traps used consisted of a 1L plastic cup placed in the ground, with the upper rim at the ground level to serve as a sleeve to minimize disturbance of edge at collection, and with a smaller 250 ml plastic cup nested inside (Spence, 1994). The inner cup was partially filled with a 70% solution of ethylene glycol, which served as killing agent and preservative. Traps were covered with a 10x10 cm PVC roof, held in place with metal wire (Appendix B). Six traps were positioned in each site at a minimum distance of 20 m from each other in two roughly parallel lines of three traps each (Appendix B). This inter-trap distance is considered to be sufficient to minimize autocorrelation of catches among pitfall traps close to each other (Digweed et al., 1995). Trapping covered the majority of the frost-free period between May and the end of August 2014, including the main activity period of adult carabid beetles. Specimens were collected and the preservative was replenished at two-week intervals, providing a total of 7 collections.

All adult carabids were identified to the species level following Lindroth (1961-1969), and named according to Bousquet (2013). Catches were standardized to the catch expected over 100 days of trapping (length of the trapping period) to minimize effects of trap disturbance (animal activity, rain or desiccation) on species abundances. Total number of individuals captured by each trap was first divided by the number of days the trap was functional and undisturbed, to get an estimate of catch/day, which was then multiplied by 100 to estimate the catch/100 days.

3.2.2. Environmental variables selection

Environmental variables were measured during summer of 2014, to describe small scale habitat conditions around each trap. These are used to describe habitat structure, and included in functional diversity analyses to infer any potential effect of habitat disturbance on functional traits relative frequencies and potential selection for specific trait combinations in areas subjected to harvest.

Environmental variables measured include total number of standing trees, both living and dead, tree species composition, canopy cover, ground cover (% of ground covered by the projection of green parts of herbaceous plants) and herbaceous vegetation composition (most abundant herbaceous species). These variables were selected to represent canopy structure around each trap, litter structure, and provide an indirect assessment of soil characteristics and small scale climate through the use ground layer plants. A complete list of variables, and the codes used to identify them in the analyses, is presented in Table 3-1.

3.2.3. Canopy cover percentage and number of trees

Canopy cover (%) was estimated in mid-July 2014, at the time of maximum foliage coverage for deciduous species, using a concave spherical densitometer modified according to Strickler (1959). A graphical description of the method is presented in Figure 3-1: for each pitfall trap, the number of nodes inside the V-sections of the densitometer, covered by the foliage projection, was considered as canopy cover; this measure was repeated for the four cardinal directions, and the sum of the four measurements considered as the total canopy cover for the trap.

Tree species composition around each trap was estimated as the dominant tree species (the tree species with the highest number of individuals, among all trees with DBH >5 cm), inside a 100 m^2 (10x10m) square centered on the trap. All living trees were counted and recorded according to species. A similar counting method was used to tally number of dead trees (standing dead trees and stumps, at least 1.3 m in height), inside the same area, with no distinction between tree species.

3.2.4. Main herbaceous species and ground cover percentage calculation

Main herbaceous species was calculated as the species that covered the majority of the area in a radius of 5 m (~78.5 m^2), centered on each pitfall trap. Percent ground cover was estimated as the projection on the ground of green leaves and live branches of understory plants below breast height (1.3 m from the ground). Photographs of 1x1m squares, centered on each pitfall trap (Fig. 3-2), were taken in late June and in mid-August 2014. The percentage of ground covered was calculated using the image analyses software ImageJ® (Abramoff et al., 2004). The software estimates the percentage of "green" and "non-green" coverage based on pixel analysis. The distinction between the two pixel categories is based on a threshold value, selected to incorporate green leaves and branches, but to exclude bare ground, litter or debris. The result is a percentage of pixel identified as cover, which was then converted into the percentage of the 1x1m square covered by green leaves (Fig. 3-2). Values obtained from each set of pictures were then averaged to obtain mean cover the summer (*Covav*), and used to calculate the variation over the same period (*Covvar*).

3.2.5. Traits selection

Species-specific traits about dietary preferences and dispersal power (wing-dimorphism) were obtained from the literature (Lindroth, 1961-1969; Larochelle, 1990). In addition, sex ratio was calculated for each species from collected samples. A complete list of traits, used in the following analyses, is given in Table 3-2, and a more in-depth description is given below. Traits values for each species are reported in Appendix D. The traits selected represent species resource requirements, dispersal ability and potential reproductive outcome, all functional components that can be affected by habitat disturbance (Bilde et al., 2004; Jelaska et al., 2009; Vanbergen et al., 2010).

3.2.6. Dietary preferences

Most of the species included in this study are predators that consume mainly invertebrate prey (Lindroth, 1961-1969, Larochelle, 1990). Although some carabid species are known to be omnivorous, consuming plant material, no species thought to be specialized for herbivory or gramnivory was included. The majority of the data about dietary preferences were taken from laboratory experiments (Larochelle, 1990), with additional data from field observation (Lindroth, 1967-1969; Larochelle, 1990). When this literature suggested a distinct dietary preference towards a species or group of species, that preference was indicated as main food source (e.g., *Lepidoptera* (*Lep*) or *Orthoptera* (*Orp*), see Table 3-2). When no main food preference was indicated in the literature, the species was listed as generalist Carnivore (*Car*) or Omnivore (*Omn*).

3.2.7. Wing dimorphism

The majority of the species collected can be classified as either macropterous (wings fully developed) or brachypterous (wings not completely developed or absent, thus not capable of flight). A small fraction of the species collected were dimorphic for wing-length; *i.e.*, different individuals of the same species can have fully developed wings or very short wings unable to sustain flight (Lindroth, 1967-1969). Most notable among these, in terms of their abundances, are *Calathus ingratus*, *Pterostichus melanarius*, and *Agonum retractum*. This trait is related to the ability of individuals of a species to move across long distances and, taken collectively, provides insight into the vagility of a species and its potential ability to colonize new areas. In fact, some evidence shows that the ratio of winged individuals can indicate if a population is still in a colonizing phase (den Boer, 1990; Niemelä, 1999; Jelaska et al., 2009; Bourassa et al., 2011).

3.2.8. Sex ratio

Sex ratios are calculated as the proportion of females (*FemaleP*) and the ratio (*MFratio*) between males and females for each species. A lower number of females could be considered as an indication of lower rates of local egg deposition, resulting in a potential lower reproductive outcome in the following generation (den Boer, 1990). Although it is known that sex ratio is influenced and, partially, determined by pitfall trap methodology (Esch et al., 2008), this effect apply in equal way to all traps and species, therefor standardizing the potential source of error.

3.2.9. Average body length

Average body length can be generally related to resource availability and habitat heterogeneity (Barton et al., 2011). Lower resources could affect larval development, thus reducing size and other traits of adult individuals (den Boer, 1990; Barton et al., 2011). Average body length for each species is based on values available in the literature, calculated as the mean value of the range usually reported in literature (Lindroth, 1967-1969).

3.2.10. Data analyses

The analyses presented include indices of functional diversity most commonly used in ecological literature (Petchey et al., 2002, 2006; Mouchet et al., 2010; Schleuter et al., 2010). These indices are based on the number of species, the number of individuals for each species and the relative values of the different traits for each species. Functional diversity indices thus describe the distribution of point clouds, each one representing a different species, in a multidimensional space of functional traits (Schleuter et al., 2010). I describe each of these analyses in more detail below.

All analyses were carried using the package *ade4*, part of the open source statistical software *R* (v. 3.1.2, R Core Team, 2014).

3.2.10.1. Functional Richness (FR) and Functional Divergence (FD)

Two main measures of functional diversity, Functional Richness and Functional Divergence (Mason et al., 2005), were calculated following Villéger et al. (2008) and Laliberté et al. (2010), and compared among forest age classes. As above, both indices are based on spatial ordination of species in a multidimensional trait space (Mason et al., 2005; Villéger et al., 2008), where the n-axes each represent one of the species traits selected, and the position of each point the trait values for each species (Fig. 3-3) (Villéger et al., 2008).

Functional Richness (FR) index indicates how much of the available trait (*i.e.*, niche space) is filled (Schleuter et al., 2010), and how much of the potential resources available are used (Mason et al., 2005). FR values represent the volume of the minimum convex hull, plotted in the multidimensional trait space: the hull vertices are the outmost species (species with traits values located at the outer limit of the species distribution), plotted according to their corresponding traits values (Villéger et al., 2008) (Fig. 3-3). This index does not account for relative species abundances, but only for their trait values. Low FR values suggest that some of the potential niches, as defined by assemblage trait distributions, are not used by the assemblage (Mason et al., 2005).

Functional Divergence (FD) is based on the average distance from the centroid of each group distribution (calculated for FR, Villéger et al., 2008). FD measures the variance of functional traits and the position of species clusters in the multidimensional trait space (Schleuter, 2010), in relation to their relative abundances. When species that are more abundant have extreme traits (*i.e.*, are very close to or are part of the minimum convex hull boundaries) compared to the rest of the assemblage, FD is higher (Fig.3-4); this in turns indicates high niche differentiation, and suggests that resource competition is ameliorated by species trait distributions (Villéger et al., 2008).

FR and FD were calculated for each forest site, using the data about trait distributions, and then averaged for each age class (Table 3-4).

3.2.10.2. RLQ analysis

RLQ ordination can be used to infer the effects of environmental characteristics on the distribution of species functional traits, and whether habitat alteration could change trait distribution among sites (Dray et al., 2008).

RLQ (Dray, 2008; Laliberté, 2010) is based on the combination of three matrices: species abundances in each sampling unit (**L**), variables describing environmental characteristics for each sampling unit (**R**), and traits for each of the species included in the analysis (**Q**). RLQ analysis is based on a double inertia analysis of two matrices (**R** and **Q**), with a link expressed in relation to a third one (**L**). The rows of **L** correspond to the rows of **R** and the columns of **L** correspond to the rows of **Q** (Doledec et al., 1996; Dray et al., 2002, 2008; ter Braak et al., 2012). The result of an RLQ analysis is an ordination plot that provides a projection of species and traits in relation to differences in sampling unit (traps) characteristics (environmental conditions). This is used to visually describe correlations between environmental characteristics around each trap and variation in traits represented in carabid beetle assemblages at the same sampling unit.

The first step of the RLQ analysis requires separate ordinations for each of the tables. In the analyses presented, Correspondence Analysis (CA) was applied to the species table (**L**). For traits data (**Q**), a Principal Component Analysis (PCA) was applied. Because the environmental table (**R**) contains both quantitative and categorical variables, I used the Hill-Smith ordination (Hill, 1976), which allows inclusion of both types of variables. The axes scores of each independent analysis are then combined in the RLQ analysis, which gives a visual description of potential effects of environmental variables on traits. If traits are close to the axes intercept, there is little differentiation and effect from habitat characteristics on their distribution among sites; if one or more traits are distant from the cluster of all traits in the ordination plot, then those traits are selected or influenced by habitat conditions. Variables values and species ordination are manually over imposed on the traits distribution to obtain the final plot (Fig. 3-10).

3.3. Results

3.3.1. Functional Richness (FR) and Functional Divergence (FD)

Average Functional Richness (FR), compared among post-harvest age classes, increases with time since last harvest (Fig 3-5). This is a first indication of a negative effect of clear-cutting on functional diversity in carabid assemblages. Lower FR indicates that part of the potential resources available are not utilized by the species present in the assemblage (Mason et al., 2005).

Figure 3-6 shows the average Functional Divergence (FD) for each stand age class. The plot shows slightly significantly lower FD values for older stands, indicating that in these stands species abundances are evenly distributed in the multidimensional trait space, while in younger stands there are fewer species, with extreme traits values, that dominate the assemblage (Mason et al., 2005). This is a second indication of the shift in the assemblage composition due to harvesting impacts.

3.3.2. RLQ analysis

The RLQ analysis shows how changes in habitat structure along the regeneration chronosequence may affect carabid beetle traits distribution. Figures 3-9 and 3-10 show the relative influence of the variables and the distribution of traits based on the combined results of all the ordinations performed on each data set. Some of the traits associated with less abundant species, located at the outer limit of species distribution, may be influenced by changes in habitat conditions. These traits are generally associated with species adapted to open habitat (*Notiophilus semistriatus*), thus the notable effect of specific environmental variables on the distribution of the traits could be related to forest harvest. Species that use

Collembola (*Col*) and *Lepidoptera* (*Lep*) as main sources of food are distinctly separated from species that primarily feed on *Dermaptera* (*Der*) and insect eggs (*Egg*). For the majority of species, however, traits distribution is homogeneous, as shown in Figures 3-9 and 3-10, which indicates that there is little or no selection for these traits.

3.4. Discussion

The results presented suggest that clear-cut harvest can affect components of carabid beetle functional diversity. The lower values of Functional Richness (Fig 3-5) in recently harvested forest plots (recent clear-cuts and 20 years old forest stands) show that the decrease of habitat heterogeneity correlated to harvesting activities can potentially reduce the variability in traits expressed by carabid assemblages. Analysis of Functional Divergence (Fig 3-6) also shows that in younger stands there are fewer species, each represented in the assemblage by a higher number of individuals, characterized by traits values closer to the outer hull of the assemblage distribution. These species are the most abundant in youngest stands, and thus their traits influence the functions of these assemblages. Their functions seem to be strongly linked to open habitats and become less relevant as the forest canopy closes.

The analyses about how small scale habitat structure acts as a filter for specific traits are inconclusive. RLQ results (Fig 3-9) show that there may be some partial effect of habitat structure on some species: environmental conditions may select for specific traits, as can be seen by some being plotted away from the axis intercept (Fig 3-10). However, the majority of species seem to be little affected by changes in habitat structure. This can be identified by the fact that the majority of the traits selected are spread homogeneously around the central area of the plot (Fig 3-9 and 3-10).

Despite the inconclusive results, this chapter presents a first step toward integrating functional diversity indices into studies about how disturbance, and specifically forest harvest, affects carabid beetle assemblages. The results do not necessarily underline that this type of analyses are not effective in characterizing functional diversity, but that the selection process of traits used to characterize assemblages, and of the variables used to describe habitat changes can have a strong impact on the outcome of the analyses. Most of carabid beetle species share food sources, have similar needs in terms of habitat condition, and have overlapping spatial distribution. These characteristics can be difficult to incorporate in functional diversity analyses and to describe using a limited list of variables; therefor variables selection assumes a crucial role in influencing the analyses results.

Despite the potential shortcoming of such analyses, functional diversity is an interesting aspect of biodiversity to explore. The ecological functions expressed by a particular assemblage may provide useful insight into mechanisms related to post-disturbance recovery processes. Comparison of the results presented in this chapter, with those from of similar analyses of forest stands affected by wildfire, for example, could increase understanding of functional differences between natural disturbance and commercial forest management. Such comparisons could contribute to understanding how the differences in the impact, magnitude and quality of natural disturbance and human activities can be reduced by adjustment of harvest protocols, in order to achieve the levels of biodiversity conservation advocated by modern forestry standards (CCFM, 2005).

3.5. Literature cited

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Table 3-1: Variables selected for the analyses

Variable name	Description
Age	Forest age (time since last harvesting)
Covav	Average ground cover (% of green leaves)
Covvar	Variation of ground cover over the summer
Mainsp	Main herbaceous species (highest % covered)
Secsp	Second most abundant herbaceous species
Mtree	Main tree species
Cancov	Canopy cover percentage
TotAlive	Total number of alive trees around the trap
D	Number of standing dead trees

Table 3-2: Life traits codes and relative descriptions

Code	**Description**
Lep	Lepidoptera as primary food source
Car	Carnivores (generalists)
Omn	Omnivores (generalists)
Orp	Orthoptera as primary food source
Der	Dermaptera as primary food source
Col	Collembola as primary food source
Egg	Arthropod eggs as primary food source
FWY	Proportion of females with wings
FWR	Proportion of females without wings
MWY	Proportion of males with wings
MWR	Proportion of males without wings
FemaleP	Proportion of females
MFratio	Males/Females ratio
AvLe	Average body length (mm)

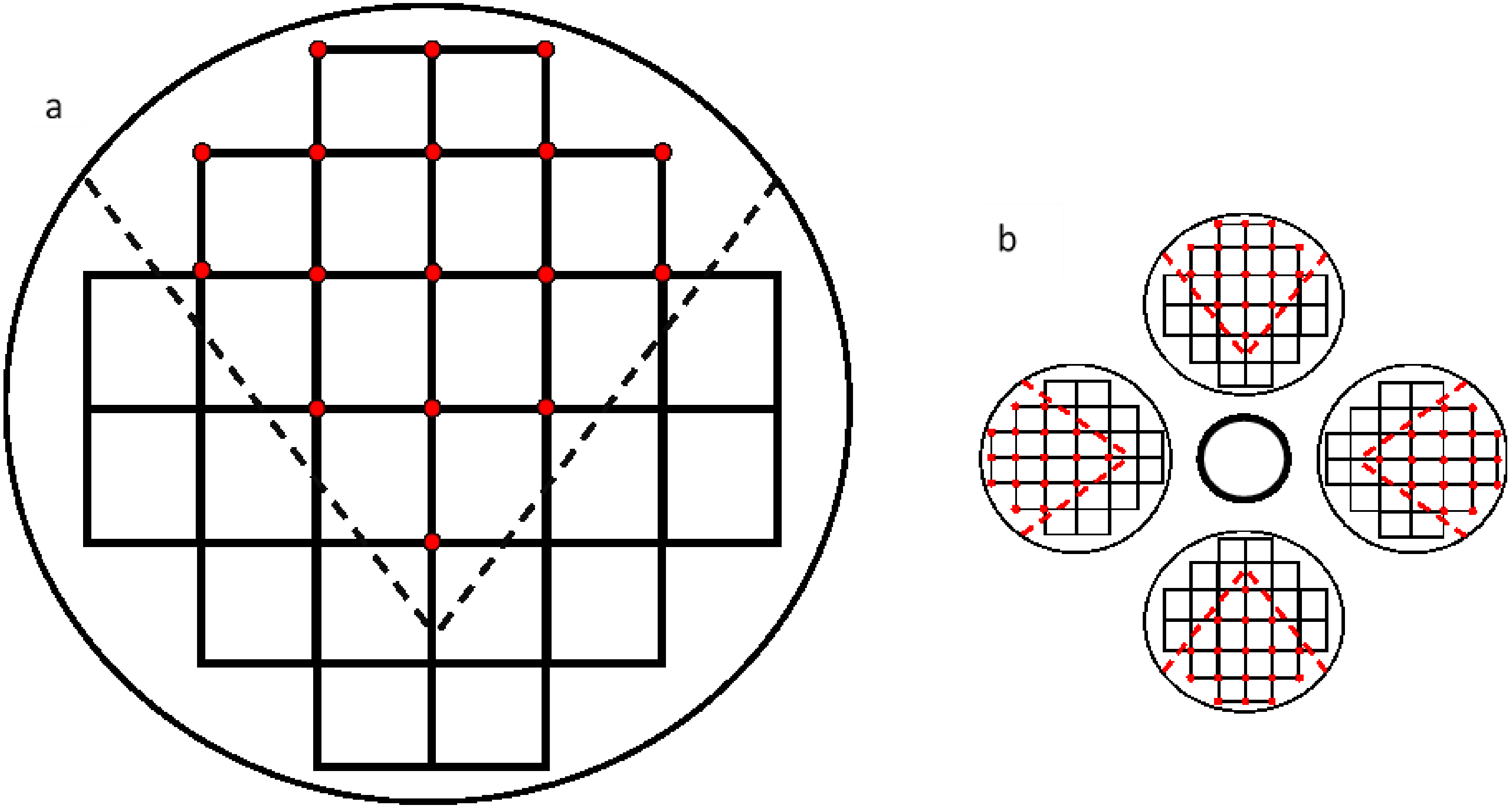


Fig 3-1: Modified method for canopy cover detection (Strickler, 1959) using a concave densitometer (a). The 17 dots (red circles) at the line intersections inside the V-shaped section (dashed line) are the ones considered when calculating canopy cover. Each point covered by the projection of the canopy is counted. The same operation is repeated four times, each time pointing the densiometer at a different main cardinal direction (N, S, E and W) around the trap (b). To calculate the percentage covered, the total number of point covered is then multiplied by 1.5 (Strickler, 1959).

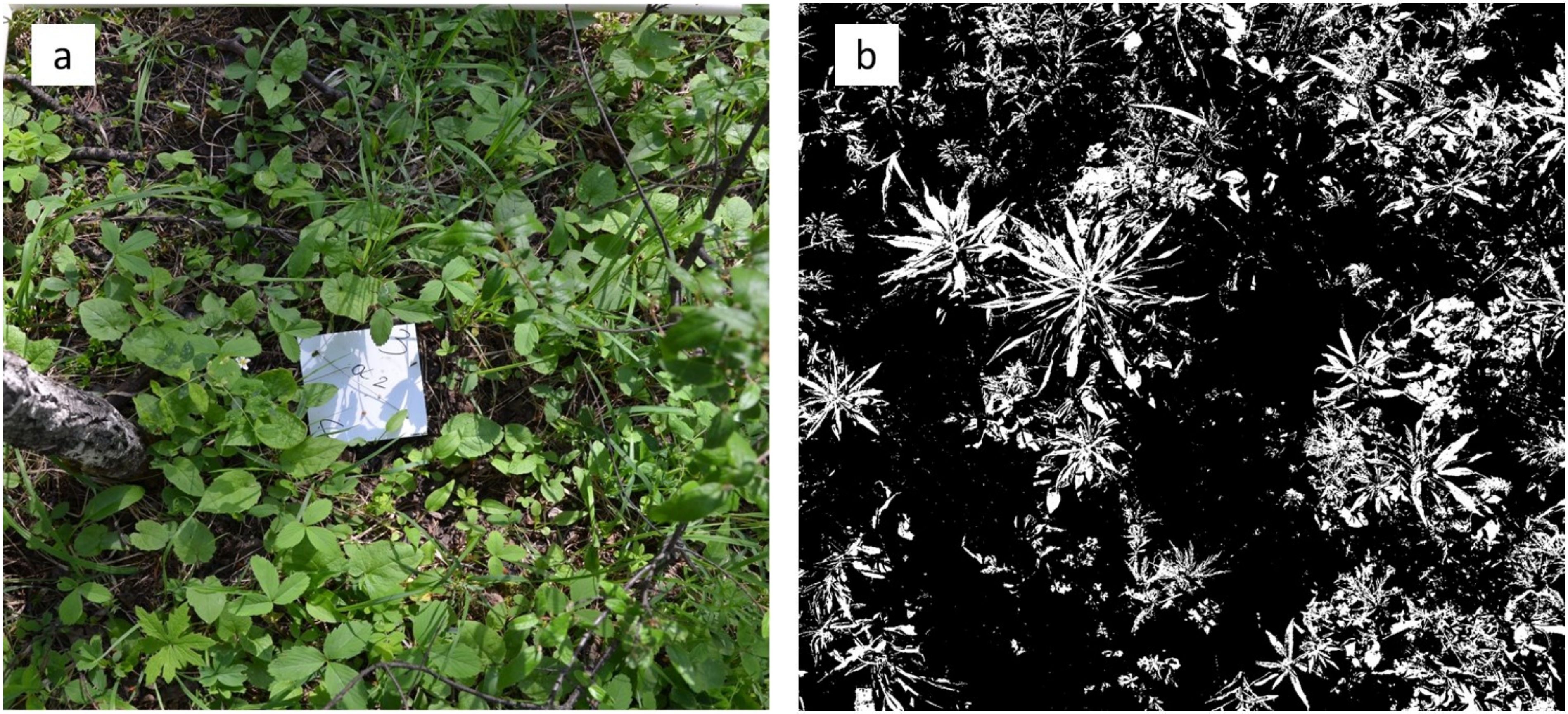


Fig 3-2: The procedure used to calculate ground cover percentage. A picture of a 1x1m square, centered on each pitfall trap (a) was taken at the end of June and in mid-August. The pictures were analyzed using the software ImageJ®, transforming the image in a black and white pixel mask (b), where white pixels represent green areas (leaves, grass), and black pixels represent bare ground or areas not covered by vegetation. The mask is then used to calculate the percentage of the area covered.

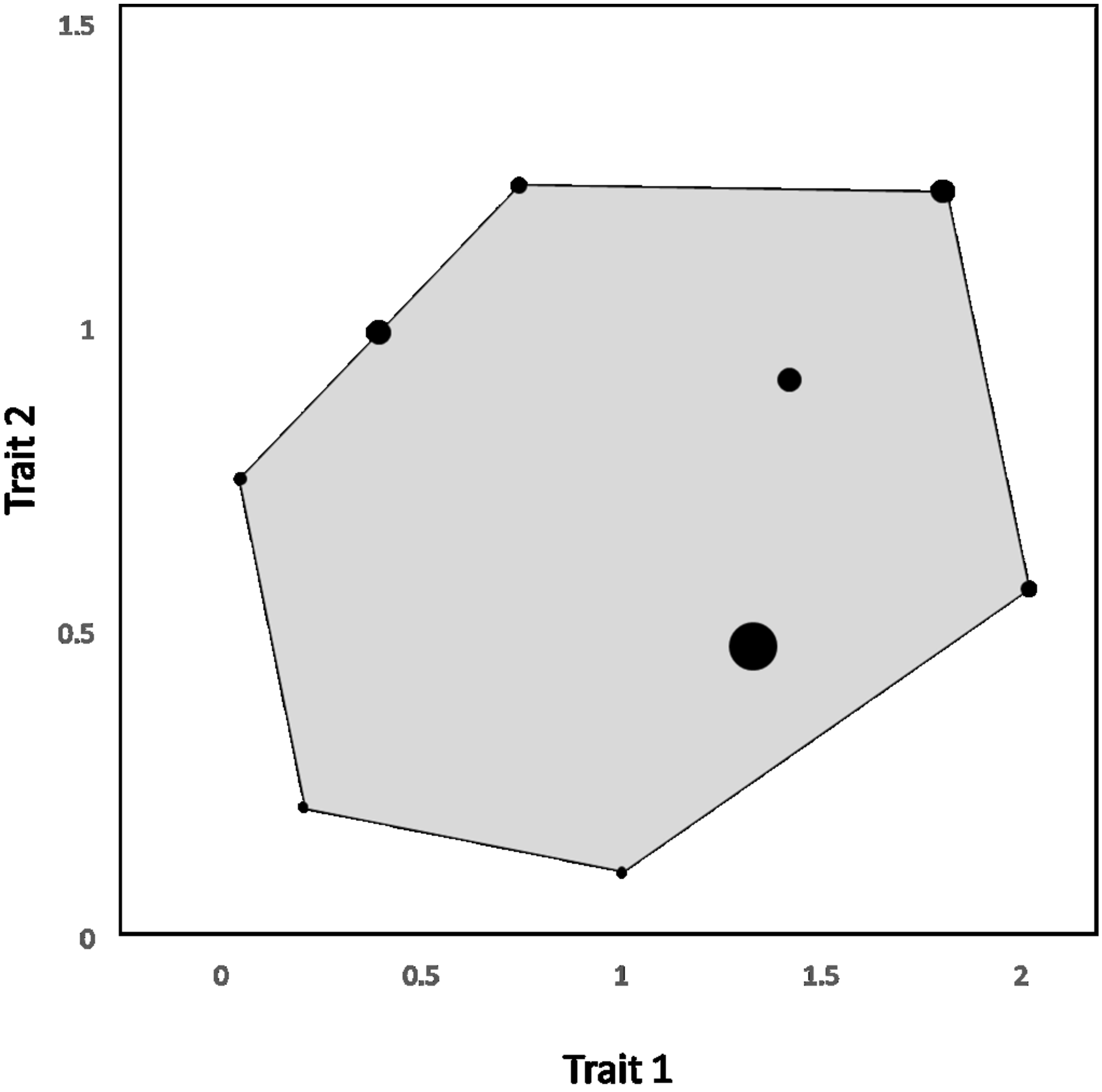


Fig 3-3: Visual depiction of Functional Richness (FR) in the multidimensional traits space. Each black circle represents a species, and their size represents their respective abundances. The volume of the convex is the total Functional Richness of the group of species considered. Adapted from Villéger et al., 2008, Fig.1, p. 2292.

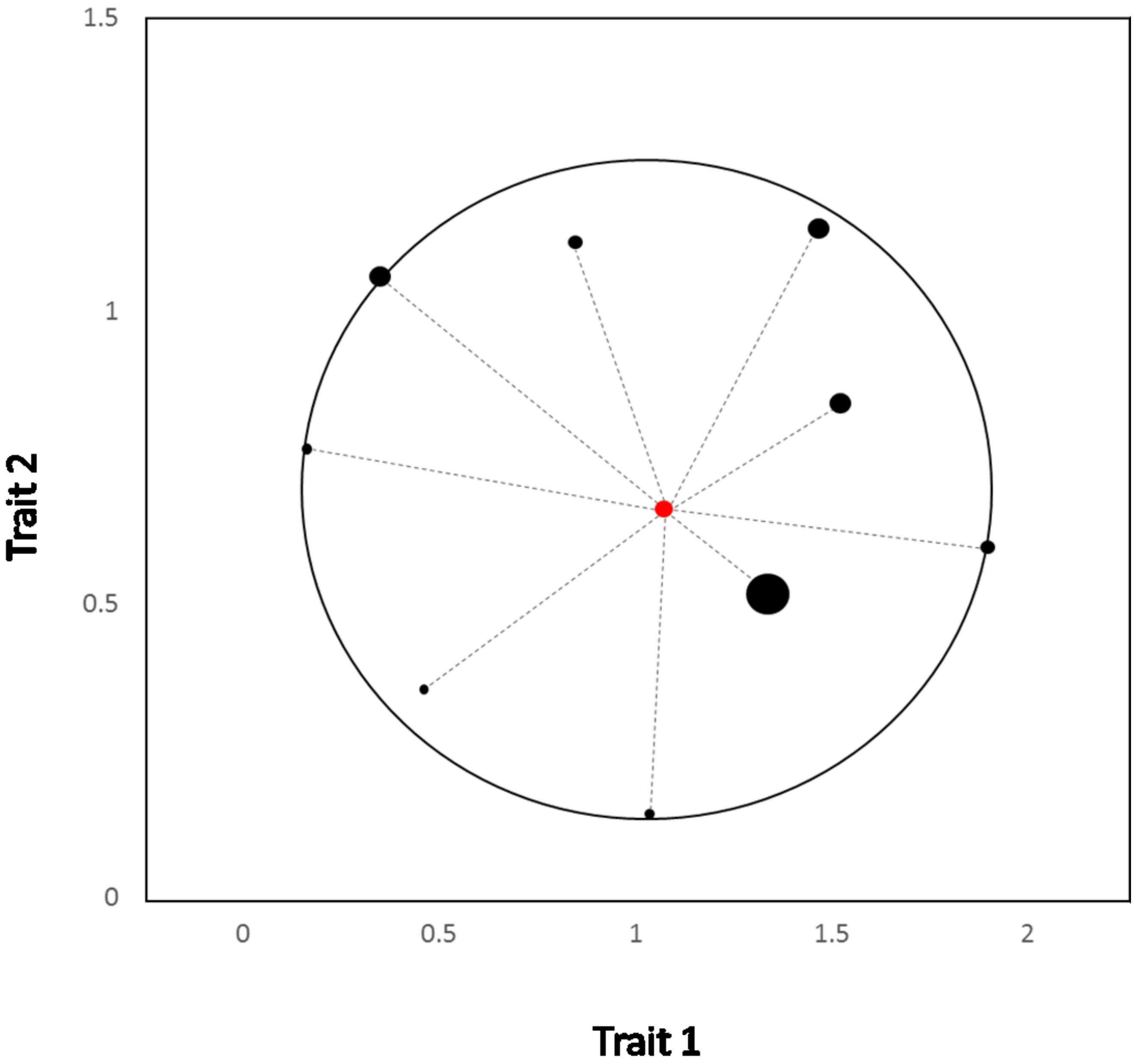


Fig 3-4: Visual depiction of Functional Divergence (FD) in the multidimensional traits space. Each black circle represents a species, and their size is proportional to their respective abundances. The red dot represents the center of gravity, or centroid, of the points cloud. The relative distance of each species from the centroid, and their abundances, influences Functional Divergence. When most abundant species have extreme traits (higher distance from the centroid), then FD is high (Villéger et al., 2008). Adapted from Villéger et al., 2008, Fig.1, p. 2292.

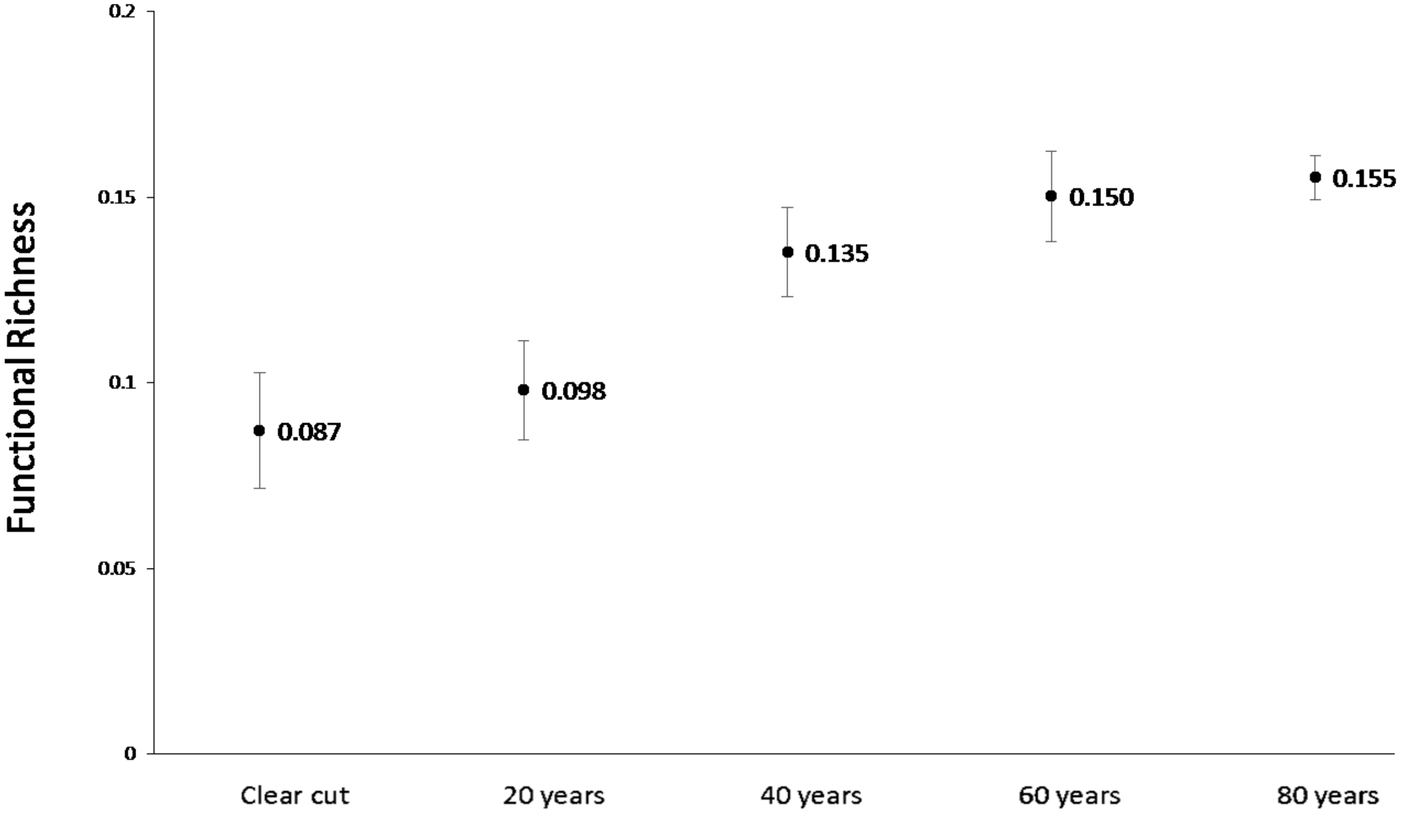


Fig 3-5: Average Functional Richness (FR) for each age class. Bars on each point represent standard error.

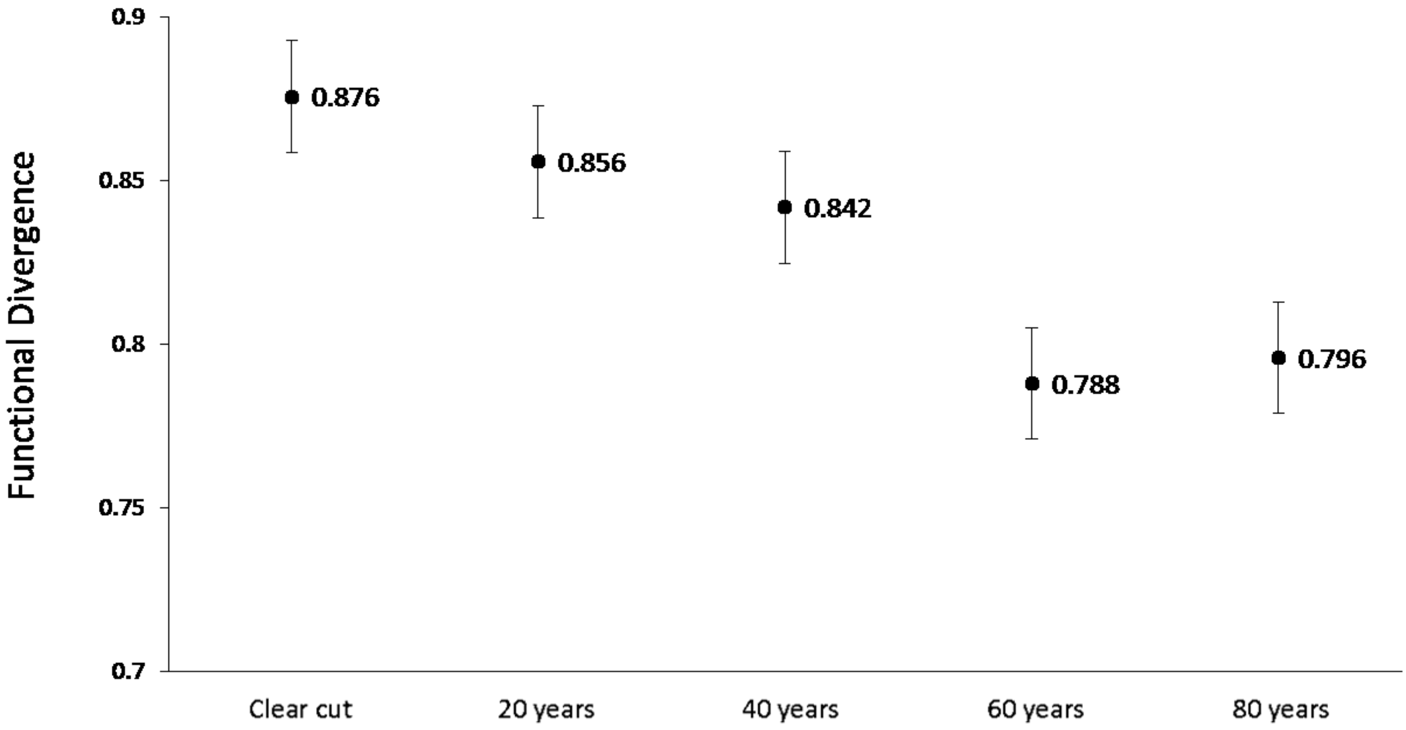


Fig 3-6: Average Functional Divergence (FD) for each age class. Bars on each point represent standard error

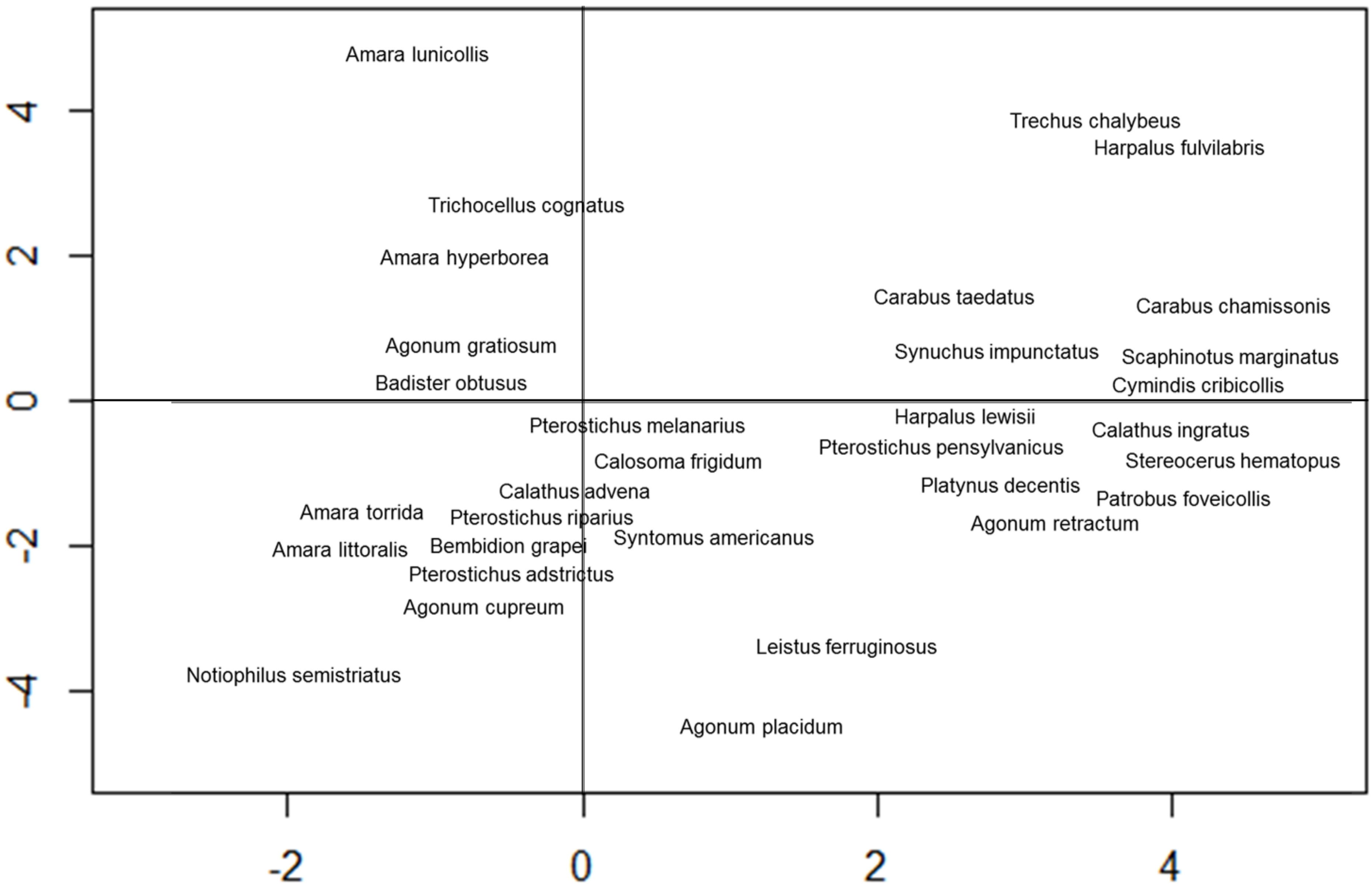


Fig 3-7: Species ordination, based on their abundances.

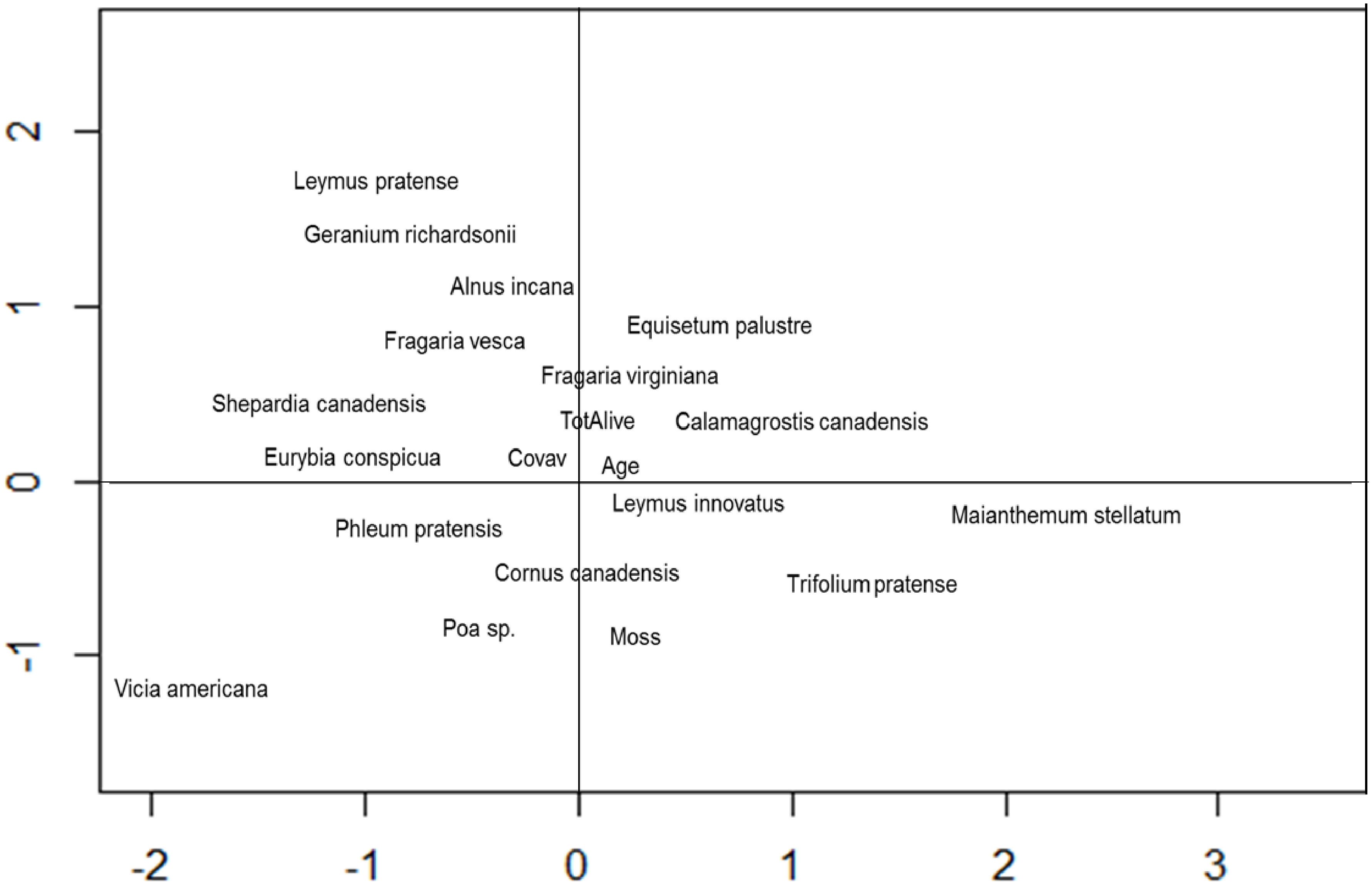
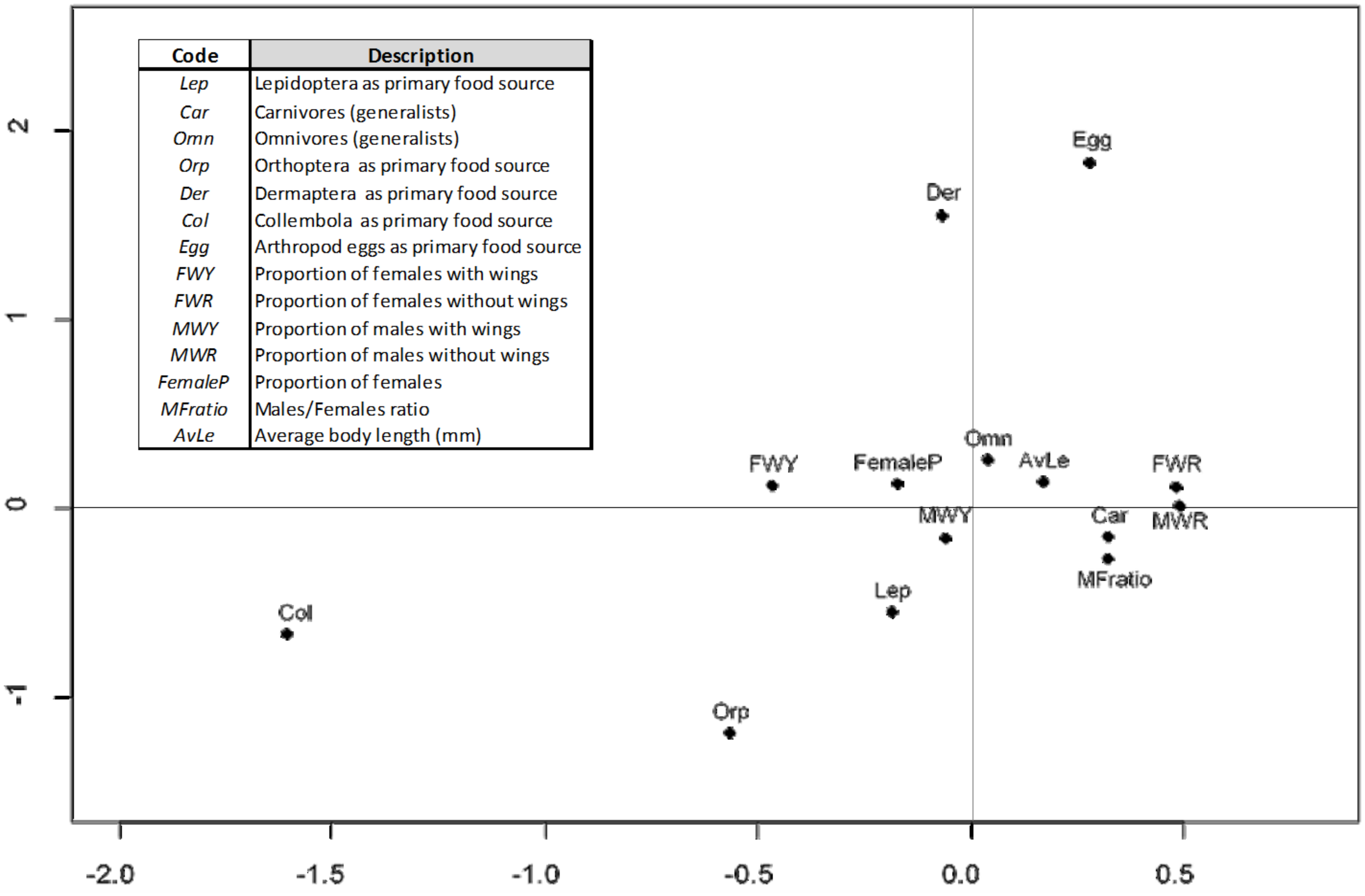
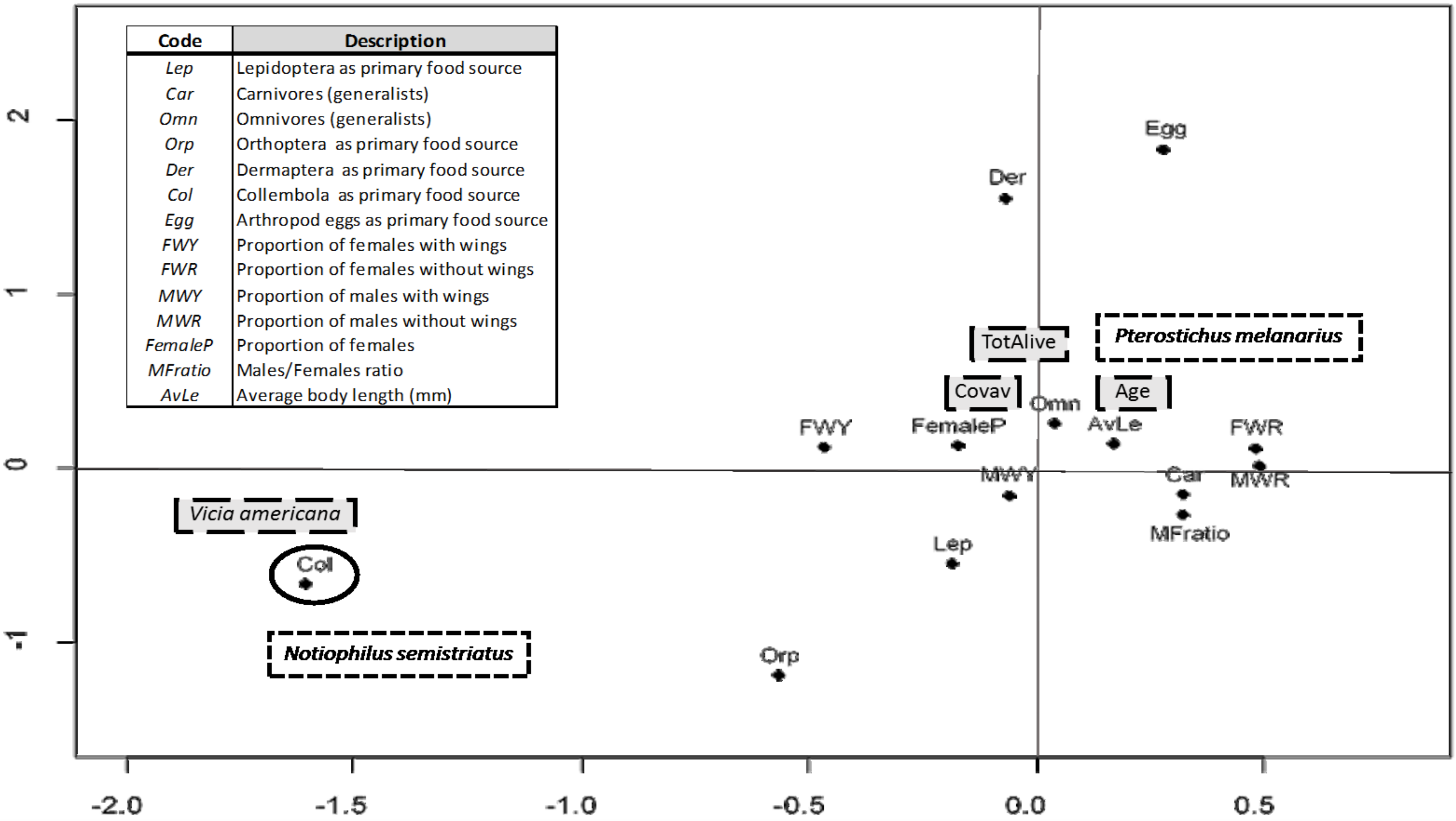


Fig 3-8: Variables ordination, based on their relative values around each trap. For graphical reasons, only some of the variables codes are shown. Plant species names represent categories of the *Mainsp* variable.



Code	Description
Lep	Lepidoptera as primary food source
Car	Carnivores (generalists)
Omn	Omnivores (generalists)
Orp	Orthoptera as primary food source
Der	Dermaptera as primary food source
Col	Collembola as primary food source
Egg	Arthropod eggs as primary food source
FWY	Proportion of females with wings
FWR	Proportion of females without wings
MWY	Proportion of males with wings
MWR	Proportion of males without wings
FemaleP	Proportion of females
MFratio	Males/Females ratio
AvLe	Average body length (mm)

Fig 3-9: Ordination indicating differences in life traits distribution between species, calculated in relation to species abundances and habitat characteristics.



Code	Description
Lep	Lepidoptera as primary food source
Car	Carnivores (generalists)
Omn	Omnivores (generalists)
Orp	Orthoptera as primary food source
Der	Dermaptera as primary food source
Col	Collembola as primary food source
Egg	Arthropod eggs as primary food source
FWY	Proportion of females with wings
FWR	Proportion of females without wings
MWY	Proportion of males with wings
MWR	Proportion of males without wings
FemaleP	Proportion of females
MFratio	Males/Females ratio
AvLe	Average body length (mm)

Fig 3-10: Example of the interpretation of the RLQ analyses. The position of the species *Notiophilus semistriatus* is based on its abundance, and is over imposed on the results presented in Fig. 3-9. In a similar way, the value of an environmental variable (Mainsp, main herbaceous species, *Vicia americana*) is over imposed, based on ordination results presented in Fig. 3-8. The position in relation to Col (Collembola) indicates that *Notiophilus semistriatus* feeds predominantly on this group, and that the distribution of this trait can be related to the presence of *Vicia Americana*. When looking at a more abundant species (*Pterostichus melanarius*), the effect of environmental variables on traits distribution is less clear.

Chapter 4- General discussion

This thesis contributes to knowledge about post-harvest recovery of carabid beetle assemblages, an important component of forest biodiversity. Understanding the impacts of forest harvest on biodiversity is essential to support sustainable forest management (SFM) policies and protocols (Attiwill, 2005; CCFM, 2005). In order to achieve such understanding, and to integrate it with ecological characteristics of the forest, it is necessary to first describe overall forest structure and diversity, explore their interactions and clarify how particular natural systems respond to and accommodate disturbance. This thesis contributes to this goal for carabid assemblages by describing how forest structural components (tree species composition, understory plant species, ground cover percentage) and physical characteristics (temperature, light intensity) can influence the recovery processes after clear-cut harvest.

First, results presented in Chapter 2 highlight how the use of forest age as the primary indicator of recovery of forests after harvest, may ignore critical aspects of the recovery mechanism for carabid beetles and, by extension, other elements of biodiversity. This provides a step forward toward improved biodiversity impact assessments in forest management strategies as required by the recent approach toward sustainable forest management (CCFM, 2005). I have demonstrated that local habitat variables are quite useful in understanding regeneration trajectories and mechanisms for carabid beetles. Thus, additional research can improve our understanding of how small scale habitat structure equivalent to that of old-growth forest may be best developed subsequent to harvest.

Second, in Chapter 3, I have shown that attempts to relate harvest prescriptions to natural disturbance might be improved by the use of diversity indicators that better account not just for the structure of assemblages, but also for functional aspects of carabid beetles. Functional diversity indicators illustrated in Chapter 3 provide a promising starting point for the implementation of such diversity measures in forestry researches. The results show a pattern of reduced functional richness and increased divergence over time after harvesting. These are a direct reflection of the reduction in species richness in relation to clear cut harvesting shown in Chapter 2: a lower number of species in younger stands, due to harvesting disturbance, means that fewer traits are represented in the assemblages so that Functional Richness was reduced. The variation in species composition and distribution of abundances among species is reflected directly by Functional Divergence: assemblages in younger stands are dominated, in terms of abundances, by few species whose traits are more extreme compared to the rest of the assemblage (*i.e. Notiophilus semistriatus*). The combination of the results of Chapter 2 and 3 show that, although stand age is important in influencing carabid beetle diversity, small scale habitat heterogeneity explains a large amount of variation in carabid beetle assemblage.

Although there are few strong and conclusive inferences from these initial analyses, the RLQ analysis hinted at the importance of impact of disturbance on rare species traits. Thus, including functional diversity measures in forest biodiversity work may help us understand how to improve harvest protocols in order to better conserve important functional aspects of ground dwelling communities. The current approach to improve harvesting methods is to simulate natural disturbances, such as wildfire (CCFM, 2005). In order to incorporate functional diversity, a possible approach is to monitor carabid beetle assemblages in post-fire forests and harvested areas, following similar regeneration chronosequences, using similar sets of environmental variables, and compare how functional diversity may different in relation to differences in disturbance source.

In summary, I have shown that an understanding of habitat features at smaller scale than usually used by forest managers can provide better explanations of recovery of carabid beetle assemblages than do simple correlations with forest stand age and large scale structure. Such understanding should then be extended to better promote recovery of carabid beetle assemblages and assemblages of other epigaeic taxa, thereby better meeting biodiversity objectives in the SFM guidelines developed by the Canada Council of Forestry Ministers (CCFM, 2005).

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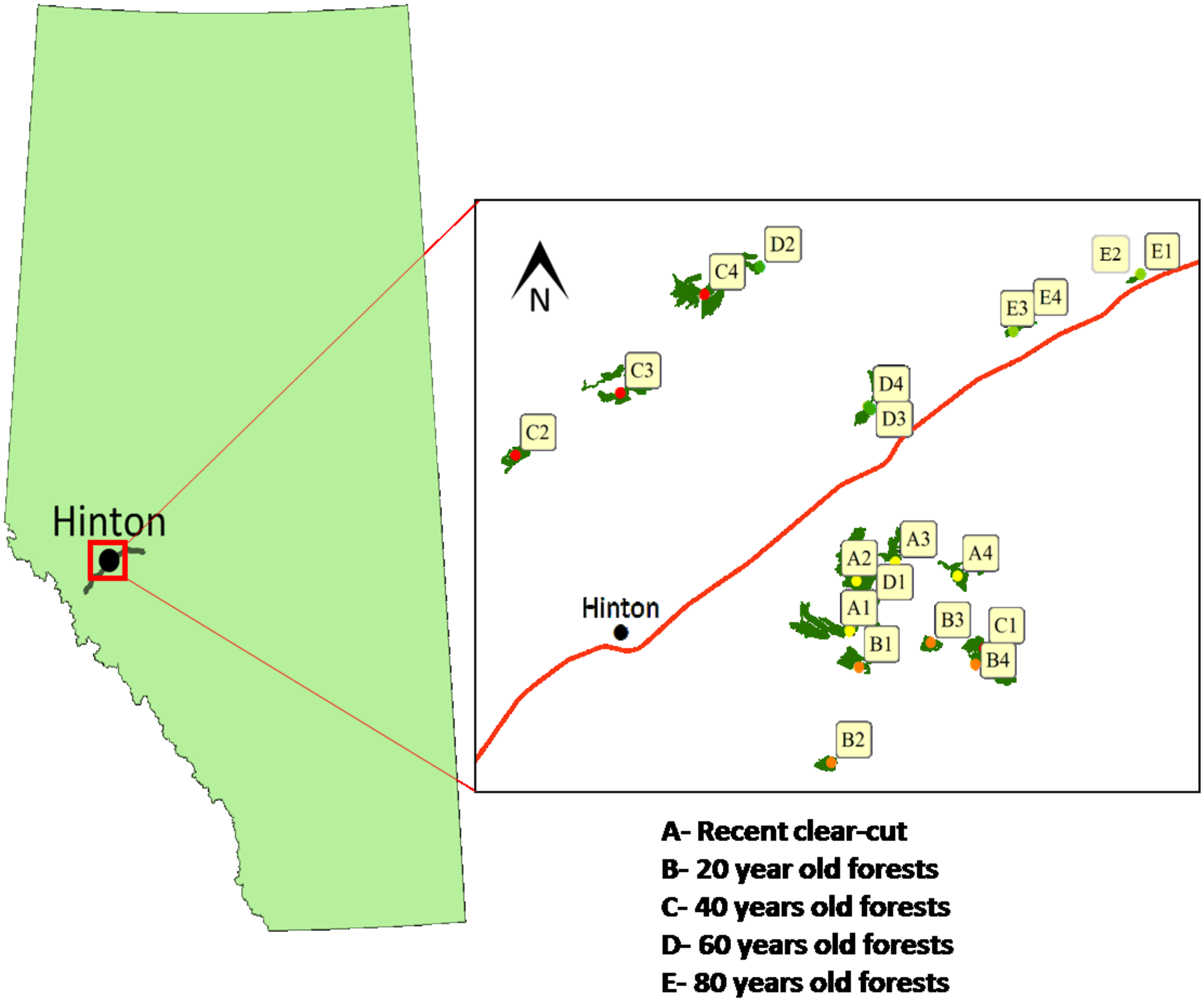
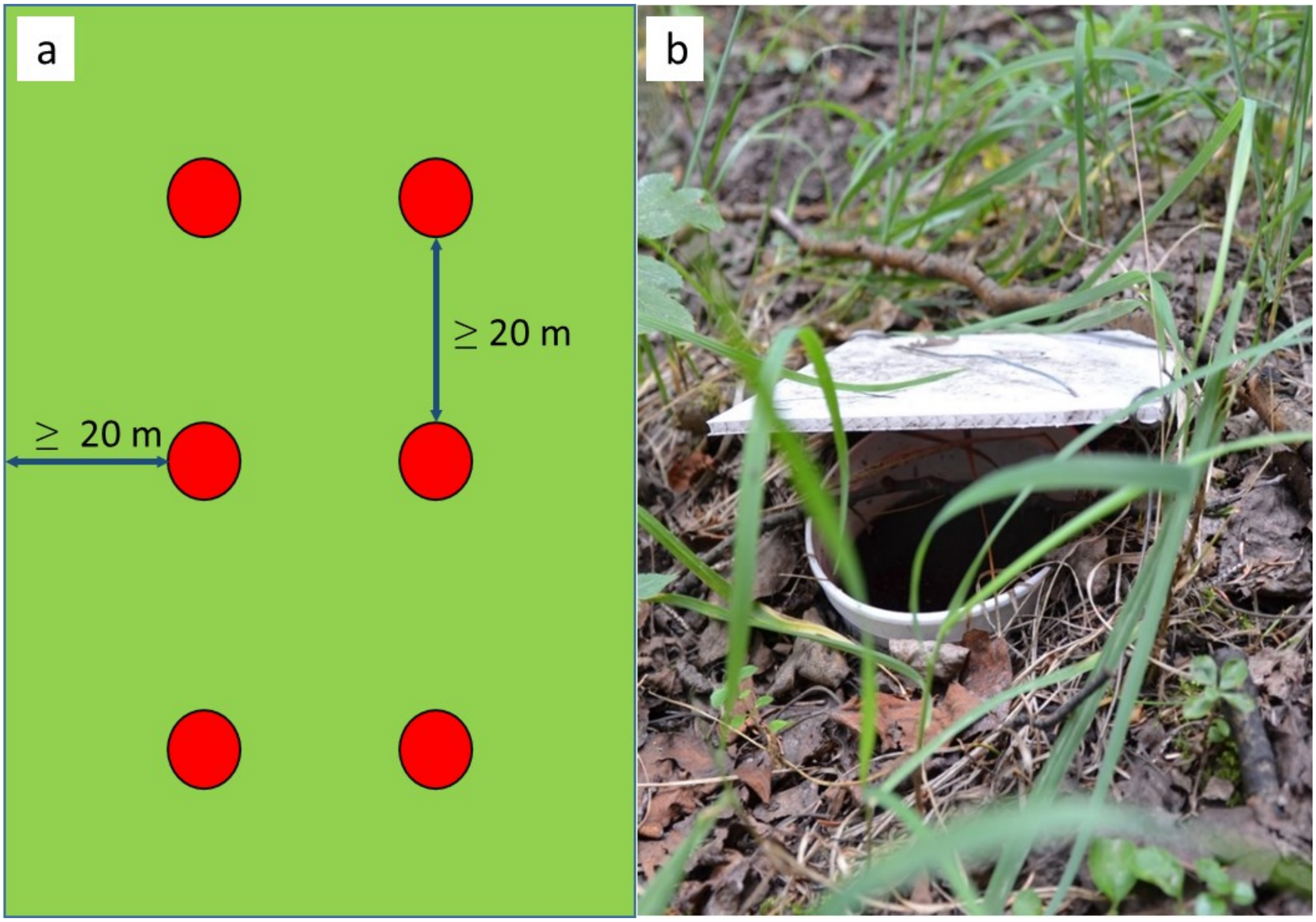
Appendix A

Sampling sites position in relation to the town of Hinton (53.4114° N, 117.5639° W), west central Alberta, Canada



Appendix B

Pitfall trap positioning schematic



In each of the selected forest stands, 6 pitfall traps were positioned in two parallel lines of three traps each, with a minimum distance between traps and from the forest stand edge of 20 m (a). Each pitfall trap consist of a 1L plastic cup, placed in the ground with the upper rim at the ground level, with a smaller 250 ml plastic cup inserted in it. The smaller cup was filled with a 70% solution of ethylene glycol, which serves as preservative for the captured carabid beetles. In order to reduce disturbance from rain or debris, traps were covered with a 10x10 cm PVC roof, hold in place with metal wire (b).

Appendix C

Total number of individuals for each species captured in each age class

Age Class	*Platynus decentis*	*Calathus ingratus*	*Pterostichus adstrictus*	*Calosoma frigidum*	*Pterostichus riparius*	*Pterostichus melanarius*	*Scaphinotus marginatus*	*Calathus advena*	*Stereocerus hematopus*	*Agonum cupreum*	*Pterostichus pennsylvanicus*
Clear cut	1	42	71	0	14	0	13	3	1	80	1
20 years	5	117	2	0	22	0	18	3	1	1	3
40 years	117	202	61	96	69	1	31	65	19	1	20
60 years	370	180	210	46	141	96	42	23	38	0	10
80 years	273	94	203	196	49	123	51	25	52	0	26

Age Class	*Trechus chalybeus*	*Synuchus impunctatus*	*Agonum retractum*	*Carabus chamissonis*	*Bembidion grapii*	*Harpalus fulvilabris*	*Carabus taedatus*	*Patrobus foevicollis*	*Agonum gratiosum*	*Syntomus americanus*	*Leistus ferruginosus*
Clear cut	6	6	0	1	14	3	2	0	0	0	0
20 years	5	6	0	1	0	1	2	1	4	2	1
40 years	9	15	8	4	0	5	2	2	0	1	1
60 years	24	1	5	11	0	2	0	0	0	0	0
80 years	2	2	5	0	0	1	1	2	0	1	1

Age Class	*Cymindis cribicollis*	*Amara littoralis*	*Notiophilus semistriatus*	*Amara lunicollis*	*Trichocellus cognatus*	*Agonum placidum*	*Harpalus lewisii*	*Amara hyperborea*	*Amara torrida*	*Badister obtusus*
Clear cut	0	2	0	2	1	0	0	1	1	0
20 years	0	1	2	0	1	0	1	0	0	0
40 years	3	0	0	0	0	0	0	0	0	0
60 years	0	0	0	0	0	1	0	0	0	0
80 years	0	0	0	0	0	0	0	0	0	1

Appendix D

Life trait values for each of the species included in the analyses.

Species	FWY	FWR	MWY	MWR	FemaleP	MFratio	AvL	Food
Agonum cupreum	1	0	1	0	0.60	0.66	8.3	Lep
Agonum gratiosum	1	0	0	0	1	0	7.8	Ca
Agonum placidum	0	0	1	0	0	0	7.8	Le
Agonum retractum	0.4	0.6	0	1	0.91	0.1	6.9	Ca
Amara hyperborea	1	0	0	0	1	0	11	Om
Amara littoralis	1	0	0	0	1	0	7.8	Or
Amara lunicollis	1	0	0	0	1	0	8.2	Der
Amara torrida	1	0	0	0	1	0	10.1	Or
Badister obtusus	1	0	0	0	1	0	5.8	Ca
Bembidion grapii	1	0	1	0	0.71	0.4	4.4	Ca
Calathus advena	1	0	1	0	0.57	0.74	9.9	Ca
Calathus ingratus	0.03	0.97	0.016	0.984	0.81	0.24	9.5	Ca
Calosoma frigidum	1	0	1	0	0.27	2.66	22	Lep
Carabus chamissonis	0	1	0	1	0.74	0.64	14.5	Ca
Carabus taedatus	0	1	0	1	0.29	2.5	21	Lep
Cymindis cribricollis	0	1	0.33	0.67	0.25	3	9.7	Om
Harpalus fulvilabris	0.38	0.63	0.5	0.5	0.67	0.5	10.3	Egg
Harpalus lewisii	0	0	1	0	0	0	13.5	Ca
Leistus ferruginosus	1	0	1	0	0.29	2.5	8.6	Ca
Notiophilus semistriatus	0	1	0	1	0.33	2	5.1	Col
Patrobus foevicollis	0	0	0.2	0.8	0	0	5.1	Ca
Platynus decentis	1	0	1	0	0.65	0.55	12	Om
Pterostichus adstrictus	1	0	1	0	0.58	0.72	11.3	Lep
Pterostichus melanarius	0.44	0.56	0.34	0.66	0.51	0.95	15.5	Ca
Pterostichus pensylvanicus	1	0	1	0	0.68	0.47	10.8	Ca
Pterostichus riparius	0.06	0.94	0.01	0.99	0.43	1.37	7.3	Ca
Scaphinotus marginatus	0	1	0	1	0.30	2.37	15.3	Ca
Stereocerus hematopus	1	0	1	0	0.34	1.94	11	Ca
Syntomus americanus	0	1	0	1	0.5	1	10	Ca
Synuchus impunctatus	0.24	0.76	0.125	0.875	0.76	0.32	10	Om
Trechus chalybeus	0.03	0.97	0.07	0.93	0.67	0.48	4.3	Egg
Trichocellus cognatus	1	0	1	0	0.5	1	4.4	Egg

Code	Description
Lep	Lepidoptera as primary food source
Car	Carnivores (generalists)
Omn	Omnivores (generalists)
Orp	Orthoptera as primary food source
Der	Dermaptera as primary food source
Col	Collembola as primary food source
Egg	Arthropod eggs as primary food source
FWY	Proportion of females with wings
FWR	Proportion of females without wings
MWY	Proportion of males with wings
MWR	Proportion of males without wings
FemaleP	Proportion of females
MFratio	Males/Females ratio
AvLe	Average body length (mm)