Disturbance, habitat variability and biodiversity of a boreal carabid (Coleoptera: Carabidae) fauna 15 years after variable retention harvest

by

Linhao Wu

A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Conservation Biology

Department of Renewable Resources
University of Alberta

Abstract

Species diversity patterns and the processes that drive them are a central focus of modern ecology. Although the *spatial* effects of habitat variation and disturbance on aggregate metrics like diversity and abundance have received considerable attention at local scales, ecologists have virtually ignored the joint influences of habitat variability and disturbance on the *temporal* variability in communities. Many such studies have dealt with carabid beetles (ground beetles), which are widely used as bioindicators to evaluate faunal response to disturbance. In this dissertation, I have studied variation of boreal ground beetle assemblages in time, in relation to the joint influences of forest cover type and disturbance as a contribution to interpreting the findings of the EMEND (Ecosystem Management Emulating Natural Disturbance) experiment in NW Alberta, Canada.

In chapter 1, I focused on α-diversity and studied how local assemblages respond to combinations of retention harvest prescription across four cover types of mixedwood forest, using a 15-year dataset. The work led to three main conclusions: (1) retention harvests better maintain ground beetle diversity than do traditional clear-cuts; (2) beetle assemblages start recovering toward pre-harvest condition immediately after harvest, instead of diverging from it; and (3) beetle assemblages in high retention treatments recover more quickly than do those in low retention treatments.

Chapter 2 identifies the species that are mostly significantly affected by harvest responsible for large post-harvest species turnover (*i.e.*, β-diversity) among harvested stands and between them and un-harvested controls. My analysis establishes that (1) retention harvests are associated with lower species turnover than are traditional clear-cuts; (2) species turnover decreases with increased retention; and (3) species turnover in response to harvest is driven mostly by forest specialists, but that the extent of turnover will vary with cover-type. I found that seven reasonably abundant species contributed most to species turnover and classified them as ‘key species’ for conservation of these carabids in the context of mixedwood forestry.

Chapter 3 links post-harvest variation to abundance of particular ground beetle species, and I model the abundance of key species, common species and rare species based on information about composition of vegetation. This chapter provides species-specific understanding of how harvest disturbance drives faunal turnover in these forests. Again, there are three main results: (1) habitat variation influences the patterns of abundance, and hence, distribution of ground beetle species and thus affects the structure of local assemblages in quite predictable ways; (2) such influences vary among ground beetle species because they have different habitat requirements; and (3) species distribution in stands harvested with retention are left more similar to un-harvested controls and recover toward forest characteristic of the early phases of boreal succession than in clear-cuts.

Overall, my dissertation provides the most extensive analysis of forest ground beetle assemblages ever undertaken in relation to anthropogenic disturbance. My dissertation contributes to a habitat-based understanding of α- and β-diversity for carabid beetles of forest systems, and clearly shows that the conservation-related effects of forestry flow from reductions in β-diversity. Thus, in the more general view, this work increases ecological understanding about species diversity patterns that contributes to building better approaches for long-term biodiversity conservation in the context of sustainable forest management.

Acknowledgements

I would first like to thank my supervisor Dr. John Spence for providing me with such great opportunity to work on this incredible interesting research, for his patience, motivation and encouragement. It is a great honor for me to be his last PhD student. I also thank my co-supervisor Dr. Fangliang He for giving me great ideas on my thesis, especially his way of critical thinking inspired me to think outside of the box all the time. I also thank supervisory committee Dr. Subhash Lele for always encouraging me to think beyond the data analysis and fully understand why we use these methods to deal with the data. In addition to my supervisory committees, I would also like to express my sincere appreciation to my thesis committee: Dr. Johan Kotze from Helsinki, Dr. Carol Frost and Dr. Scott Nielsen for their insightful comments on my thesis and their encouragement.

I would also like to thank Dr. Colin Bergeron and Dr. Jaime Pinzon for their great help during my PhD study. Whenever I had a question, I could always go to their office and had a nice discussion. I also thank Dr. Colin Bergeron and Silvia Ronzani for teaching me how to identify ground beetles and helped me with identification of difficult groups of beetles. I thank Silvia Ronzani, Jeffery Anderson and Jessica Iltgen for helping me in the field. Those great field memories will always be in my heart. I also thank Amy Hayden, Laureen Echiverri, Matthew Robinson, Caroline Franklin and EMEND core crews for all the support in the field. I also thank Jim Witiw in Daishowa-Marubeni International Ltd. (DMI) for providing me with site information of EMEND. I thank David Langor from CFS for all the encouragement. I also thank all people who involved in the EMEND project in the past 20 years for providing me with such great long-term data.

My sincere thanks also go to my colleagues in the Spence lab and He lab: Jaime Pinzon, Colin Bergeron, Seung-Il Lee, Jared Amos, Aaron Bell, Vincent Belluz, Zoltan Domahidi, Sonya Odsen, Claudio La Rocca, Silvia Ronzani, Jian Zhang, Xiaofeng Ruan, Youhua Chen, Dingliang Xing. We had great time working together in the lab and established great friendship.

I would also like to thank my previous supervisor, Dr. Xiangrong Wang for introducing to me to the field of Ecology. I thank all the teachers who taught me in elementary school, middle school, high school, Tonji Univeristy, Fudan Univeristy and University of Alberta. I thank all the friends in China and in Canada for their encouragement.

Last but not the least, I thank my parents, Xingen Wu and Ping Li for everything they did for me. Their love for me has always been the most powerful support. I would not complete this journey without their love.

Financial support was provided by the Chinese Scholarship Council, DMI, Canfor, CFS, Government of Alberta, Forest Resource Improvement Association of Alberta (FRIAA) and NSERC Discovery Grant to John Spence, as well as the Alberta Conservation Association Grants in Biodiversity to Linhao Wu.

Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

Understanding the determinants of species diversity patterns and the processes driving them is of central interest in ecology (Gatson 2000, Tscharntke et al. 2012). Habitat-associated factors including both biotic and abiotic conditions play important roles in location of species in landscapes (Hutchinson 1957, Holt 2009), and determine the distribution of species on local to regional spatial scales (Peterson 2001, Guisan and Zimmermann 2000). At local spatial scales, the importance of habitat, especially the structure and complexity of vegetation, has long been emphasized for explaining animal distributions (MacArthur and MacArthur 1961), and has been the subject of investigation for many taxa. Since the work of Pickett and White (1985), however, increasing numbers of researchers have focused on disturbance in trying to understand patterns of species distribution (Muotka and Virtanen 1995, Devictor et al, 2008).

Therefore, understanding the joint effects of habitat variability and disturbance on species distributions has been a recent focus of ecological studies (McClain and Barry 2010, Parisien and Moritz 2009, Moreno-Rueda and Pizarro 2009). In Canada, several large-scale studies consider species distributions of various taxa within the boreal ecosystem. For example, the EMEND (Ecosystem Management Emulating Natural Disturbance) project in Northwestern Alberta (Spence et al., 1999) seeks to determine the effects of forest cover type and disturbance on species distributions across a wide range of taxa (Bergeron et al. 2017) and to apply such knowledge to improve conservation of biodiversity and the sustainability of forestry on managed landscapes.

Retention harvesting has been increasingly applied as an alternative to traditional clear-cutting over the past two decades in forestry worldwide (Lindenmayer and Franklin 2002, Lindenmayer et al. 2012). In contrast to clear-cutting, stands harvested leaving a significant proportion of green trees, standing as 'retention', are more similar in structure to those left by natural disturbance (Franklin et al. 1997). Because maintenance and re-establishment of native forest biodiversity is a central goal of the retention harvesting approach (Baker et al. 2013), understanding the impacts on species distributions is central to its assessing value. It is thought to be better for biodiversity conservation management than clear-cutting because retention harvests (1) can 'lifeboat' sensitive species through the early stages of stand regeneration; (2) increase structural variation in regenerating lands; and (3) promote connectivity in forest landscapes (Franklin et al. 1997, Gustafsson et al. 2010).

Short-term impacts of retention harvests on forest biodiversity have been widely studied. We know, for example, that retention harvest can effectively maintain forest-dependent plants in managed landscapes (Baker et al 2016), and that retention patches serve as potential refugia for bryophytes and lichens (Perhans et al 2009). Harvest intensity also influences ground beetle populations and the structure of their assemblages in boreal mixedwood forests, with recovery of forest assemblages being demonstrably faster with increasing retention (Jacobs et al. 2008, Work et al. 2013). Taken together, published short-term studies nonetheless generally indicate that retention harvest has profound effects on forest characteristics that affect biodiversity maintenance. Such effects differ among organisms, green tree retention patterns and forest types (Hyvarinen et al. 2006, Koivula 2002, Sullivan et al. 2001, Sullivan et al. 2008, Pinzon et al. 2012), and many studies are attempting to understand them in an effort to develop more effective forest harvest and regeneration strategies.

Although harvesting can have severe and long-lasting effects on biodiversity of forest ecosystems (Lindenmayer and Franklin 2002), only a few studies have examined long-term responses of biotic assemblages to retention harvest at particular sites (Pinzon et al. 2016, Roberts et al. 2016). Since a central goal of retention harvest is to conserve and facilitate recovery of biodiversity to pre-harvest conditions, long-term studies are needed to measure recovery and evaluate the extent to which retention harvest meets these goals.

Biodiversity is a useful concept, but it is not easily distilled as a variable that can be practically measured. Thus, use of 'indicator species' has evolved as a practical method to evaluate biotic recovery from ecosystem disturbances and, in particular, to assess progress in meeting "sustainable forest management" targets (Lindenmayer et al. 2000). Because ground beetles (Coleoptera: Carabidae) are diverse, but well known taxonomically, sensitive to environmental changes (Rainio and Niemelä 2003, Work et al. 2008, Koivula 2011), and react strongly to industrial-scale harvests (Niemelä et al. 1992, Buddle et al. 2006), they have been widely used as good bioindicators to assess the conservation value of variable retention harvesting, and they have been particularly well studied at EMEND (Jacobs et al. 2008, Work et al. 2010, Blanche et al. 2013, Bergeron et al. 2017).

This thesis further develops that theme, focusing on responses of ground beetle assemblages to various retention harvests in four cover types in the mixed wood boreal forest of NW Alberta, Canada, using a 15 years dataset. Although only a mid-term study from the perspective of forest succession, these data are among the longest term records available for forest carabids from anywhere in the world.

In chapter 1, I showed (1) retention harvests better maintain ground beetle diversity than do traditional clear-cuts; (2) beetle assemblages start recovering toward pre-harvest condition immediately after harvest, instead of diverging from it; and (3) beetle assemblages in high retention treatments recover more quickly than do those in low retention treatments. After testing these general hypotheses in first data chapter, I then continued to explore which species are most affected by harvest and thus caused large species turnover between harvested stands and controls post-harvest.

Since Whittaker (1960, 1972) introduced the concept of partitioning regional (gamma) diversity into local (alpha) and turnover (beta) components, academic interest in the concept of beta diversity has steadily increased (Harrison et al. 1992, Lennon et al. 2001, Koleff et al. 2003, Jost 2007, Anderson et al. 2011). Species turnover links regional species pools to local alpha diversity by quantifying compositional differences among sites (Harrison et al 1992, Soininen et al 2007), and therefore, understanding beta diversity is essential for evaluating and managing conservation efforts on landscapes. Thus, ecologists are exploring patterns of beta diversity to understand how and why assemblages of species differ from one location to another (Vellend 2010).

Species turnover is driven by powerful ecological processes, reflecting geography, environment and the dispersal ability of organisms in the regional pool (Soininen et al 2007). Most published studies have focused on large organisms at broader scales to explore geographical patterns in biodiversity (Condit 2002, Qian et al. 2005, Hillebrand 2004). However, more local disturbances such as forest harvesting can also impact biodiversity (Lindenmayer and Franklin 2002), and promote large species turnover across habitat even at relatively small scales (Work et al. 2010, Pinzon et al. 2016).

In initial studies of retention effects, intensity appears to influence arthropod populations and assemblages, with more similar species composition (less species turnover) associated with increased retention (Jacobs et al. 2008, Work et al. 2010, Pinzon et al. 2012). Ground beetles are strongly associated with particular tree species (Bergeron et al 2011) and, based on characteristic habitats, can be classified into habitat generalists, forest generalists and forest specialists (Niemelä and Spence 1992); forest specialists appeared to be more sensitive to harvest intensity (Work et al 2010).

Therefore, in the second data chapter, I focused on differences in post-harvest species turnover in ground beetle assemblages between four intensities of retention harvests and uncut boreal forest across the mixed-wood cover-types and over the 15 years period encompassed by my data set. I showed (1) retention harvests are associated with lower species turnover than are traditional clear-cuts; (2) species turnover decreases with increased retention; and (3) species turnover in response to harvest is driven mostly by forest specialists, but that the extent of turnover will vary with cover-type.

After determining key species which contributed most to species turnover in chapter 2, I then linked post-harvest habitat variation to abundance of ground beetle species in chapter 3, modeling abundance of key species, common species and rare species to understory vegetation. This contributes to understanding of how harvest disturbance drives faunal turnover in different kinds of forest.

Forest habitats are significantly influenced by the intensity of harvest. For example, graminoid cover increases in low retention stands while bryophyte cover remains higher in high retention stands (Pinzon et al. 2016). Therefore, it has been suggested that high retention harvests can 'lifeboat' sensitive species through the early stages of stand regeneration to maintain and more quickly re-establish native forest biodiversity (Frankin et al. 1997, Gustafsson et al. 2010, Lindenmayer and Franklin 2002, Lindenmayer et al. 2012).

Habitat variation shaped by harvesting is expected to drive ground beetle species distribution through impacts on particular habitats in relation to habitat preference of beetles and variable reproductive success of the species in affected habitats (Koivula et al. 1999, Niemelä et al. 1992, Jacobs et al. 2008, Begeron et al. 2011). Understanding these interactions should help guide practical retention harvest so that its implementation reduces undesired influence on ground beetles, and through extension of the general principle, all biodiversity that is negatively affected at the stand scale.

Therefore, the main goal of my last data chapter is to describe the distribution of ground beetles in stands regenerating after harvest in relation to habitat variability, as shaped by pre-harvest cover-type a decade or more after variable retention harvest. I showed that (1) habitat variation influences the distribution of ground beetle species and local structure of assemblages in predictable ways; (2) such influences vary among ground beetle species because of different habitat requirements; and (3) species distribution in stands harvested with retention are more similar to un-harvested controls than to clear-cuts.

In conclusion, while the *spatial* effects of habitat variation and disturbance on aggregate metrics like diversity and abundance have received considerable attention, ecologists have virtually ignored the joint influences of habitat variability and disturbance on *temporal* variability in communities. Thus, in this dissertation, I have studied variation of ground beetle assemblages in time, in relation to the joint influences of forest cover type and disturbance. This is an important issue because significant interactions between the character of forest habitats and disturbance suggests that a similar level of disturbance could have very different effects on beetle assemblages in different habitats. Attempts to manage biodiversity on harvested landscape will undoubtedly fail if such interactions are ignored. I believe that my dissertation will contribute useful information about spatial dynamics of ground beetle populations, but also, in the more general view, to building better approaches to a long-term biodiversity conservation in the context of sustainable forest management.

Chapter 2

Recovery of a boreal carabid (Coleoptera: Carabidae) fauna 15 years after variable retention harvest

2.1 Introduction

Retention harvesting has been increasingly applied over traditional clear-cutting over the past two decades in global forestry (Lindenmayer and Franklin 2002, Lindenmayer et al. 2012). In contrast to clear-cutting, stands harvested with a significant proportion of green trees left, are more similar in structure to those left by natural disturbance (Franklin et al. 1997). Maintenance and re-establishment of native forest biodiversity is a central goal of the retention harvesting approach (Baker et al. 2013). It is thought to be better for biodiversity conservation management than clear-cutting because retention harvests (1) 'lifeboat' sensitive species through the early stages of stand regeneration; (2) increase structural variation in regenerating lands; and (3) promote connectivity in forest landscapes (Franklin et al. 1997, Gustafsson et al. 2010).

Short-term impacts of retention harvests on forest biodiversity have been widely studied. We know, for example, that retention harvest can effectively maintain forest-dependent plants in managed landscapes (Baker et al 2016), and that retention patches serve as potential refugia for bryophytes and lichens (Perhans et al 2009). Harvest intensity also influences ground beetle populations and the structure of assemblages in boreal mixedwood forests, with recovery of forest assemblages faster with increasing retention (Jacobs et al. 2008, Work et al. 2013). Overall, published short-term studies nonetheless generally indicate that retention harvest still has profound effects on forest characteristics that affect biodiversity maintenance. However, such effects differ among organisms, green tree retention patterns and forest types (Hyvarinen et al. 2006, Koivula 2002, Sullivan et al. 2001, Sullivan et al. 2008, Pinzon et al. 2012).

Harvesting can have severe and long-lasting effects on biodiversity of forest ecosystems (Lindenmayer and Franklin 2002); however, only a few studies have examined long-term responses of biotic assemblages to retention harvest at particular sites (Pinzon et al. 2016, Roberts et al. 2016). Since a central goal of retention harvest is to conserve and facilitate recovery of biodiversity to pre-harvest conditions, long-term studies are needed to evaluate the extent to which retention harvest meets these goals.

Biodiversity is a useful concept but not easily distilled as a variable that can be practically measured. Thus, use of 'indicator species' has evolved as a practical method to evaluate recovery from ecosystem disturbances and, in particular, to assess progress in meeting "sustainable forest management" targets (Lindenmayer et al. 2000). Because ground beetles (Coleoptera: Carabidae) are diverse, but well known taxonomically, sensitive to environmental changes (Rainio and Niemela 2003, Work et al. 2008, Koivula 2011), and react strongly to industrial-scale harvests (Niemela et al. 1992, Buddle et al. 2006), they have been widely used as good biodindicators to assess the conservation value ofvariable retention harvesting.

In this chapter, I focus on responses of ground beetle assemblages to various retention harvests in four cover types in the mixed wood boreal forest of NW Alberta, Canada, using a 15-year dataset. My hypothesis is that (1) retention harvests better maintain ground beetle diversity than do traditional clear-cuts; (2) beetle assemblages start recovering toward pre-harvest condition immediately after harvest, instead of diverging from it; and (3) beetle assemblages in high retention treatments recover more quickly than do those in low retention treatments.

2.2 Methods

2.2.1 Study area

This study was conducted at the EMEND (Ecosystem Management Emulating Natural Disturbance) research site where an experimental design of retention harvesting was implemented during 1998-99 across a range of upland mixedwood sites all comprising merchantable forest. EMEND is located ~90 km northwest of Peace River, Alberta, Canada (56°46′13″ N, 118°22′28″ W). Forests on the EMEND landscape are typical western boreal mixedwood, main deciduous species including trembling aspen, *Populus tremuloides* Michaux, and balsam poplar, *Populus balsamifera* L., in early successional stages, and mainly conifer species including white spruce, *Picea glauca* (Moench) Voss and black spruce, *Picea mariana* (Miller), in later successional stages (Pinzon et al 2016).

The EMEND design allocated a range of innovative harvest treatments to each of four dominant forest cover types, classified as (Work et al. 2004):

(i) deciduous-dominated (DDOM): mainly *Populus* species with less than 30% coniferous

trees in the canopy,

(ii) deciduous with a coniferous understory (DDOMU): mainly *Populus* canopy with significant amounts of white spruce in the understory,

(iii) mixed stands (MX): canopy layer with approximately equal proportions of deciduous and coniferous components, and

(iv) conifer-dominated (CDOM): with conifers, mainly white spruce, representing greater than 70% of the canopy

2.2.2 Experimental design and beetle sampling

The EMEND experiment was designed to explore interactions between stand cover type and forest harvest through stand-level manipulation of green-tree retention. Green tree retention was left in c. 10-ha compartments harvested for the first time in 1999 in the following percentages of original stand basal area: 2% (R0), 10% (R10), 20% (R20), 50% (R50) and 75% (R75); each replicate block also included an uncut (CT) compartment (i.e., R100). Three blocks of replicate 10-ha compartments were established in stands classified before harvest as belonging to each of the four cover types (i.e., there were 4x6 = 24 cover type x retention combinations), providing 72 compartments in total [Fig. 2.1. Full details of the experimental design are provided by Spence et al. (1999) and Work et al. (2010)].

Ground beetles were collected throughout EMEND using pitfall traps in 1999, 2000, 2004, 2009 and 2014, with these years corresponding to 1, 2, 5, 10 and 15 years post-harvest, respectively. Pitfall traps (12 cm diameter) were dug into ground with their upper rims level with the soil surface, filled with approximately 200 ml ethylene glycol as a killing agent and preservative, and covered with a suspended plastic roof to avoid flooding (Spence and Niemela 1994). Traps were installed at either end of three randomly chosen 40 m transects in a subset of the six EMEND permanent sampling plots (PSPs) in each 10-ha forest compartment (Work et al. 2010). Thus, each compartment was sampled by a total of six traps. Each trap was visited 4-5 times at approximate 3-week intervals to bracket the frost-free season from mid-May to late August in each of the 5 years. Ground beetles were also collected in 1998 in what were designated as un-harvested control compartments, intended to represent pre-harvest conditions. Ground beetles were sorted and identified to species using Lindroth (1961, 1963, 1966, 1968, 1969a,b).

2.2.3 Analysis

Ground beetles were pooled by compartment in each collection year. Catch of ground beetles was standardized to number of individuals per 100 trap-days to minimize the sampling effort as a result of trap disturbance. The capture rate of pitfall trap may be biased due to uneven chance among different beetle species to be caught across treatments. Since this study focuses on relative difference of beetle assemblages in time and space, it is not that necessary to know the absolute beetle abundance. Thus, pitfall trap data was analyzed unbiased in this study through chapter 2 to chapter 4.

Estimated ground beetle richness was calculated for 5 post-harvest periods (1, 2, 5, 10 and 15 years post-harvest) and 6 treatments (R0, R10, R20, R50, R75 and CT) for each forest cover type using coverage-based rarefaction (Chao and Jost 2012). Unlike the traditional rarefaction method, which uses samples with the lowest number of individuals as a threshold for comparison, in coverage-based rarefaction, assemblages are compared from the perspective of equal completeness (i.e., coverage), not equal sample size, which means we compare species richness for the same proportion of individuals from each community. Thus, comparisons of species richness are based on characteristics of the communities, rather than on standardizing the surveyor's sampling efforts. Because carabid sampling at EMEND required collective large sampling efforts across years and uneven sampling efforts was inevitable, coverage-based rarefaction will then make the best use of all data regardless of uneven sampling efforts which were mostly due to unexpected trap disturbance.

Temporal species turnover is described by the total change in species (appearances and disappearances) as well as the proportion of species that either appear or disappear between time points (Collins et al. 2008, Cleland et al. 2013). Comparisons were paired between samples from 2, 5, 10 and 15 years post-harvest, and 1 year, respectively. Total species turnover = (Species gained + Species lost)/Total species observed in both time points (MacArthur and Wilson 1963, Diamond 1969).

Canonical Redundancy Analysis (RDA; Legendre and Legendre 2012) was used to assess the response of species composition of ground beetle assemblages to three factors (time, cover type, harvest treatment and their interactions; the interactions are defined as new dummy variables resulting from combination of both main factors). RDA not only illustrates the dissimilarity of different assemblages but also estimates the variance explained by each component constructed by the analytical procedures. Therefore, RDA explains how time, cover type, harvest treatment and their interactions contribute the clustering or scatter of beetle assemblages. Significance of the final model, explanatory variables and RDA axis were tested based on P values generated from 999 permutations.

All analyses were computed in R v 3.2.4 (R Core team 2015) using iNEXT (Hsieh, Ma and Chao 2016) for coverage-based rarefaction, codyn (Hallett et al. 2016) for temporal species turnover and vegan (Oksanen et al. 2015) for RDA analysis.

2.3 Results

A total of 52,437 ground beetles, comprising 76 species were collected. Among those species, 13 species accounted for 95.7% of the total individuals. *Pterostichus adstrictus*, *Platynus decentis* and *Calathus ingratus* were the three most abundant species, together accounting for 55.6% of the total catch. In contrast, 38.2% of the species were represented by singletons (24 spp.) and doubletons (5 spp.). Overall species richness was highest 5 years after harvest (46 spp.) and lowest pre-harvest (15 spp.).

2.3.1 Ground beetle richness

Estimated species richness was compared among combinations of harvest treatments and time periods at the same coverage value respectively (Fig. 2.2), with 96.5% sample completeness (coverage value) for deciduous-dominated stands, 94.8% sample completeness for deciduous/spruce stands, 94.3% for mixed stands and 96.3% for conifer stands. Within each forest type, the estimated species richness in most treatments, both 1 and 2 yr after harvest, was lower and differed significantly from (no overlap in 95% confidence intervals) that of un-harvested controls (dashed horizontal lines in Fig. 2.2), suggesting substantial species loss right after harvest. Clear-cut (R0) experienced the most dramatic changes in richness among all treatments in all forest types (Fig. 2.2). In all remaining treatments in deciduous and deciduous/spruce units, estimated richness remained relatively stable and was equal to or a little bit lower than that of un-harvested controls 15 yr after harvest (Fig. 2.2a, b). In mixed and conifer stands, however, estimated richness fluctuated more and finally surpassed or equaled to that of un-harvested controls in mixed stands (Fig. 2.2c), and was significantly higher than un-harvested controls in conifer stands (Fig. 2.2d).

2.3.2 Temporal ground beetle turnover

Temporal species turnover indicates that in general there were greater fluctuations in the ground beetle species present in the harvested treatments than the controls in four forest cover types (Fig. 2.3). The highest species turnover occurred 5 years after harvest across most retention levels, illustrating dramatic changes in species composition over the first 5 years after harvest (Fig. 2.3). Within harvested treatments, there was higher species turnover in low retention levels (R0-R20) than high retention levels (R50-R75). In short, species composition changed dramatically with increasing harvest intensity.

Partitioning total turnover by appearances and disappearances, there were lower proportions of appearances and higher proportion of disappearances in low retention treatments (R0-R20) than in high retention (R50 and R75) treatments 2 and 5 years post-harvest, indicating that more species were lost in low retention treatments during the early post-harvest stage (Fig. 2.3a, d) in these two cover types. In contrast, there were generally higher proportions of both appearance and disappearance of ground beetle species in low retention treatments (R0-R20) than high retention treatments (R50 and R75) in deciduous/spruce stands and mixed stands from 2 to 10 years post-harvest (Fig. 2.3b, c), suggesting both tremendous beetle species loss and gains in each time periods; i.e., the assemblages of recovering stands are highly dynamic

2.3.3 Ground beetle assemblages

Harvesting had an important long-lasting effect on ground beetle assemblages in terms of species composition in each forest cover type through 15 years post-harvest. Significant effects of time, forest cover type, harvest treatment, and their interactions were detected; however, the three-way interaction was not significant. Therefore, a final model without three-way interaction was established ($F_{63, 308}$=4.7; P<0.001). Significant differences in species composition were detected among years ($F_{5, 308}$=20.5; P<0.001), cover types ($F_{3, 308}$=26.2; P<0.001), treatments ($F_{5, 308}$=5.9; P<0.001), and their interactions: year × cover type ($F_{15, 308}$=1.86; P<0.001) (Fig. 2.4), year × treatment ($F_{20, 308}$=1.82; P<0.001) (Fig. 2.5), cover type × treatment ($F_{15, 308}$=1.51; P<0.01) (Fig. 2.6). The model explained 38.7% (adjusted R^2) of the total variance, with axis 1 and axis 2 explaining 37.6% and 21.7% of the constrained variance, respectively.

No significant differences in assemblage composition were detected between pre-harvest, 1- and 2- years post-harvest; however, these assemblages significantly differed from those found 5 and 10 years post-harvest (Fig. 2.4). Generally, the ordination reveals vertical pattern from top to bottom in the direction of axis 2 reflecting changes during pre-harvest to 10 years post-harvest, but then the trend goes up in 15 years post-harvest, suggesting the beginnings of real recovery of ground beetle assemblages toward the pre-harvest state (Fig. 2.4). Carabid assemblages 15 years post-harvest more or less overlapped in structure with pre-harvest assemblages in deciduous-dominated stands and deciduous/spruce stands. In contrast, however, assemblages in mixed and conifer stands moved further away from pre-harvest states, becoming more similar to those in deciduous and deciduous/spruce stands (Fig. 2.4a, b). Within each time period, assemblages in deciduous stands evidently differed from those in the other three forest cover types while assemblages from mixed and conifer stands largely overlapped in structure (Fig. 2.4).

Significant impacts of harvest intensity on ground beetle assemblages were observed in the ordination during each time. A vertical disturbance gradient, increasing from top to bottom in the ordination, and following harvest intensity from clear-cuts to un-harvested controls, was evident in the data from 1- and 2-yrs post-harvest (Fig. 2.5b, c). Then the vertical disturbance gradient gradually became horizontal, increasing from right to left, from 5- to 15-yrs post-harvest (Fig. 2.5d, e, f). Nonetheless, no matter the actual direction of change in ordination space, the disturbance gradient remained evident, suggesting that harvest intensity consistently played a major role in changes of ground beetle assemblages after harvest. Assemblages found in higher retention treatments were clearly more similar in species compositions to those of controls. Based on 95% confidence intervals around harvest treatment centroids (ellipses), the carabid assemblages of clear-cuts differed quite significantly from those of other harvest treatments 2-, 5- and 15-yrs post-harvest (Fig. 2.5c, d, f); Interestingly, the difference was a little less obvious 10-yrs post-harvest because of a large overlap of the confidence ellipses among low retention levels (R0-R20) (Fig. 2.5b, e), suggesting that beetle assemblages uniformly recovered faster in retention treatments than in clear-cuts.

Interaction of cover type and treatment was also significant, but not as evident as were the other two interactions (Fig. 2.6). A clear difference between clear-cuts and un-harvested controls was evident in all cover types; however, there was a large overlap of confidence ellipses among retention treatments and clear-cuts, and only treatments with highest retention level (R75) had assemblages clearly closer to those of un-harvested controls, especially in deciduous/spruce stands.

2.4 Discussion

Our results strongly support our first hypothesis. Clearly, retention harvest helps to maintain forest biodiversity better than traditional clear-cutting, and variation in harvest intensity promotes recovery for the ground beetle fauna along different trajectories. Given our 15 year time frame, which is longer than most published studies, our results suggest long-lasting effects of retention harvest and a dynamic recovery of biodiversity after harvest.

We found no general retention threshold that better conserves these boreal ground beetle assemblages, consistent with the results of ground-dwelling spiders in the same study area (Pinzon et al. 2016). Thus, a mixed treatment of harvest intensity (variable retention) may best conserve ground beetle biodiversity, contrasting with predictions of our third hypothesis. Although beetle assemblages recover faster in retention treatments than in clear-cuts, we did not find that any particular retention level was optimal. Assemblages in higher retention treatments (R50 and R75) did not generally recover faster than in lower retention treatments (R10 and R20). Thus, even 10% retention is better for faunal recovery than the former approach of clear-cutting. Our conclusion about thresholds has the following caveat: elements characteristic of the pre-harvest fauna in spruce dominated stands appear to be better conserved with higher retention levels, although such level are not economically feasible in present-day boreal forestry.

The temporal effects on position of ground beetle assemblages in our ordination corroborates our second hypothesis, i.e, beetle assemblages began recovering toward the pre-harvest condition 15 yrs after harvest instead of continuing to diverge from it. Moreover, our results showed that the recovery of ground beetle assemblages is not just a hint or a sign, like the recovery of ground-dwelling spiders found in the same area 10 years post-harvest (Pinzon et al. 2016). They recover more quickly than we thought especially in deciduous and deciduous/spruce stands.

However, recovery of ground beetle assemblages differed across forest cover types. They converged strongly toward the pre-harvest condition in deciduous and deciduous/spruce stands

15 years post-harvest, but by this time in mixed and conifer stands, had become more similar to those of originally deciduous and deciduous/spruce stands. The pattern shows that conifer associated assemblages are less resistant and resilient to harvesting, and suggests that recovery requires a re-set to the state typical of deciduous stands that are earlier in the successional sequence (Rowe 1972, Keenan and Kimmins 1993). In other words, and unsurprisingly, carabid assemblages follow the successional trajectories of the recovering forest after harvest.

Harvested stands of mixed wood forest generally regenerate through a deciduous phase, regardless of pre-harvest cover type (Gradowski et al. 2010). Therefore, following harvest of mixed and conifer stands the recovering forest becomes similar to that of originally deciduous stands through a strong pulse of deciduous trees regeneration, providing ideal habitat to deciduous associated ground beetle species. Previously studies in the same area have also showed that harvesting has more significant immediate influence on both ground beetle and spider species in late successional stands than in early successional stands (Work et al. 2010, Pinzon et al. 2016). Therefore, cover types should be carefully considered before retention harvest is applied and higher retention levels will more effectively conserve mature forest associated species and facilitate recover of beetle assemblages to the pre-harvest condition.

Although our 15-year study is relatively long in comparison to other published work, it is still a short time when compared to normal forest rotation times (80-90 years) in the western boreal forest of Canada. Recovery of beetle assemblages is evident 15 years after harvest but ground beetle assemblages remain quite different from the pre-harvest condition in late successional stands. Therefore, long-term studies are required to evaluate the long-lasting effects of retention harvesting on biodiversity. The EMEND project that was designed to run for 80 years should provide an excellent example of post-harvest recovery through future observations. The present study clearly suggests that retention forestry will promote more rapid recovery of biodiversity than would be seen under a clear-cut harvest regime.

Our results have two important implications for forest management, and for the conservation of biodiversity in managed forest landscapes. First, variable retention harvests will promote and maintain biodiversity better than clear-cutting. Higher retention levels promote faster recovery and so an important consideration for biodiversity conservation is the trade-off between in-block retention and total area that must be harvested to meet economically sustainable requirements for volume. Second, if the goal is recover biodiversity toward pre-harvest states, higher retention levels are needed in conifer dominated stands compared to deciduous dominated stands. Other work at EMEND suggests that post-harvest silviculture prescriptions can promote more rapid recovery of coniferous forests (Gradowski et al. 2010), but for the moment is remains unclear whether this accelerates recovery of other biotic elements.

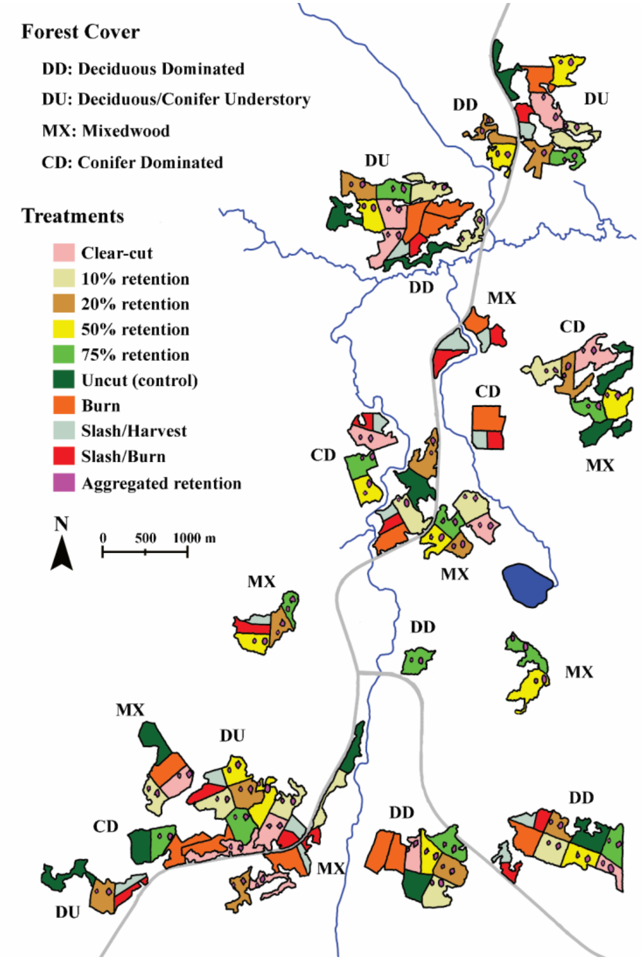


Fig. 2.1. Map of the EMEND (Ecosystem Management by Emulating Natural Disturbance) experimental site. Compartments of harvesting treatments and un-harvested controls in four forest cover types.

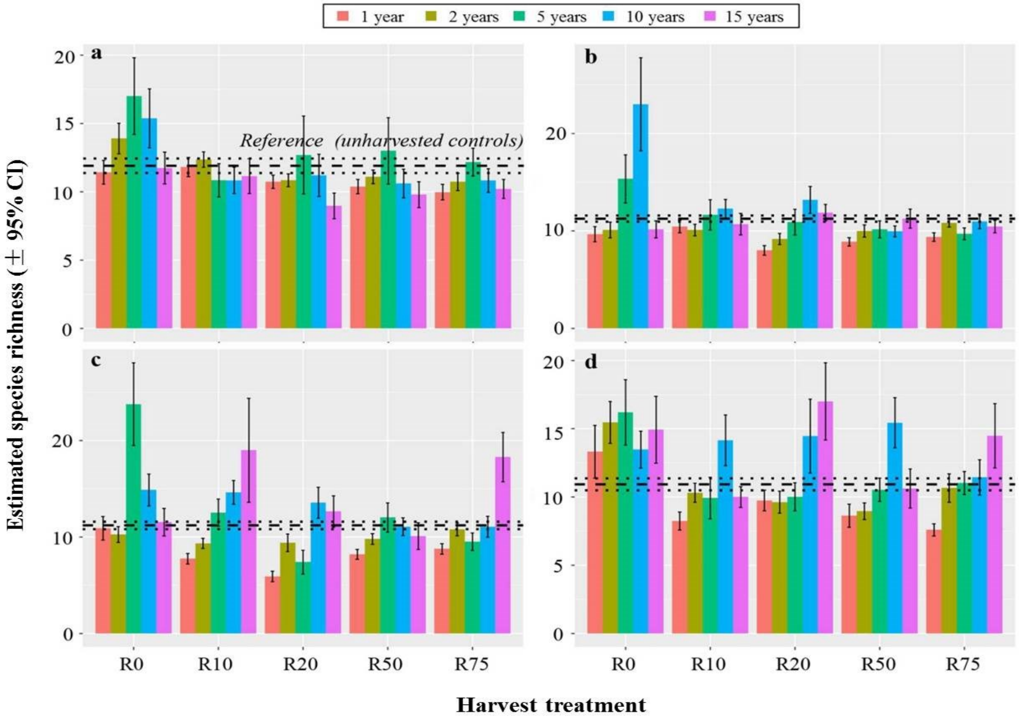
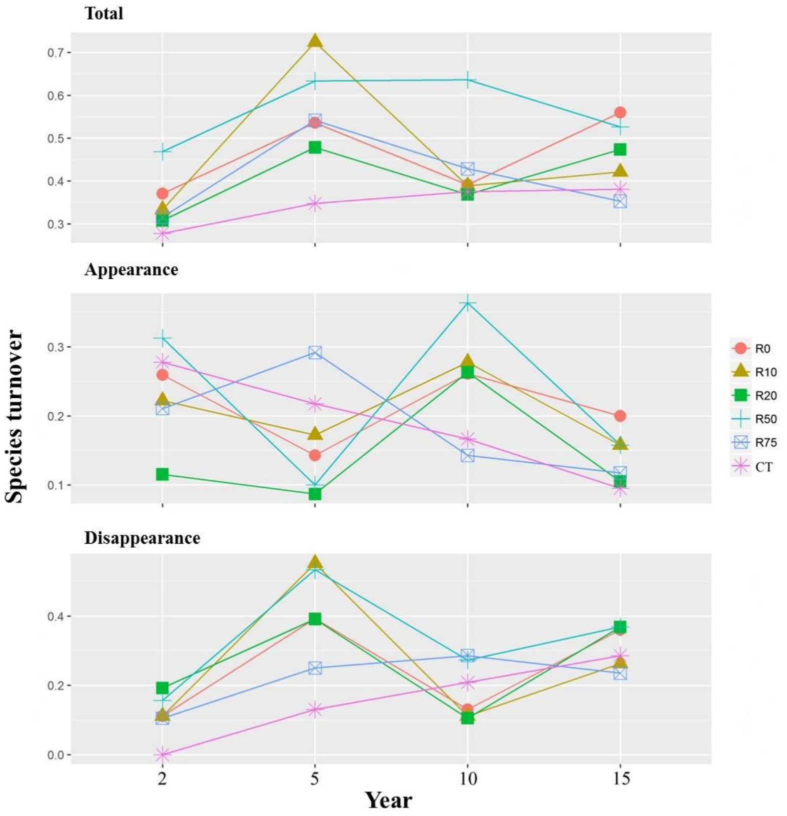
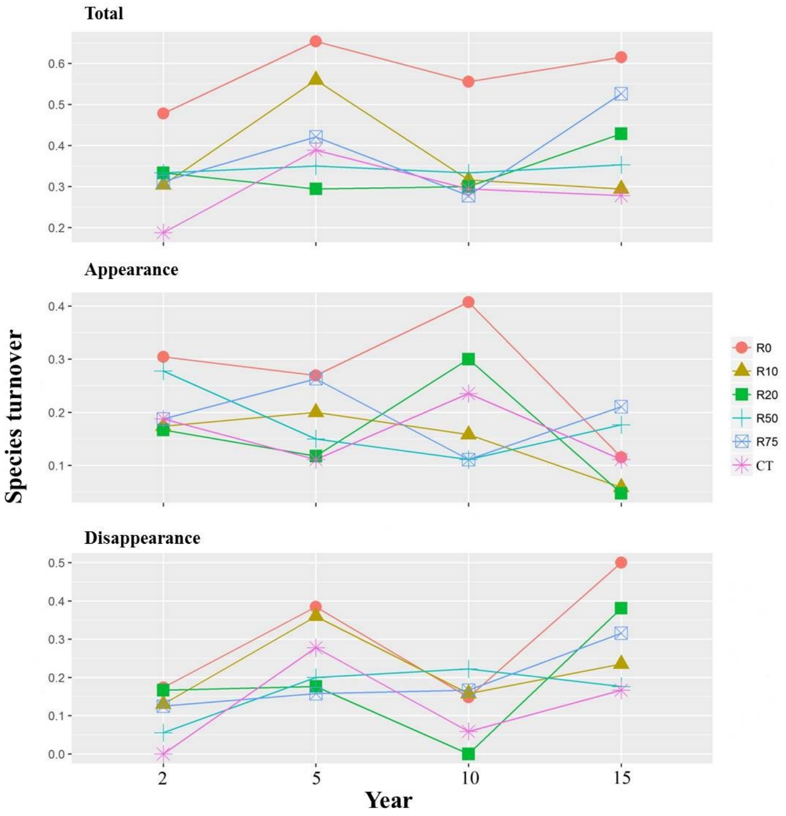


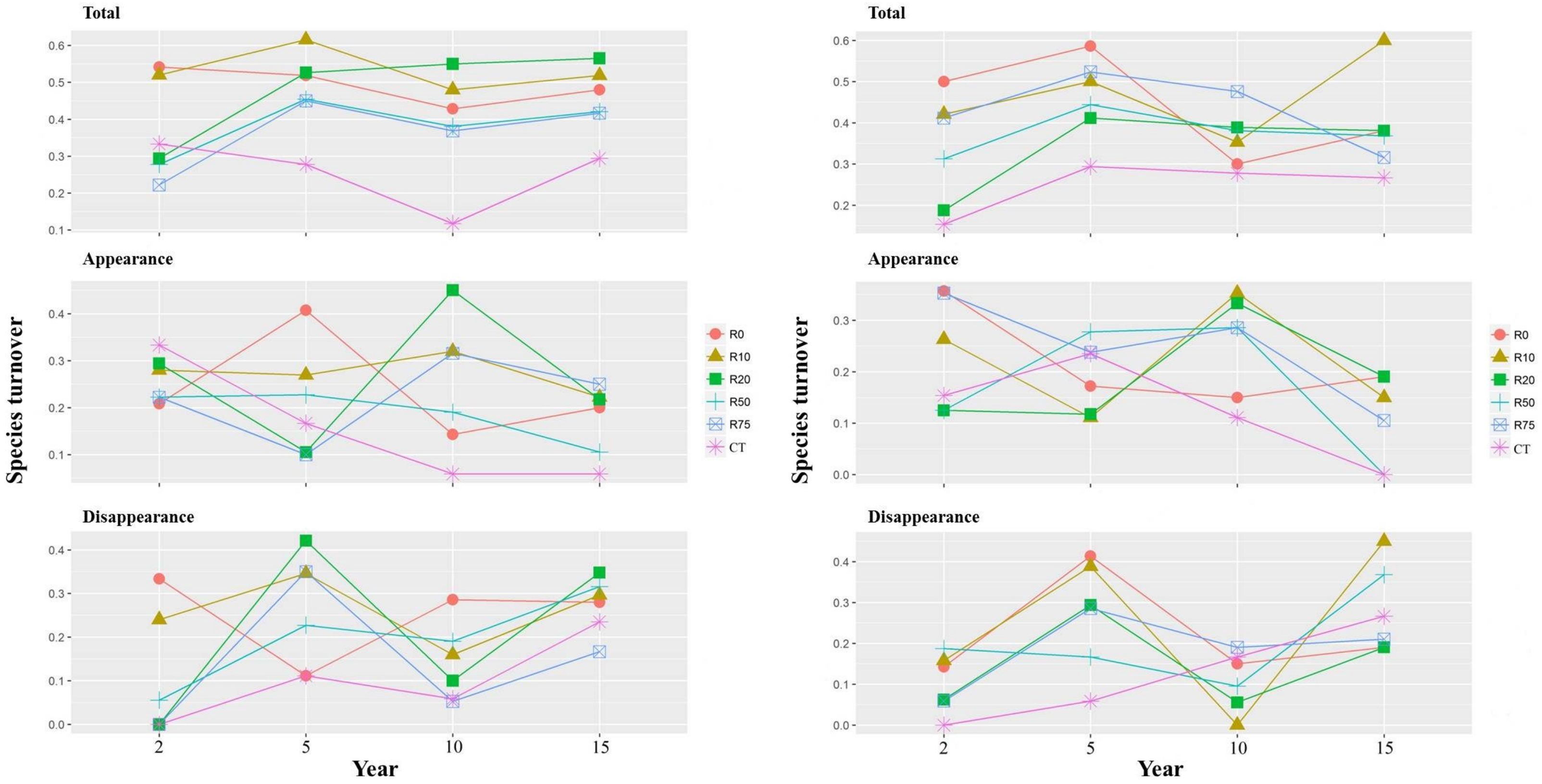
Fig. 2.2. Estimated species richness (± 95% confidence interval; CI) of ground beetles in each of the five harvest retention treatments (R0, R10, R20, R50, R75) 1, 2, 5, 10, 15 years post-harvest. Estimations are calculated using coverage-based rarefactions (Chao and Jost 2012) of samples with equal completeness for each forest cover type. Values are compared to a reference richness (mean [dashed line] ± 95% CI [dotted line]) based on pooled data from unharvested controls using the same corresponding coverage value. (a) Deciduous-dominated stands (coverage level, 96.5%; reference, 11.90 ± 0.53). (b) Deciduous-dominated stands with spruce understory (coverage level, 94.8%; reference, 11.27 ± 0.32). (c) Mixed stands (coverage level, 11.21 ± 0.39). (d) conifer-dominated stands (coverage level, 10.93 ± 0.43).


Total
0.7
0.6
0.5
0.4
0.3
Appearance
0.3
0.2
0.1
Disappearance
0.4
0.2
0.0
Species turnover
R0
R10
R20
R50
R75
CT
2
5
10
15
Year

a


Total
0.6
0.5
0.4
0.3
0.2
Appearance
0.4
0.3
0.2
0.1
Disappearance
0.5
0.4
0.3
0.2
0.1
0.0
Species turnover
R0
R10
R20
R50
R75
CT
2
5
10
15
Year

b



c d

Fig. 2.3. Temporal species turnover in (a) deciduous-dominated stands, (b) deciduous dominated stands with spruce understory, (c) mixed stands, and (d) conifer stands. Species turnover (values close to 0 represent low species turnover, values close to 1 represent high species turnover). Species turnover: Total = Appearance + Disappearance.

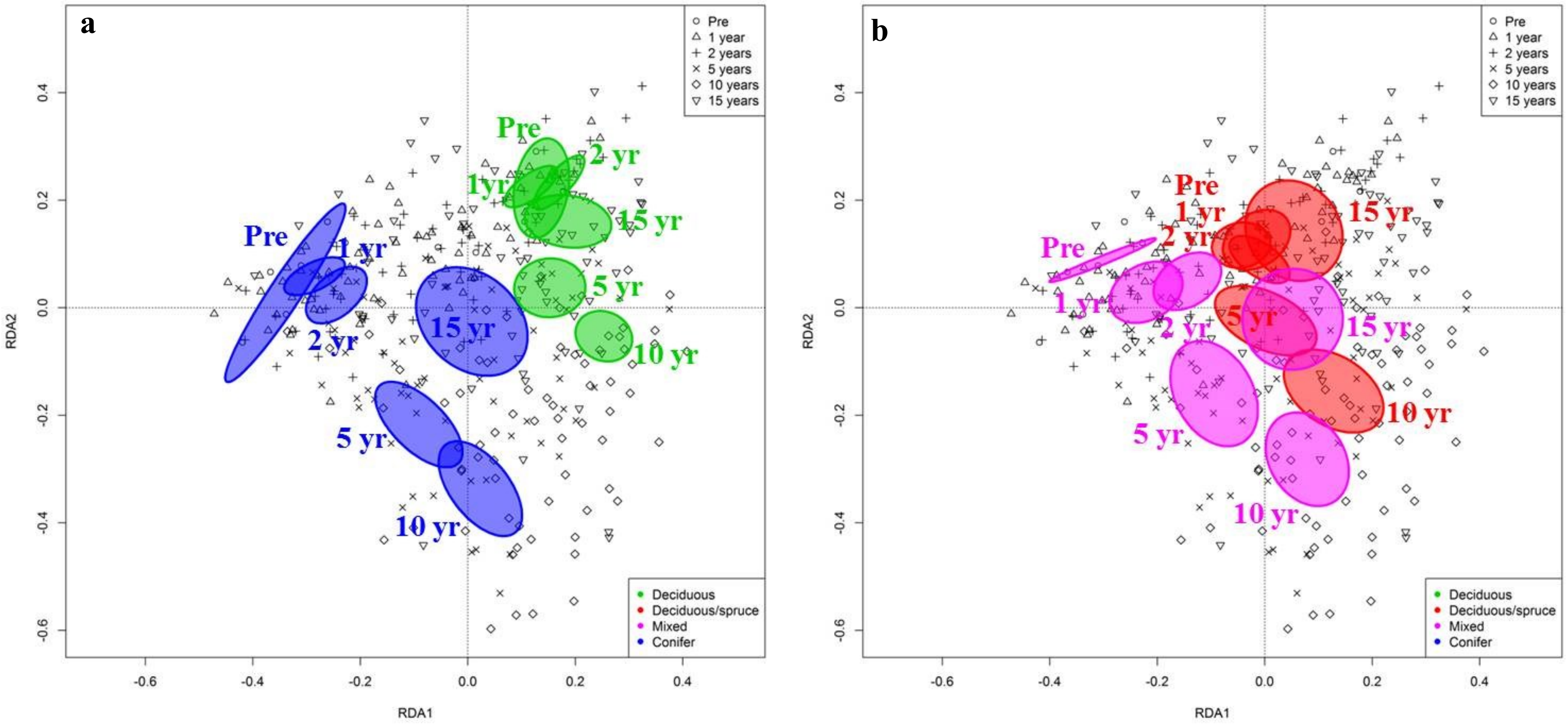
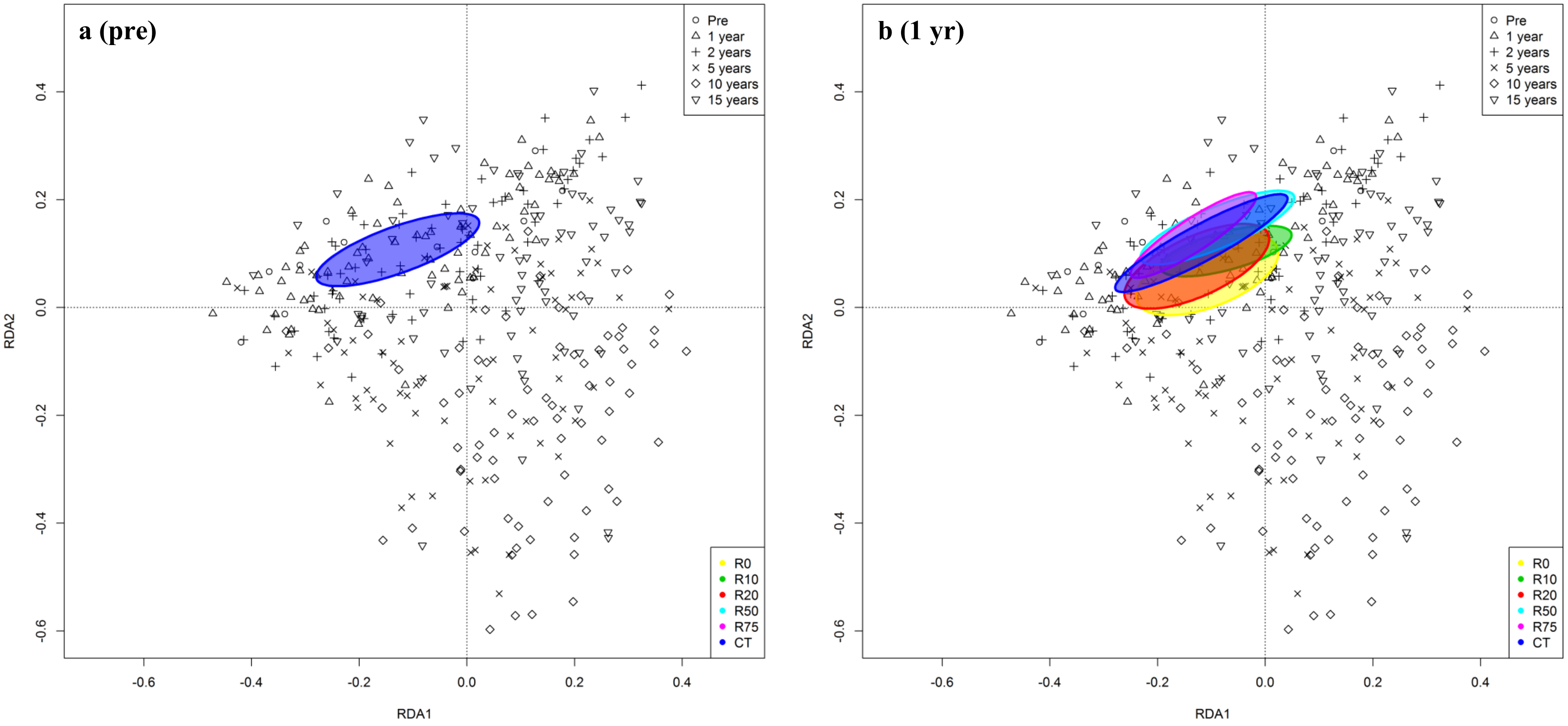
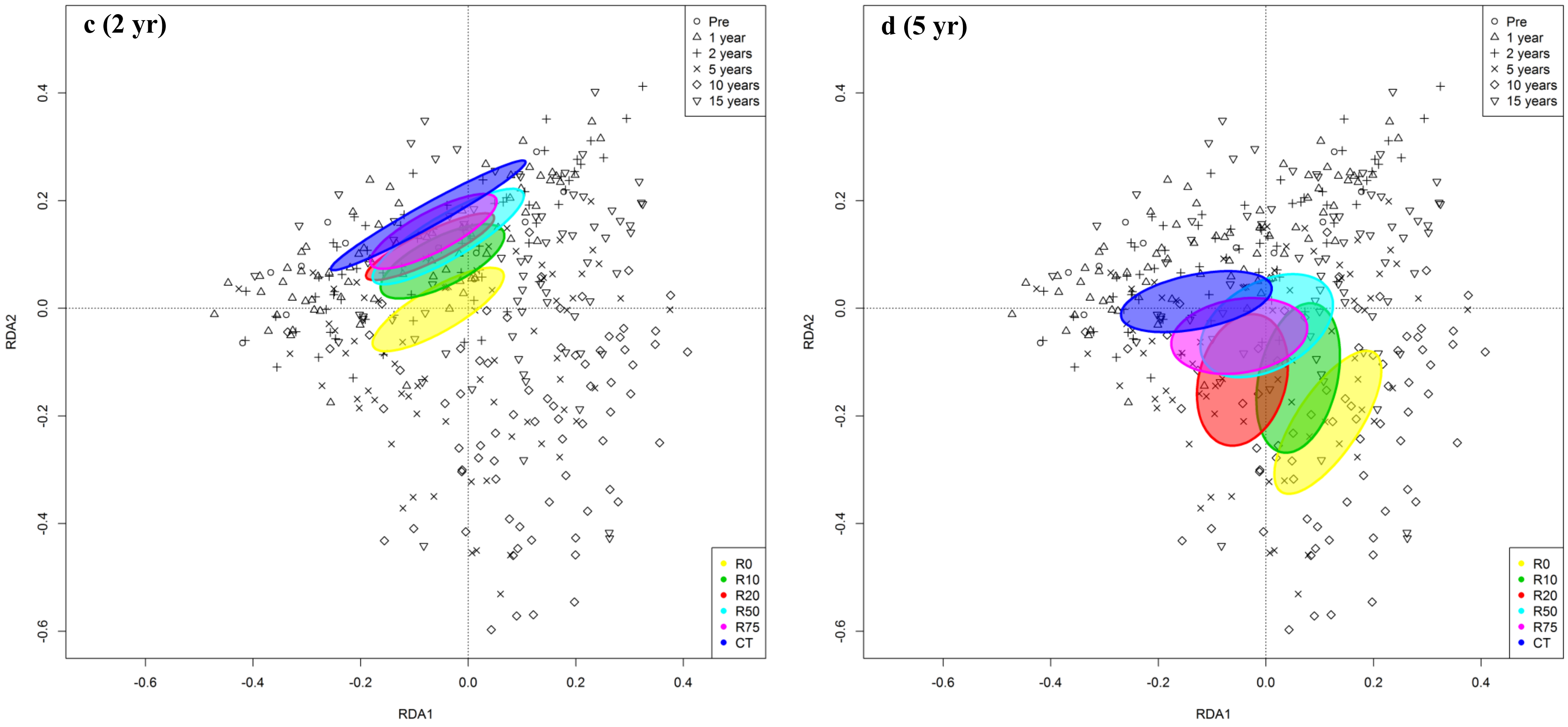


Fig. 2.4. Responses of ground beetle assemblages to variable retention harvest 1, 2, 5, 10 and 15 yr following variable retention harvest in stands with different forest cover type. Effects of time by forest cover type interaction, panel (a) showing ellipses for deciduous and conifer stands, panel (b) showing ellipses for deciduous/spruce and mixed stands. Colored ellipses represent 95% CI around group centroids.


a (pre)
b (1 yr)
Pre
1 year
2 years
5 years
10 years
15 years
R0
R10
R20
R50
R75
CT
RDA1
RDA2
-0.6
-0.4
-0.2
0.0
0.2
0.4


c (2 yr)
d (5 yr)
Pre
1 year
2 years
5 years
10 years
15 years
R0
R10
R20
R50
R75
CT
RDA1
RDA2
-0.6
-0.4
-0.2
0.0
0.2
0.4

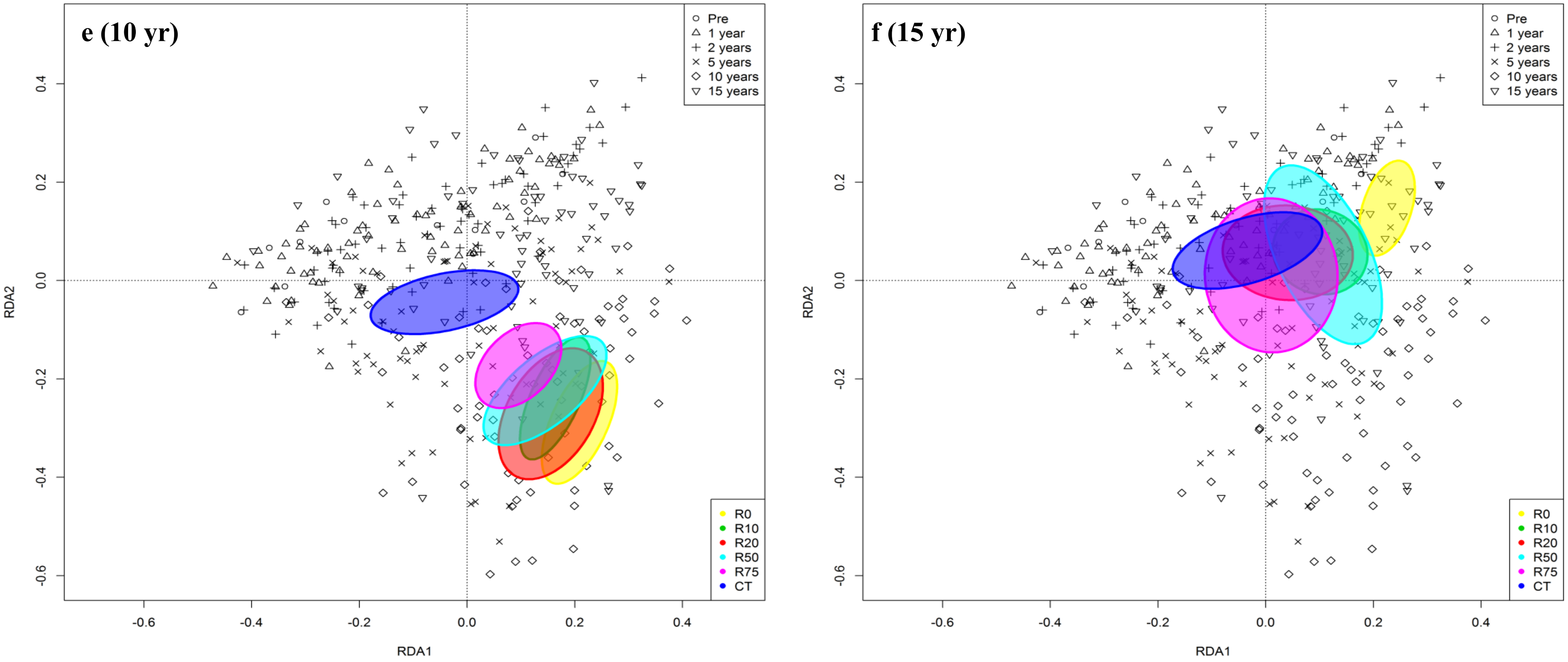
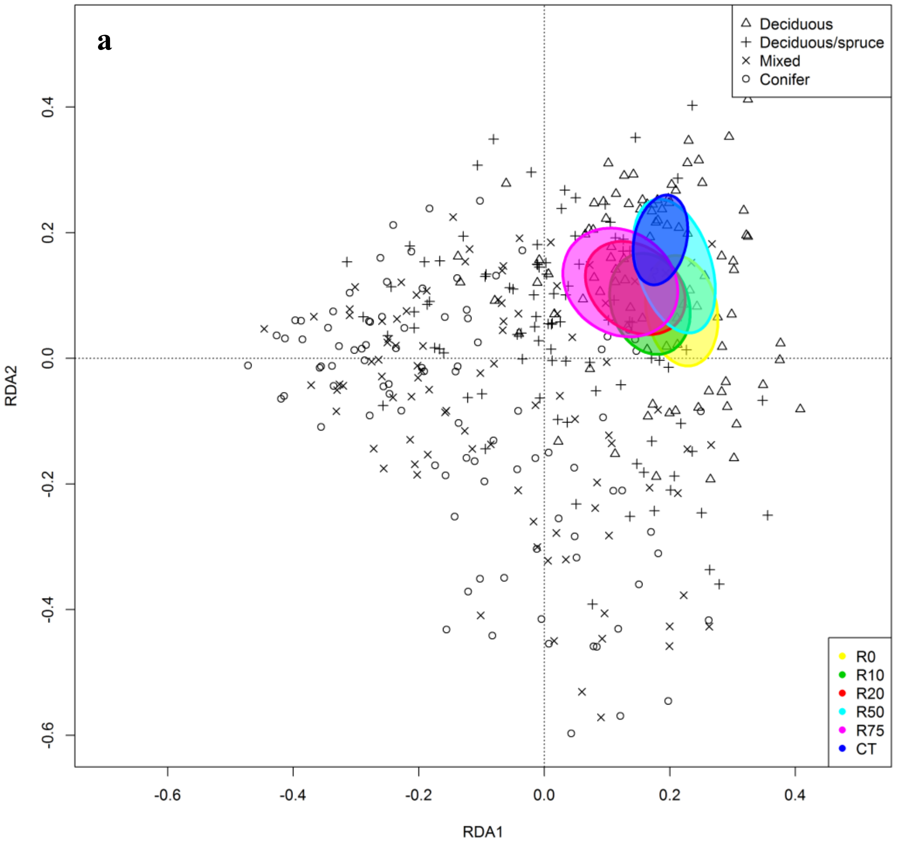
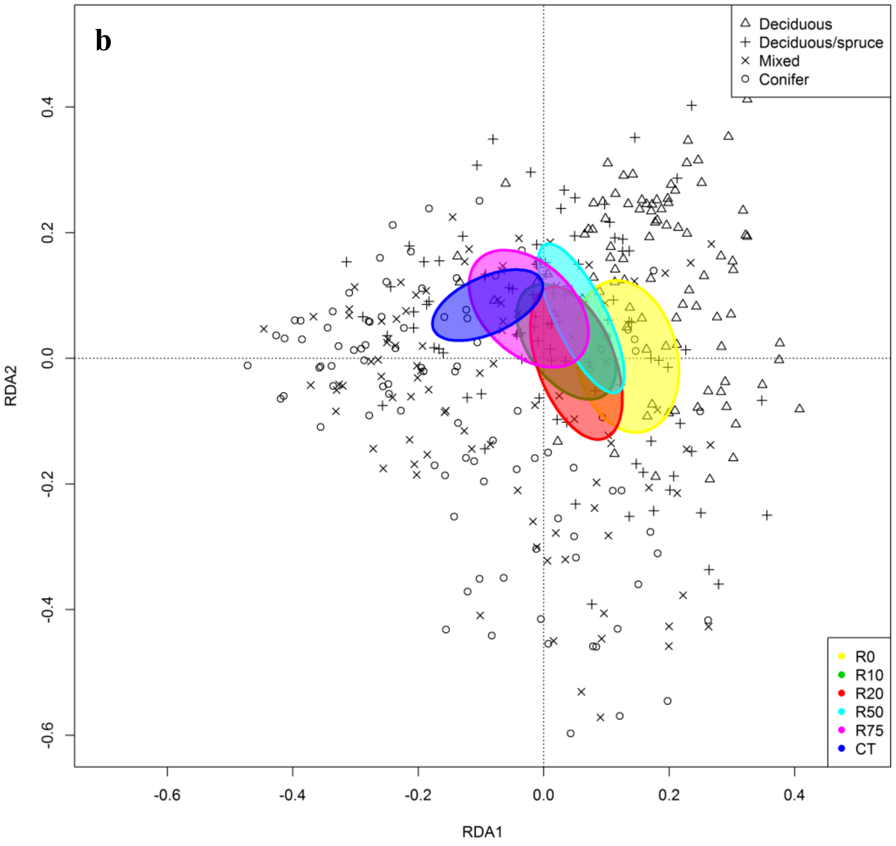


Fig. 2.5. Responses of ground beetle assemblages to variable retention harvest 1, 2, 5, 10 and 15 yr following variable retention harvest in stands with different forest cover type. The ordination plot is the same as in Fig. 2.4, in this figure showing effects of time by harvest treatment interaction, panel (a) showing ellipses for controls before harvesting, panel (b)-(f) showing ellipses for all harvest treatments 1, 2, 5, 10 and 15 yr post-harvest respectively.


a
Deciduous
Deciduous/spruce
Mixed
Conifer
R0
R10
R20
R50
R75
CT
RDA2
RDA1
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.6
-0.4
-0.2
0.0
0.2
0.4


b
Deciduous
Deciduous/spruce
Mixed
Conifer
R0
R10
R20
R50
R75
CT
RDA2
RDA1
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.6
-0.4
-0.2
0.0
0.2
0.4

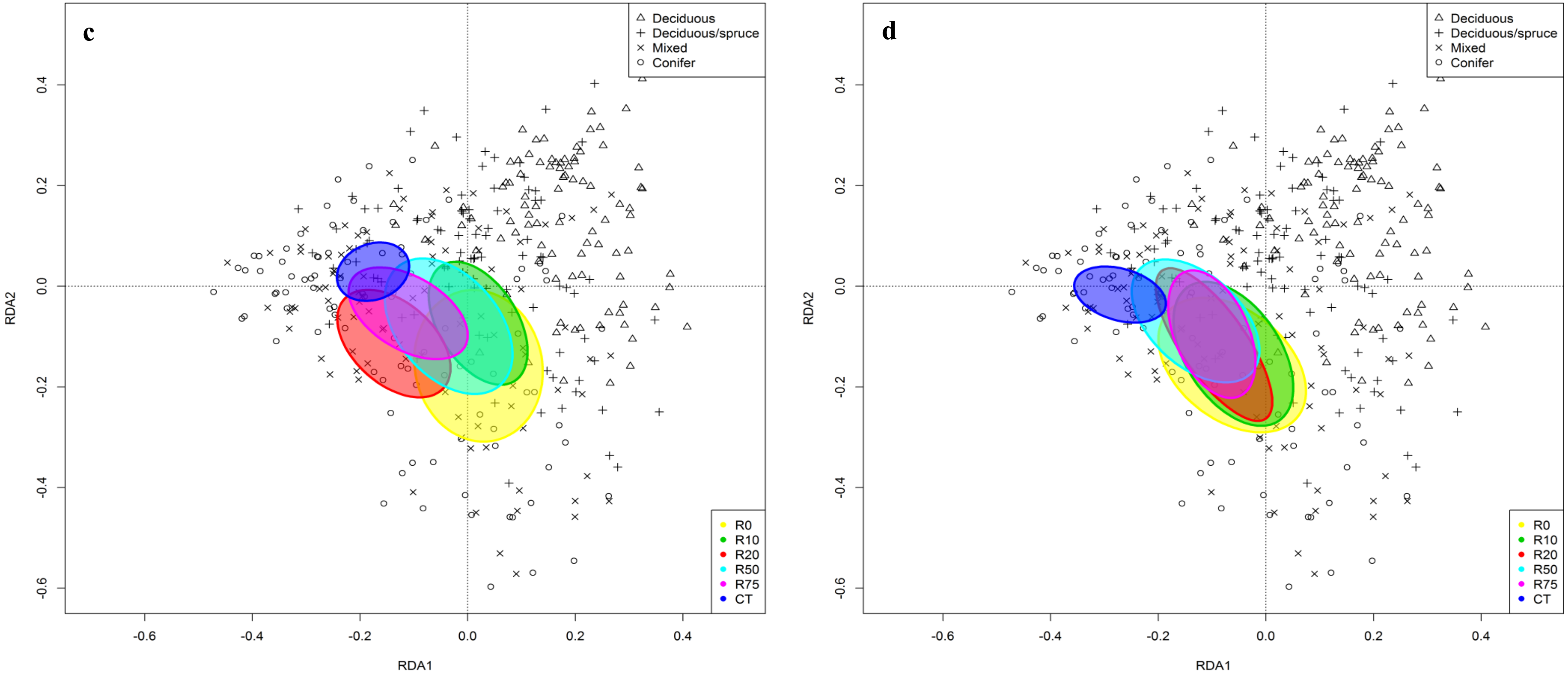


Fig. 2.6. Responses of ground beetle assemblages to variable retention harvest 1, 2, 5, 10 and 15 yr following variable retention harvest in stands with different forest cover type. The ordination plot is the same as in Fig. 2.4, in this figure showing effects of forest cover type by harvest treatment interaction, panels showing ellipses for all treatments in (a) deciduous stands, (b) deciduous/spruce stands, (c) mixed stands, and (d) conifer stands.

Chapter 3

Turnover of boreal ground-beetle (Coleoptera: Carabidae) species and variable retention harvest: beta diversity in space and time

3.1 Introduction

Since Whittaker (1960, 1972) introduced the concept of partitioning regional (gamma) diversity into local (alpha) and turnover (beta) components, interest in beta diversity has steadily increased (Harrison et al. 1992, Lennon et al. 2001, Koleff et al. 2003, Jost 2007, Anderson et al. 2011). Species turnover links regional species pools to local alpha diversity by quantifying compositional differences among sites (Harrison et al 1992, Soininen et al 2007), and therefore, understanding beta diversity is essential for evaluating and managing conservation efforts on landscapes. Thus, ecologists are exploring patterns of beta diversity to understand how and why assemblages of species differ from one location to another (Vellend 2010).

Species turnover is driven by powerful ecological processes, reflecting geography, environment and the dispersal ability of organisms in the regional pool (Soininen et al 2007). Most published studies have focused on large organisms at broader scales to explore geographical patterns in biodiversity (Condit 2002, Qian et al. 2005, Hillebrand 2004). However, local disturbances such as forest harvesting can also impact biodiversity (Lindenmayer and Franklin 2002), and lead to large species turnover across habitat even at relatively small scales (Work et al. 2010, Pinzon et al. 2016).

Retention harvest is increasingly suggested as an alternative to clear cutting that better conserves biodiversity than clear cutting. Such harvests can ‘lifeboat’ sensitive species through the early stages of stand regeneration, to maintain and more quickly re-establish native forest biodiversity (Frankin et al. 1997, Gustafsson et al. 2010, Lindenmayer and Franklin 2002, Lindenmayer et al. 2012). In initial studies of retention effects, intensity appears to influence arthropod populations and assemblages, with more similar species composition (less species turnover) associated with increased retention (Jacobs et al. 2008, Work et al. 2010, Pinzon et al. 2012).

Ground beetles (Coleoptera: Carabidae) are sensitive to environmental changes (Rainio and Niemelä 2003, Work et al. 2008, Koivula 2011), and react strongly to industrial-scale harvests (Niemelä et al. 1992, Buddle et al. 2006); thus, they have been widely used as bioindicators to assess the conservation value of retention harvesting. Ground beetles are strongly associated with particular tree species (Bergeron et al 2011) and, based on characteristic habitats, can be classified into habitat generalists, forest generalists and forest specialists (Niemelä and Spence 1992); forest specialists appeared to be more sensitive to harvest intensity (Work et al 2010).

In this paper, we focus on differences in post-harvest species turnover in ground beetle assemblages over 15 years between four intensities of retention harvests and uncut boreal forest in the mixed-wood cover-type. We tested the hypotheses that (1) retention harvests are associated with less species turnover than traditional clear-cuts; (2) species turnover decreases with increased retention; and (3) species turnover in response to harvest is driven mostly by forest specialists, but that extent of turnover will vary with cover-type.

3.2 Methods

3.2.1 Study area

This study was conducted at the EMEND (Ecolsystem Management Emulating Natural Disturbance) research site where an experimental design developed to compare effects of varying intensity of retention harvest was applied during 1998-99 across a range of typical upland mixedwood sites with merchantable timber. The

EMEND landscape is located ~90 km northwest of Peace River, Alberta, Canada (56°46′13″ N, 118°22′28″ W). The main broadleaf deciduous species include trembling aspen, *Populus tremuloides* Michaux, and balsam poplar, *Populus balsamifera* L., in early successional stages, and mainly the conifer species, white spruce, *Picea glauca* (Moench) Voss, black spruce, *Picea mariana* (Miller) and eastern larch, *Larix laricina* (DuRoi) K. Koch in later successional stages (Pinzon et al 2016).

3.2.2 Experimental design and beetle sampling

The EMEND experiment was designed to explore interactions between stand cover-type and forest harvest through stand-level manipulation of green-tree retention. The design allocated a range of retention harvest treatments to each of four regionally dominant forest cover-types. Green tree retention was left in c. 10-ha compartments harvested for the first time in 1999 in the following percentages of original stand basal area: 2% (R0), 10% (R10), 20% (R50), 50% (R50) and 75% (R75); each replicate block also included an uncut (CT) compartment (i.e., R100). Three blocks of replicate 10-ha compartments were established in stands classified before harvest as belonging to each of the following four cover-types (Work et al. 2004) :

(v) deciduous-dominated (DDOM): mainly *Populus* species with less than 30% coniferous trees in the canopy,

(vi) deciduous with a coniferous understory (DDOMU): mainly *Populus* canopy with significant amounts of white spruce in the understory,

(vii) mixed stands (MX): canopy layer with approximately equal proportions of deciduous and coniferous components, and

(viii) conifer-dominated (CDOM): with conifers, mainly white spruce, representing greater than 70% of the canopy

Thus, there were 4 x 6 = 24 cover type x retention combinations, comprising 72 compartments in total [Fig. 3.1. Full details of the experimental design are provided by Spence et al. (1999) and Work et al. (2010)].

Ground beetles were collected in all the EMEND compartments using pitfall traps in 1999, 2000, 2004, 2009 and 2014, with these years corresponding to 1, 2, 5, 10 and 15 years post-harvest, respectively. Pitfall traps (12 cm diameter) were dug into ground with their upper rims level with the soil surface, filled with approximately 200 ml ethylene glycol as a killing agent and preservative, and covered with a suspended plastic roof to minimize flooding and accumulation of debris (Spence and Niemelä 1994). Traps were installed at either end of three randomly chosen 40 m transects in a subset of the six EMEND permanent sampling plots (PSPs) in each 10-ha forest compartment (Work et al. 2010). Trapping spanned the frost free season from mid-May to late August in each of the 5 years. During these periods each trap was visited 5 scenarios at approximate 3-week intervals to collect the accumulated catch, make in required trap adjustments and replenish the preservative. Ground beetles were sorted and identified to species using Lindroth (1961, 1963, 1966, 1968, 1969a,b) and named following Bousquet and Larochelle (1993).

3.2.3 Analysis

Ground beetle catches were pooled by compartments over each collection year and standardized to number of individuals per 100 trap-days to minimize effects of occasional trap disturbance on the data.

Species turnover for each compartment was assessed using pairwise Bray-Curtis dissimilarity with relevant control stands and then averaged to each harvest treatment. Higher dissimilarities indicate greater differences from controls which means greater species turnover.

Repeated calculation of species turnover using Bray-Curtis dissimilarity but removing one species at each time (Jackknife Method), was used to determine which species contributed most to species turnover. Key species were designated as those that drove the highest species turnover. Overall, determinations of key species were based on 100 scenarios (i.e., there were 5x5x4 = 100 year period x cover type x retention combinations).

All calculations were made in R v 3.2.4 (R Core team 2015) using vegan (Oksanen et al. 2015) for species turnover.

3.3 Results

A total of 50,493 individual ground beetles, representing 76 species comprise the overall dataset. Thirteen species accounted for 97.0% of the total individuals, with *P. adstrictus*, *P. decentis* and *C. ingratus* the three most abundant species, together accounting for 55.5% of the total catch. In contrast, 38.2% of the species were represented by singletons (24 spp.) and doubletons (5 spp.).

3.3.1 Species turnover

Ground beetle species turnover for harvested stands differed significantly among post-harvest periods ($F_{4, 288}$=7.35; P<0.001), forest cover types ($F_{3, 288}$=3.92; P<0.01) and harvest treatment ($F_{4, 288}$=3.19; P<0.05).

In data pooled across all cover-types, species turnover (values of dissimilarity from controls) generally decreased with increased retention after year 1. Thus, during post-harvest recovery carabid composition was more similar to that of un-harvested controls in compartments with higher green tree retention (Fig. 3.2). Clear-cut stands differed most from controls (0.55), followed by R10, R20 and R50 (0.54, 0.52 and 0.51 respectively), and with lowest dissimilarity in R75 (0.47) (Table. 3.1).

Species turnover was lowest 15 years post-harvest (0.39) and highest 2 years post-harvest (0.58) in deciduous stands (Table 3.2), indicating carabid assemblages in harvested stands 15 years post-harvest had become more similar in species composition to control sites than they were more immediately after harvest. In contrast, species turnover was highest 15 years post-harvest (0.58 and 0.66) in mixed and conifer stands respectively, suggesting that departure of carabid assemblages in harvested compartments from control assemblages increased with time in these two cover types (Table 3.2).

3.3.2 Key species that leads to species turnover

Overall, thirteen species were determined to be key species contributing most to species turnover. Among those species, *P. adstrictus*, *C. advena* and *S. haematopus* were designated most frequently (respectively 22, 21 and 14 out of 100 scenarios) (Table 3.4). *P. adstrictus* is a habitat generalist species while *C. advena* and *S. haematopus* are forest specialists associated with mature conifer forests ((Niemelä & Spence 1992, Jacobs et al. 2008). Moreover, populations of *C. advena* are especially common in old-growth coniferous (Jacobs et al 2008).

Responses of key species were mediated by cover-type. *P. adstrictus,* for example, was the most frequent key species, occurring in 9 out of 25 scenarios for deciduous dominated stands (Table 3.3), suggesting that species turnover in deciduous dominated stands is mainly caused by changes in populations of this open-habitat generalist. Although *C. frigidum* was most frequently designated as the key species driving turnover in 7 out of 25 scenarios for deciduous stands with conifer understory (Table 3.3), *P. adstrictus* was the second most frequent key species for these stands (6 out of 25 scenarios, Table. 3).

C. advena was the most frequent key species occurring 10 out of 25 scenarios in mixed stands (Table 3), and *C. advena* (8 out of 25 scenarios for these stands, Table 3.3) together with *S. haematopus* (7 out of 25 scenarios for these stands , Table 3.3) were the two key species that most frequently drove turnover in conifer stands.

The identity of key species also changed profoundly during the 15 years after harvest. For example, increases in *C. frigidum* and *P. adstrictus* were the main drivers of turnover in pure deciduous stands and those with spruce understory 1 and 2 years post-harvest. With regeneration of aspen in these stands creating forest floor conditions more similar to those beneath closed canopies, the key species identified by my analysis were mainly forest specialists. For example, appearance of *A. retractum* and *P. decentis* drove turnover in deciduous stands, and *S. haematopus* became the key species for deciduous stands with spruce understory by year 15 post-harvest.

C. advena and *S. haematopus* were generally the two most frequent key species for mixed and conifer stands, except that *P. adstrictus* was designated as the only key species in mixed stands 2 years post-harvest (Table 3.3). This likely reflected the domination of this open-habitat specialist and the loss of forest specialists in harvested stands 2 years post-harvest. However, the data support the general theme that species turnover in mixed and conifer stands was consistently caused by loss of species associated with mature conifer stands after harvest.

Identity of key species varied with harvest intensity but without apparent general pattern. However, interestingly, *A. retractum* was identified as the key species during turnover in R0 and R10 mixed stands 15 years post-harvest (Table 3.3), suggesting that deciduous forest specialists became more abundant in mixed stands harvested to low retention.

3.4 Discussion

The results strongly supported our first hypothesis, clearly showing that retention harvests were associated with less species turnover than were traditional clear-cuts. Species turnover decreased with increasing retention level for pooled data from four cover-types. However, this pattern was not observed in the first year after harvest. We assume that, in the spring and summer after harvest, newly emerged and overwintered adults of forest specialist carabids are actively moving to escape post-harvest conditions and are trapped at higher than normal rates.

In addition, species turnover in deciduous stands was lowest 15 years post-harvest but highest in mixed and conifer stands 15 years post-harvest, suggesting strong recovery of carabid assemblages toward those typical of un-harvested conditions in deciduous stands but an apparent departure from control assemblages in coniferous compartments. This pattern is also consistent with results presented in the previous chapter, showing that conifer associated assemblages are less resistant and resilient to harvesting.

Responses of designated key species were mediated by cover-type. *C. advena* and *S. haematopus* were the two most key species most frequently found driving turnover in mixed and conifer stands. In general, these species are all associated with mature coniferous forest and respond positively to conditions under dense canopy, suggesting that species turnover in mixed and conifer stands were mainly driven by the loss of forest specialists due to harvesting. Thus higher retention level is needed to maintain populations of species associated with old or mature coniferous over early post-harvest periods.

C. frigidum was designated as the most frequent key species in compartments cut as deciduous canopy with spruce understory, especially for the 1 and 2 year post-harvest periods. Adults and larvae of *C. frigidum* feed on caterpillars (Cameron & Reeves, 1990), and thus, outbreak populations of Large Aspen Tortrix (*Choristoneura conflictana*) that occurred in Alberta in 2000 and 2001 (Jacobs et al 2008) are the likely cause of the observed surge of *C. frigidum*. Therefore, more *C. frigidum* were trapped in the controls for this cover-type likely due to abundant food resources, and the difference in abundance between harvested stands and controls was associated with greater species turnover 1 and 2 years post-harvest.

The identity of key species driving turnover also changed profoundly over the 15 years after harvest as the forest regenerated. *P. adstrictus* is considered as a habitat generalist (Niemelä & Spence 1992), but it also prospers in open habitats (Jacobs et al. 2008, Niemelä & Spence 1993, Spence et al 1996). It was the key species 1 and 2 years post-harvest in deciduous stands, deciduous stands with spruce understory and even in mixed stands. The domination of this open-habitat species right after harvest was greater than the loss of forest specialists, therefore, accounting for more species turnover. But since populations of *P. adstrictus* dropped notably in abundance 5 years post-harvest with closing of the canopy (Jacobs et al 2008), deciduous associated species such as *A. retractum* and *P. decentis*, became the major drivers of species turnover in deciduous stands, and *C. advena* and *S. haematopus* retook the first position of driving species turnover in mixed and conifer stands.

Harvested stands of mixed wood forest generally regenerate through a deciduous phase, regardless of pre-harvest cover type (Gradowski et al. 2010). Therefore, mixed stands following harvest recover more similar to that of originally deciduous stands through a strong pulse of deciduous trees regeneration. This provides ideal habitat for ground beetle species associated with deciduous stands, especially in stands harvested to low retention. Because of such changes, the key species in low retention mixed stands switched from the open habitat generalist, *P. adstrictus,* to the conifer forest specialist, *C. advena*, and to the deciduous forest specialist, *A. retractum*. In other words, the identity of the key species changed dramatically with changes of habitat condition, suggesting that low retention levels in late successional stands were not only insufficient to preserve mature conifer associated species, but also supported development of deciduous associated species. Thus, beetle assemblages became more similar to those of deciduous control compartments, and moved further away from the un-harvested control condition for late successional cover-types.

Our results have two important implications for supporting native biodiversity through forest management. First, retention harvests will maintain biodiversity better than clear-cutting and higher retention levels are associated with less species turnover. Second, maintaining forest specialists is critical for promoting biodiversity, and higher retention levels are needed in conifer stands to maintain old conifer forest specialists and conserve pre-harvest biodiversity of ground-beetles.

Table 3.1 Average species turnover for each retention level

Retention level	**Average species turnover**
R0	0.55
R10	0.54
R20	0.52
R50	0.51
R75	0.47

Table 3.2 Average species turnover for four cover-types (DD=deciduous-dominated stands, DU=deciduous-dominated stands with spruce understory, MX=mixed stands, CD=conifer stands) each year post-harvest.

Cover-type	**Year post-harvest**	**Average species turnover**
DD	1	0.46
DD	2	0.58
DD	5	0.50
DD	10	0.43
DD	15	0.39
DU	1	0.42
DU	2	0.54
DU	5	0.62
DU	10	0.54
DU	15	0.59
MX	1	0.53
MX	2	0.55
MX	5	0.56
MX	10	0.46
MX	15	0.58
CD	1	0.38
CD	2	0.51
CD	5	0.59
CD	10	0.51
CD	15	0.66

Table 3.3 Key species that contributes most to species turnover 1, 2, 5, 10 and 15 yr post-harvest in four cover types (DD=deciduous-dominated stands, DU=deciduous-dominated stands with spruce understory, MX=mixed stands, CD=conifer stands) with R0, R10, R20, R50 and R75 retention level.

Year post-harvest	**Cover type**	**Retention level**	**Species turnover**	**Minimum species turnover after removing key species**	**Key species**
1	DD	R0	0.33	0.28	*Calosoma frigidum*
1	DD	R10	0.44	0.41	*Pterostichus adstrictus*
1	DD	R20	0.54	0.47	*Pterostichus adstrictus*
1	DD	R50	0.59	0.55	*Calosoma frigidum*
1	DD	R75	0.41	0.40	*Pterostichus pensylvanicus*
1	DU	R0	0.40	0.37	*Calosoma frigidum*
1	DU	R10	0.42	0.39	*Pterostichus adstrictus*
1	DU	R20	0.48	0.45	*Calosoma frigidum*
1	DU	R50	0.39	0.36	*Pterostichus adstrictus*

1	DU	R75	0.41	0.37	*Calosoma frigidum*
1	MX	R0	0.52	0.49	*Pterostichus adstrictus*
1	MX	R10	0.52	0.48	*Calathus advena*
1	MX	R20	0.53	0.50	*Calathus ingratus*
1	MX	R50	0.56	0.54	*Calathus advena*
1	MX	R75	0.51	0.48	*Calathus advena*
1	CD	R0	0.49	0.48	*Platynus decentis*
1	CD	R10	0.36	0.32	*Platynus decentis*
1	CD	R20	0.37	0.32	*Calathus advena*
1	CD	R50	0.30	0.27	*Platynus decentis*
1	CD	R75	0.41	0.38	*Calathus ingratus*
2	DD	R0	0.50	0.44	*Pterostichus adstrictus*
2	DD	R10	0.64	0.61	*Pterostichus adstrictus*
2	DD	R20	0.66	0.60	*Pterostichus adstrictus*

2	DD	R50	0.67	0.65	*Pterostichus adstrictus*
2	DD	R75	0.43	0.38	*Pterostichus adstrictus*
2	DU	R0	0.58	0.52	*Pterostichus adstrictus*
2	DU	R10	0.55	0.52	*Calosoma frigidum*
2	DU	R20	0.55	0.49	*Calosoma frigidum*
2	DU	R50	0.52	0.47	*Calosoma frigidum*
2	DU	R75	0.55	0.49	*Calosoma frigidum*
2	MX	R0	0.59	0.35	*Pterostichus adstrictus*
2	MX	R10	0.61	0.52	*Pterostichus adstrictus*
2	MX	R20	0.46	0.38	*Pterostichus adstrictus*
2	MX	R50	0.58	0.45	*Pterostichus adstrictus*
2	MX	R75	0.53	0.47	*Pterostichus adstrictus*
2	CD	R0	0.51	0.50	*Sericoda quadripunctata*
2	CD	R10	0.53	0.48	*Pterostichus adstrictus*

2	CD	R20	0.58	0.55	*Calathus advena*
2	CD	R50	0.44	0.41	*Calathus advena*
2	CD	R75	0.48	0.45	*Platynus decentis*
5	DD	R0	0.59	0.57	*Calathus ingratus*
5	DD	R10	0.42	0.41	*Trechus chalybeus*
5	DD	R20	0.53	0.49	*Stereocerus haematopus*
5	DD	R50	0.50	0.49	*Agonum retractum*
5	DD	R75	0.43	0.40	*Pterostichus adstrictus*
5	DU	R0	0.79	0.74	*Calathus ingratus*
5	DU	R10	0.58	0.56	*Calathus advena*
5	DU	R20	0.69	0.63	*Calathus ingratus*
5	DU	R50	0.59	0.57	*Calathus advena*
5	DU	R75	0.47	0.44	*Stereocerus haematopus*
5	MX	R0	0.56	0.50	*Calathus advena*

5	MX	R10	0.56	0.50	*Calathus advena*
5	MX	R20	0.60	0.55	*Calathus advena*
5	MX	R50	0.55	0.52	*Calathus advena*
5	MX	R75	0.53	0.51	*Platynus decentis*
5	CD	R0	0.66	0.60	*Calathus advena*
5	CD	R10	0.67	0.60	*Calathus advena*
5	CD	R20	0.68	0.65	*Stereocerus haematopus*
5	CD	R50	0.45	0.41	*Calathus advena*
5	CD	R75	0.47	0.44	*Calathus advena*
10	DD	R0	0.48	0.47	*Platynus decentis*
10	DD	R10	0.45	0.44	*Patrobus foveocollis*
10	DD	R20	0.46	0.44	*Calathus ingratus*
10	DD	R50	0.42	0.40	*Trechus chalybeus*
10	DD	R75	0.34	0.32	*Pterostichus pensylvanicus*

10	DU	R0	0.73	0.72	*Stereocerus haematopus*
10	DU	R10	0.57	0.55	*Trechus chalybeus*
10	DU	R20	0.54	0.52	*Agonum retractum*
10	DU	R50	0.54	0.52	*Agonum retractum*
10	DU	R75	0.33	0.31	*Calathus advena*
10	MX	R0	0.53	0.49	*Synuchus impunctatus*
10	MX	R10	0.45	0.42	*Calathus advena*
10	MX	R20	0.43	0.39	*Platynus decentis*
10	MX	R50	0.44	0.41	*Calathus advena*
10	MX	R75	0.45	0.42	*Calathus advena*
10	CD	R0	0.58	0.54	*Synuchus impunctatus*
10	CD	R10	0.49	0.45	*Stereocerus haematopus*
10	CD	R20	0.63	0.60	*Stereocerus haematopus*
10	CD	R50	0.45	0.43	*Calathus advena*

10	CD	R75	0.38	0.35	*Trechus chalybeus*
15	DD	R0	0.33	0.32	*Stereocerus haematopus*
15	DD	R10	0.46	0.41	*Pterostichus adstrictus*
15	DD	R20	0.42	0.36	*Platynus decentis*
15	DD	R50	0.39	0.38	*Patrobus foveocollis*
15	DD	R75	0.38	0.29	*Elaphrus lapponicus*
15	DU	R0	0.50	0.47	*Pterostichus adstrictus*
15	DU	R10	0.67	0.65	*Pterostichus adstrictus*
15	DU	R20	0.64	0.61	*Stereocerus haematopus*
15	DU	R50	0.57	0.54	*Stereocerus haematopus*
15	DU	R75	0.59	0.56	*Pterostichus adstrictus*
15	MX	R0	0.52	0.46	*Agonum retractum*
15	MX	R10	0.47	0.44	*Agonum retractum*
15	MX	R20	0.62	0.60	*Calathus ingratus*

15	MX	R50	0.69	0.66	*Calathus ingratus*
15	MX	R75	0.58	0.55	*Stereocerus haematopus*
15	CD	R0	0.63	0.59	*Stereocerus haematopus*
15	CD	R10	0.65	0.58	*Stereocerus haematopus*
15	CD	R20	0.69	0.64	*Stereocerus haematopus*
15	CD	R50	0.65	0.61	*Platynus decentis*
15	CD	R75	0.67	0.62	*Stereocerus haematopus*

Table 3.4 Key species frequency table (derived from table 3.3)

Species	**Frequency**
Pterostichus adstrictus	22
Calathus advena	21
Stereocerus haematopus	14
Calosoma frigidum	9
Platynus decentis	9
Calathus ingratus	8
Agonum retractum	5
Trechus chalybeus	4
Patrobus foveocollis	2
Pterostichus pensylvanicus	2
Synuchus impunctatus	2
Elaphurs lapponicus	1
Sericoda quadripunctata	1

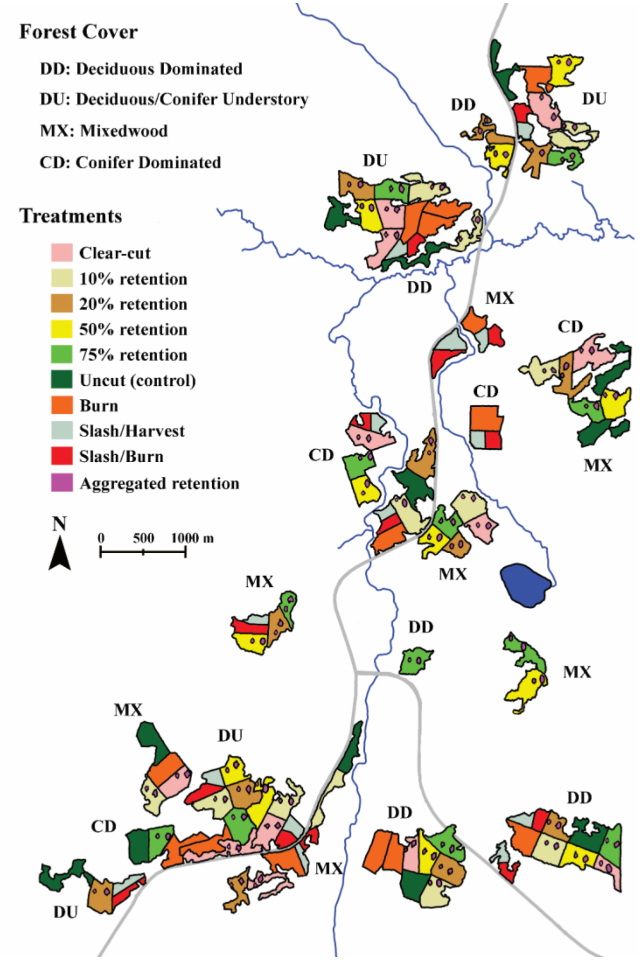


Fig. 3.1. Map of the EMEND (Ecosystem Management by Emulating Natural Disturbance) experimental site. Compartments of harvesting treatments and un-harvested controls in four forest cover types.

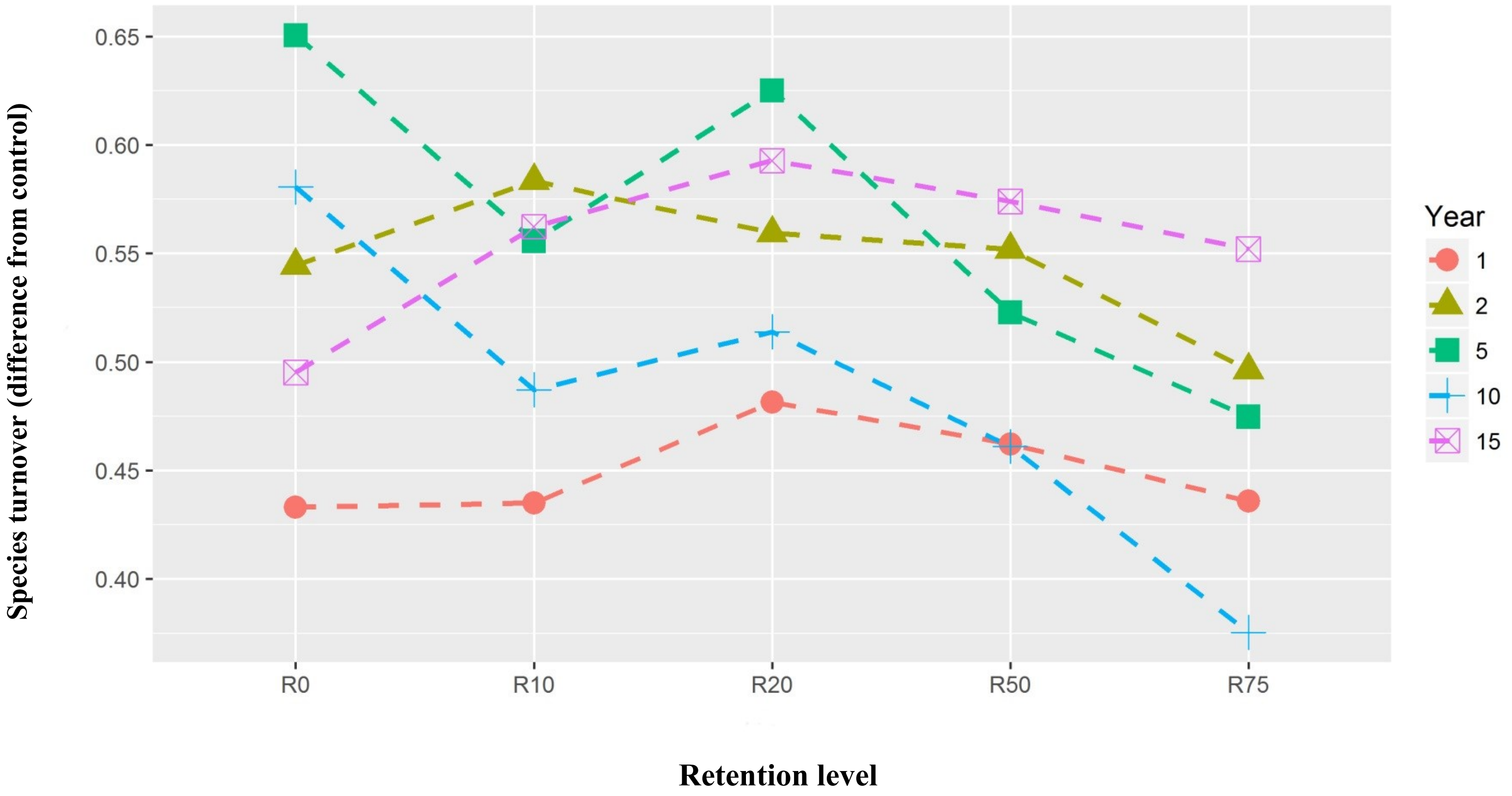


Fig. 3.2. Species turnover in carabid assemblages, measured as the Bray-Curtis dissimilarity between un-harvested controls and harvest treatments regardless of cover-types, 1, 2, 5, 10 and15 years post-harvest. Differences from control (value closer to 1 represent very dissimilar assemblages, therefore very high species turnover while values close to 0 represent very similar assemblages which indicating very little species turnover).

Chapter 4

Habitat variability and carabid (Coleoptera: Carabidae) distribution after retention harvest in a mixedwood boreal forest

4.1 Introduction

Understanding the determinants of species diversity patterns and the processes driving them is of central interest in ecology (Gatson 2000, Tscharntke et al. 2012). Habitat-associated factors including both biotic and abiotic conditions play important roles in determining location of species in landscapes (Hutchinson 1957, Holt 2009), and partly drive the distribution of species from local to regional spatial scales (Guisan and Zimmermann 2000, Peterson 2001). At local scales, the importance of habitat, especially the structure complexity of vegetation, has long been emphasized for explaining animal distributions (e.g., MacArthur and MacArthur 1961), and this linkage has been the subject of investigation for many taxa (Bell et al. 1991, Nash et al. 2014, Lengyel et al. 2016).

Local disturbances such as logging greatly change forest structure, and have huge impacts on biodiversity (Lindenmayer and Franklin 2002). Retention harvest is increasingly suggested as an alternative better than clear cutting for biodiversity conservation because it retains both elements of pre-harvest structural variation in regenerating stands and characteristics of old forests on landscapes (Franklin et al. 1997, Gustafsson et al. 2010). Forest habitats are significantly influenced by the intensity of harvest. For example, graminoid cover increases in low retention stands while more significant bryophyte cover remains in stands with higher retention (Pinzon et al. 2016). Therefore, it has been suggested that green-tree retention harvests can 'lifeboat' sensitive species through the early stages of stand regeneration to maintain and more quickly re-establish native forest biodiversity (Frankin et al.

1997, Gustafsson et al. 2010, Lindenmayer and Franklin 2002, Lindenmayer et al. 2012).

Ground beetles (Coleoptera: Carabidae) are sensitive to environmental changes (Rainio and Niemelä 2003, Work et al. 2008, Koivula 2011), and react strongly to industrial-scale harvests (Niemelä et al. 1992, Buddle et al. 2006). Thus, they have been widely used as bioindicators to assess the conservation value of management practices, such as retention harvesting. Habitat variation shaped by harvesting is expected to alter ground beetle species distributions through impacts on particular habitats in relation to species-specific habitat affinities of beetles and variation in reproductive success of their populations in affected habitats (Niemelä et al. 1992, Koivula et al. 1999, Jacobs et al. 2008, Bergeron et al. 2011). Understanding these interactions could guide practical improvements in retention harvesting toward minimizing negative influence on ground beetle biodiversity.

The main goal of this study is to describe the distribution of ground beetles in regenerating stands in relation to habitat variability that has flowed from pre-harvest cover-type a decade or more after variable retention harvest. Our hypotheses are that (1) habitat variation influences the distribution of ground beetle species and local structure of assemblages in predictable ways; (2) such influences vary among ground beetle species reflecting different habitat requirements and affinities; and (3) species distribution in stands harvested with retention are more similar to un-harvested controls ten years post-harvest than they are to clear-cuts.

4.2 Methods

4.2.1 Study area

This study was conducted at the EMEND (Ecosystem Management Emulating Natural Disturbance) research site where the effects of varying the intensity of retention harvest are being compared across a range of upland mixedwood sites representative of the merchantable forest of the region. The EMEND landscape is located ~90 km northwest of Peace River, Alberta, Canada (56°46′13″ N, 118°22′28″ W) and includes typical mixedwood forests typical of the western Boreal region of North America. The main broadleaf deciduous species are trembling aspen, *Populus tremuloides* Michaux, and balsam poplar, *Populus balsamifera* L., which dominate early successional stages. Later successional stages are dominated by the conifer species, white spruce, *Picea glauca* (Moench) Voss, black spruce, *Picea mariana* (Miller) and eastern larch, *Larix laricina* (DuRoi) K. Koch (Pinzon et al 2016).

4.2.2 Experimental design

The EMEND design allocated a range of retention harvest treatments to each of the four forest cover-types that represents the common successional stages of the boreal mixedwood. Harvest prescriptions for green tree retention were executed in c. 10-ha compartments of pristine forest harvested for the first time in 1999 to establish harvest treatments leaving the following percentages of original stand basal area: 2% (R0), 10% (R10), 20% (R20), 50% (R50) and 75% (R75); each replicate block also included an uncut (CT) compartment (i.e., R100). Three blocks of replicated compartments were established in stands classified before harvest as belonging to each of the following four cover-types (Work et al. 2004) :

(ix) deciduous-dominated (DDOM): mainly *Populus* species with coniferous trees accounting for < 30% of the canopy,

(x) deciduous with a coniferous understory (DDOMU): mainly *Populus* canopy with significant amounts of white spruce in the understory (<70% of canopy height),

(xi) mixed stands (MX): canopy layer with approximately equal proportions of deciduous and coniferous components, and

(xii) coniferous-dominated (CDOM): conifers, mainly white spruce, representing > 70% of the canopy

In total, there were 4 x 6 = 24 cover type x retention combinations each replicated three times, comprising 72 compartments in total [Fig. 4.1. Full details of the EMEND experimental design are provided by Spence et al. (1999) and Work et al. (2010)].

4.2.3 *Beetle sampling*

Ground beetles were collected in all the EMEND compartments using pitfall traps in 2000, 2004 and 2009, with these years corresponding to 2, 5 and 10 years post-harvest, respectively. Pitfall traps (1L in volume, 12 cm diameter) were dug into ground with their upper rims level with the soil surface, filled with approximately 200 ml ethylene glycol as a killing agent and preservative, and covered with a suspended plastic roof to minimize flooding and accumulation of debris (Spence and Niemelä 1994, Bergeron et al. 2013). Traps were installed at both ends of three 40 m transects, a subset of transects randomly chosen from the six EMEND permanent sampling plots (PSPs) in each 10-ha forest compartment (Work et al. 2010). Trapping spanned the frost free season from mid-May to late August in each of the 3 years. During these periods each trap was visited 5 times at approximate 3-week intervals to retrieve the accumulated catch, make any required trap adjustments and replenish the preservative. Ground beetles were sorted and identified to species using Lindroth (1961, 1963, 1966, 1968, 1969a,b) and named following Bousquet and Larochelle (1993).

4.2.4 Habitat variables

Percent cover of bryophytes, forbs, graminoids, lichens, low-shrubs (LShrub), tall-shrubs (TShrub) and trees were estimated on each plot in 2001, 2004 and 2009. Shrubs and trees were recorded from a 5 x 5 m quadrat at the center of the six PSPs in each compartment while other habitat variables were recorded from a 2 x 2 m quadrat within each of the shrub plots. Averages of percent cover of each vegetation group for the three transects were used for the analyses presented here.

4.2.5 Analysis

Ground beetles were pooled by compartment over each year of collection. Catches were standardized to number of individuals per 100 trap-days to minimize effects of occasional trap disturbance on the data. Trap disturbance during each collection period ranged from 2%-5% and is thought to have little influence on the data. In addition to this, standardized catches were rounded to integer counts before used as response variable in negative binomial models.

Ground beetles were categorized to three groups, 1) seven key carabid beetle species, *Pterostichus adstrictus* Eschscholtz, *Calathus advena* (LeConte), *Stereocerus haematopus* (Dejean), *Calosoma frigidum* Kirby, *Platynus decentis* (Say), *Calathus ingratus* Dejean and *Agonum retractum* LeConte; 2) seven common species*, Patrobus foveocollis* (Eschscholtz), *Pterostichus pensylvanicus* LeConte, *Trechus chalybeus* Dejean, *Carabus chamissonis* Fischer von Waldheim, *Synuchus impunctatus* (Say), *Trechus apicalis* Motschulsky and *Pterostichus punctatissimus* (Randall); and 3) 53 rare species, each accounting for < 0.4% of the catch. The seven key species were selected not only because they were generally more abundant, but more importantly, because they were the species that contributed most significantly to species turnover between harvested stands and controls according to analyses of previous chapter. The seven common species were selected because of their relatively high abundance in the overall catch. The remaining 53 rare species, collectively accounted for only 2.7% of the total catch so that low numbers prevented independent analyses for each species.

Using understory vegetation variables, I attempted to explain abundance patterns of each of the seven key, and seven common carabid species and the pooled abundance of rare species. Because our abundance data were all over-dispersed (variance/mean >1), Generalized Linear Models (GLM) following a Negative Binomial distribution (log link functions) were used to model relationships between carabid species abundance and habitat variables. Backward selection of variables was used to designate the final model. Because it is not possible to obtain model R^2 from GLM's, model goodness of fit was estimated using McFadden's pseudo-R^2 (McFadden 1974), which is calculated as 1-(residual deviance/null deviance), where the residual deviance represents the full model and the null deviance corresponds to a model with the intercept only (Zuur et al. 2009). Two models were explored for each species. Model 1 used the percent cover of bryophytes, forbs, graminoids, lichens, low-shrubs (LShrub), tall-shrubs (TShrub) and trees as predictor variables. Model 2 focused on habitat defined in terms of shrubs and trees alone and employed the overall percent cover of low-shrubs (LShrub), tall-shrubs (TShrub) and trees of each of the main species at EMEND (*Abies balsamea*, *Betula papyrifera*, *Larix laricina*, *Picea glauca*, *Picea mariana*, *Pinus contorta*, *Populus balsamifera* and *Populus tremuloides*) to predict beetle abundance.

Three-way ANOVA was used to examine the effects of Year, Treatment and Cover type on abundance of seven key, seven common and 53 rare species. Moreover, two-way ANOVA was used to examine the effects of Year and Cover type on abundance of these species in controls to establish patterns of background variation.

All analyses were computed in R v 3.2.4 (R Core team 2015) using *MASS* package (Venables and Ripley 2002) for GLMs.

4.3 Results

A total of 32,823 ground beetles, comprising 67 species was collected. Among those species, 14 species accounted for 97.3% of the total individuals. *Pterostichus adstrictus*, *Calathus ingratus* and *Platynus decentis* were the three most abundant species, together accounting for 55.5% of the total catch. Carabid catch was highest 2 years post-harvest (19, 725 individuals), followed by notable reductions in samples 5 years and 10 years post-harvest (5747 and 7351individuals, respectively). However, carabid catch in controls kept increasing post-harvest (1481, 1650 and 1786 individuals, respectively), suggesting that harvest reduced overall populations of ground beetles locally.

4.3.1 Patterns in understory vegetation

Higher percent cover of byrophytes was observed in compartments of originally mixed and conifer stands harvested to higher (75%) retention, and this pattern remained throughout the post-harvest period (Fig 4.2). Percent cover of forbs increased after harvest, especially in mixed and conifer stands (Fig. 4.2). In general, higher percent cover of forbs and graminoids was observed in lower retention compartments and this pattern remained apparent throughout the ten years of study (Fig. 4.2). There were more low-shrubs and tall-shrubs in deciduous stands than in conifer stands. Moreover, in compartments with lower retention levels, cover of low-shrubs decreased but that of tall-shrubs increased during the years after harvest (Fig. 4.2). Of course, percent cover of trees was higher in higher retention compartments 2 years after harvest and remained so through the post-harvest period studied. Even as saplings grew to reach tree status in harvested compartments and tree cover increased as a result, still more trees remained in compartments harvested to higher retention (50%-75%) prescriptions (Fig. 4.2).

Percent cover of both *P. balsamifera* and *P. tremuloides* was, of course, higher in deciduous than in conifer stands (Fig 4.3). However, percent cover of *P. tremuloides* increased in compartments harvested to lower retention, not only in stands dominated by deciduous cover before harvest, but also in stands that were originally either mixed or conifer (Fig. 4.3). Clearly, there was significant deciduous regeneration in both deciduous and conifer compartments. Nonetheless, percent cover of *P. glauca* was higher after retention harvest in both originally mixed and conifer compartments and this pattern remained through the post-harvest period (Fig. 4.3).

4.3.2 Patterns of carabid abundance

(a) key species

The abundance of the seven key carabid species was significantly explained by Model 1, which included percent cover of bryophytes, forbs, graminoids, lichens, low-shrubs (LShrub), tall-shrubs (TShrub) and trees (Table 4.1). Moreover, except for *C. frigidum*, the abundance of each of the key and common carabid species, and the overall abundance of rare species was also more or less explained in Model 2, which included only the percent cover of particular tree species (Table 4.2). Overall, patterns in actual abundance for the seven key carabid species could be reasonably (R^2=0.16-0.41 in Model 1 and R^2=0.12-0.30 in Model 2) predicted by both models (Fig. 4.4a-g). Results for each species are discussed below.

i. P. adstrictus

Significant differences in abundance of *P. adstrictus* were detected among years ($F_{2, 144}$=86.71; P<0.001), treatments ($F_{5, 144}$=3.23; P<0.001), cover types ($F_{3, 144}$=3.04; P<0.05), and there were two significant interactions: year × treatment ($F_{10, 144}$=9.59; P<0.001), year ×cover type ($F_{6, 144}$=7.59; P<0.001). However, neither the treatment × cover type interaction nor the three-way interaction was significant. (Table 1, Appendix). The abundance of *P. adstrictus* varied significantly over time in controls ($F_{2, 36}$=86.71; P<0.001) (Table 2, Appendix), with abundance generally increasing post-harvest (Actual abundance column in Fig. 4.4a). Interestingly, abundance of *P. adstrictus* in controls did not differ across cover types (Table 2, Appendix), suggesting that the significant effects for cover types and interactions involving cover types must depend on treatments and annual variation.

The abundance of *P. adstrictus* was extremely high in clear-cut and low retention compartments 2 years post-harvest, but the abundance of this species fell significantly in these compartments 5 and 10 years post-harvest (Actual abundance column in Fig.

4.4a). Higher percent cover of bryophytes, forbs, trees and tall shrubs were negatively associated with abundance of *P. adstrictus*, while higher percent cover of low shrubs positively influenced its abundance (Table 4.1). Moreover, higher percent cover of *B. papyrifera*, *P. mariana* and *P. tremuloides* were negatively associated with abundance of *P. adstrictus*, suggesting that *P. adstrictus* populations responded positively to more open canopies and that denser forest, especially with strong representation of these tree species, were not high quality habitat for this species (Table 4.2).

ii. C. advena

Significant differences in abundance of *C. advena* were detected among years ($F_{2, 144}$=24.27; P<0.001), treatments ($F_{5, 144}$=5.84; P<0.001), cover types ($F_{3, 144}$=10.49; P<0.001). In addition, the year × treatment ($F_{10, 144}$=2.46; P<0.01) and year ×cover type ($F_{6, 144}$=4.05; P<0.001) interactions were significant, as for *P. adstrictus*. However, response to treatment did not vary among the four cover types (Table 3, Appendix). Abundance of *C. advena* varied significantly over time in controls ($F_{2, 36}$=3.85; P<0.05) (Table 4, Appendix), increasing from year 2 to year 5 and then decreasing again between year 5 and year 10 post-harvest (Actual abundance column in Fig. 4.4b).

Abundance of *C. advena* differed significantly among cover types ($F_{3, 144}$=10.49) (Table 3, Appendix), with populations that were much more abundant in conifer than in deciduous compartments (Actual abundance column in Fig. 4b). In addition, *C. advena* was abundant (> 12(mean) individuals/compartments) only in harvested compartments with higher retention (>50%) immediately after harvest, and in controls 5 and 10 years post-harvest (Actual abundance column in Fig. 4.4b). Abundance of *C. advena* was negatively influenced by higher percent cover of forbs, tall shrubs, *P. balsamifera* and *P. tremuloides* (Table 4.1, 4.2). In contrast, *C. advena* was more abundant with increasing percent cover of *A. balsamea* and *P. glauca* (Table 4.2).

Thus, populations of *C. advena* were more abundant in conifer than in deciduous compartments, but recovery after harvest was relatively poor in all cover types.

iii. S. haematopus

Significant differences in abundance of *S. haematopus* were detected among years ($F_{2, 144}$=20.20; P<0.001), treatments ($F_{5, 144}$=2.39; P<0.05), cover types ($F_{3, 144}$=4.84; P<0.01), but only the year × treatment ($F_{10, 144}$=2.76; P<0.01) interaction was significant (Table 5, Appendix). No temporal variation was detected in abundance of *S. haematopus* in controls, however, its abundance differed significantly among cover types ($F_{3, 36}$=3.34; P<0.05) (Table 6, Appendix), being generally higher in conifer than in deciduous compartments.

Individuals of *S. haematopus* were also captured more commonly with increasing retention level (Actual abundance column in Fig. 4.4c). Higher percentages of graminoids, low shrubs, tall shrubs, *B. papyrifera*, *P. balsamifera* and *P. tremuloides* negatively influenced the abundance of *S. haematopus* (Table 4.1, 4.2). Abundance of *S. haematopus* was positively associated with higher percent cover of *P. glauca* (Table 4.2), and so this species can be classified as a conifer associated species.

iv. C. frigidum

Significant differences in abundance of *C. frigidum* were only detected among years ($F_{2, 144}$=5.63; P<0.01) and cover types ($F_{3, 144}$=2.86; P<0.05) (Table 7, Appendix). Although mean abundance of *C. frigidum* varied among years, it also varied dramatically among cover types (3.5 ± 1.2 individuals/compartment in DD, 9.0 ± 9.0 in DU, 0.1 ± 0.1 in MX and 0.1 ± 0.1 in CD), so inter-annual differences were not significant (8.5 ± 6.6 individuals/compartment in year 2, 0.6 ± 0.3 in year 5 and 0.4 ± 0.2 in year 10) (Table 8, Appendix).

Individuals of *C. frigidum* were found mostly in deciduous stands (Actual abundance column in Fig 4.2d). Individuals of this species were more abundant with higher percent cover of tall shrubs and trees, while increasing percent cover of bryophytes, forbs and lichens negatively affected its abundance (Table 4.1). These effects were important to predict the distribution of *C. frigidum* because, unlike the other key species, the abundance of *C. frigidum* was not be adequately explained by Model 2.

v. P. decentis

Significant differences in abundance of *P. decentis* were detected among years ($F_{2, 144}$=53.80; P<0.001), treatments ($F_{5, 144}$=3.89; P<0.01), cover types ($F_{3, 144}$=52.76; P<0.001), and the year × treatment ($F_{10, 144}$=4.23; P<0.001), year × cover type ($F_{6, 144}$=23.65; P<0.01) interactions were significant. For *P. decentis*, the three-way interaction was also significant ($F_{30, 144}$=2.13; P<0.01) (Table 9, Appendix). Abundance of *P. decentis* varied significantly in controls ($F_{2, 36}$=6.50; P<0.05) (Table 10, Appendix), generally decreasing from year 2 to year 5 and then increasing again from year 5 to year 10 post-harvest (Actual abundance column in Fig. 4.4e) as noted above for *C. advena*. Its abundance in controls also differed among cover types but followed the same trend ($F_{3, 36}$=8.47; P<0.001) (Table 10, Appendix).

More *P. decentis* were collected from deciduous compartments than from coniferous compartments, and more individuals were found in controls and high retention compartments in deciduous stands (Actual abundance column in Fig. 4.4e). Increasing percent cover of bryophytes, forbs, low shrubs, tall shrubs, *P. glauca* and *P. mariana* negatively influenced the abundance of *P. decentis* (Table 4.1, 4.2). Abundance of this species, however, was positively influenced by higher percent cover of *P. balsamifera*, clearly suggesting that *P. decentis* should be considered as a deciduous associated species (Table 4.2).

vi. C. ingratus

Significant differences in abundance of *C. ingratus* were detected among years ($F_{2, 144}$=34.32; P<0.001), treatments ($F_{5, 144}$=2.39; P<0.05), cover types ($F_{3, 144}$=6.84; P<0.001). Both the year × treatment ($F_{10, 144}$=6.27; P<0.001) and year × cover type ($F_{6, 144}$=8.34; P<0.001) interactions, and three-way interaction were also significant ($F_{30, 144}$=2.13; P<0.01) (Table 11, Appendix). No consistent temporal variation (18.7±2.9 individuals/compartment in year 2, 35.0±7.1 in year 5 and 25.5±3.2 in year 10) or cover type differences (25.3±4.8 individuals/compartment in DD, 35.5±8.0 in DU, 24.1±3.2 in MX and 20.7±6.0 in CD) were detected in the abundance of *C. ingratus* in controls (Table 12, Appendix).

Populations of *C. ingratus* were more evenly distributed across all retention compartments and cover-types, with increased abundance of this species noted in both high retention stands and controls (Actual abundance column in Fig. 4.4f). Higher percent cover of forbs, graminoids, tall shrubs, *P. mariana* and *P. tremuloides* negatively affected the abundance of *C. ingratus*, while the coverage of low shrubs positively influenced its abundance (Table 4.1, 4.2).

vii. A. retractum

Finally, significant differences in abundance of *A. retractum* were detected among years ($F_{2, 144}$=47.94; P<0.001), treatments ($F_{5, 144}$=3.42; P<0.01), cover types ($F_{3, 144}$=47.96; P<0.001). For this species, all two-way interactions: year × treatment ($F_{10, 144}$=4.09; P<0.001), year × cover type ($F_{6, 144}$=26.61; P<0.001), treatment × cover type ($F_{15, 144}$=1.88; P<0.05) and the three-way interaction were also significant ($F_{30, 144}$=2.47; P<0.001) (Table 13, Appendix), making it challenging to interpret the significant main effects. No temporal variation was detected in the abundance of *A. retractum* in controls, however, its abundance differed among cover types ($F_{3, 36}$=9.86; P<0.001) (Table 14, Appendix).

There were more *A. retractum* in deciduous than in coniferous compartments (Actual abundance column in Fig. 4.4g); however, increasing numbers of *A. retractum* were found over the 10-year study in compartments that had been harvested in originally mixed and conifer compartments, likely reflecting their regeneration to mainly deciduous saplings (Actual abundance column in Fig. 4.4g). Coverage of bryophytes, forbs, graminoids, tall shrubs, *P. glauca* and *P. mariana* negatively influenced the abundance of *A. retractum* (Table 4.1, 4.2). In contrast, percent cover of low shrubs and *P. tremuloides* positively affected its abundance (Table 4.2). Thus, *A. retractum* is properly considered as a deciduous associated species.

(b) common species

For the seven common carabid species, abundance was significantly explained by Model 1 (Table 4.1), but, unlike for the key species, Model 2 offered good predictions for only a few species (Table 4.2). The details of understory vegetation were apparently more important in predicting habitat use by these species.

i. P. foveocollis

Significant differences in abundance of *P. foveocollis* were detected among years ($F_{2, 144}$=23.75; P<0.001), treatments ($F_{5, 144}$=3.22; P<0.01), cover types ($F_{3, 144}$=18.62; P<0.001). The year × treatment ($F_{10, 144}$=1.98; P<0.05), year × cover type ($F_{6, 144}$=7.17; P<0.001) and three-way interaction were also significant ($F_{30, 144}$=1.55; P<0.05) (Table 15, Appendix). No temporal variation was detected in the abundance of *P. foveocollis* in controls, however, its abundance differed among cover types ($F_{3, 36}$=3.78; P<0.05) (Table 16, Appendix).

Abundance of *P. foveocollis* was generally higher in deciduous than in coniferous compartments (Fig. 4.4h). Abundance of this species was positively associated with percent cover of low shrubs and *P. balsamifera*, but negatively associated with bryophytes and higher coverage of *P. glauca* (Table 4.1, 4.2). Therefore, *P. foveocollis* should be considered as a deciduous associated species.

ii. P. pensylvanicus

Significant differences in abundance of *P. pensylvanicus* were detected only among years ($F_{2,\,144}$=13.43; P<0.001) and cover types ($F_{3,\,144}$=21.89; P<0.001), and the year × cover type interaction was significant ($F_{6,\,144}$=7.19; P<0.001) (Table 17, Appendix). There were no significant differences in abundance among years or cover types for *P. pensylvanicus* in controls (Table 18, Appendix).

Significantly more individuals of *P. pensylvanicus* were collected in deciduous stands than in coniferous stands (Fig. 4.4i). Coverage of bryophytes, lichens and tall shrubs all negatively influenced the abundance of *P. pensylvanicus* (Table 4.1), as did percent cover of *P. glauca* and *P. mariana*. In contrast, abundance was positively influenced by higher coverage of *P. tremuloides* (Table 4.2). Thus, *P. pensylvanicus* is properly considered as a deciduous associated species.

iii. T. chalybeus

No significant differences in its abundance were detected among treatments and cover types for *T. chalybeus* (Table 19, Appendix). Significant variation in populations of this species appeared to be purely temporal in nature (Table 19 and 20, Appendix).

Populations of *T. chalybeus* were more or less evenly distributed across all retention stands and all cover-types 5 and 10 years post-harvest but, interestingly, not a single individual of this species was collected two years post-harvest (Fig. 4.4j). Higher percent cover of bryophytes, forbs, lichens, low shrubs and tall shrubs were positively associated with the abundance of *T. chalybeus* (Table 4.1), as did percent cover of *B. papyrifera* and *P. tremuloides* (Table 4.2).

iv. C. chamissonis

Significant differences in abundance of *C. chamissonis* were only detected among years ($F_{2, 144}=9.87$; $P<0.001$) and cover types ($F_{3, 144}=3.83$; $P<0.05$), but the significant year × cover type interaction showed that variation among years depended on the cover type ($F_{6, 144}=3.58$; $P<0.01$) (Table 21, Appendix). The abundance of *C. chamissonis* in controls varied over time ($F_{2, 36}=4.29$; $P<0.05$) (Table 21, Appendix), in a pattern similar to that seen for *C. advena* and *P. adstrictus* above, i.e., populations generally increased from year 2 to year 5 and then decreased between year 5 to year 10 (Fig. 4.4k).

Abundance of *C. chamissonis* in controls differed among cover types ($F_{3, 36}=8.47$; $P<0.001$) (Table 22, Appendix).There were more *C. chamissonis* in lower retention deciduous stands 2 years post-harvest; however, individuals of this species were collected more abundantly in higher retention stands across all cover-types 5 and 10 years post-harvest (Actual abundance column in Fig. 4.4k). Higher percent cover of bryophytes, graminoids, tall shrubs and *B. papyrifera* negatively affected the abundance of *C. chamissonis*, while the overall abundance of trees and especially *P. glauca* positively influenced its abundance (Table 4.1, 4.2). Thus, *C. chamissonis* should be considered as being mainly associated with coniferous trees (Table 4.2).

v. *S. impunctatus*

Significant differences in abundance of *S.impunctatus* were detected only among years ($F_{2, 144}=38.41$; $P<0.001$) and treatments ($F_{3, 144}=3.00$; $P<0.05$), with a significant interaction showing that treatment effects depend on year ($F_{10, 144}=1.92$; $P<0.05$) (Table 23, Appendix). Differences among treatments seem to have generated most of the variation because there were no significant differences in abundance of *S.impunctatus* among either years or cover types in controls (Table 24, Appendix).

Generally, individuals of *S.impunctatus* were collected more abundantly in more open compartments with lower retention across all cover-types (Fig. 4.4l). Increasing percent cover of forbs, graminoids and low shrubs, along with higher percent cover of *P. mariana* positively influenced the abundance of *S.impunctatus* (Table 4.1, 4.2).

vi. T. apicalis

No significant differences in abundance of *T.apicalis* were detected among treatments or cover types (Table 25, Appendix). Purely temporal variation accounted for all significant changes of population that were observed (Table 25, 26, Appendix).

There were no clear post-harvest patterns of variation in abundance of *T.apicalis* in relation to variation in retention level across cover-types (Fig. 4.4m). Higher percent cover of both tall shrubs and trees, particularly *P. glauca*, *P. balsamifera* and *P. tremuloides*, was negatively associated with the abundance of *T.apicalis*, while its abundance increased with higher percent cover of graminoids (Table 4.1, 4.2). From these data, I conclude that *T.apicalis*, although found in forest, should be considered as being associated with more open-habitat.

vii. P. punctatissimus

Significant differences in abundance of *P. punctatissimus* were only detected among years ($F_{2, 144}$=4.34; $P<0.05$) and cover types ($F_{3, 144}$=3.31; $P<0.05$) (Table 27, Appendix). However, there were no significant differences among either years or cover types in abundance of *P. punctatissimus* in controls (Table 28, Appendix), suggesting that the dynamics observed for this species were mainly a function of variation in harvest intensity.

Individuals of *P. punctatissimus* were collected more abundantly in coniferous than in deciduous compartments (Fig. 4.4n). The abundance of *P. punctatissimus* was positively associated with higher percent cover of both forbs and graminoids; however, its abundance was negatively affected by low and tall shrubs and percent cover of *P. balsamifera*. (Table 4.1, 4.2).

(c) Rare species

Significant differences in total abundance of 53 rare species were detected among all three driving variables: years ($F_{2,\,144}$=6.60; $P<0.01$), treatments ($F_{5,\,144}$=4.48; $P<0.001$), cover types ($F_{3,\,144}$=5.04; $P<0.01$), and the year × cover type interaction was significant ($F_{6,\,144}$=2.97; $P<0.01$) (Table 29, Appendix). There were no significant differences among years or cover types in total abundance of 53 rare species in controls (Table 30, Appendix).

The total collective abundance of 53 rare species was poorly explained by either model. The R^2 for percent cover of understory = 0.06 (Table 4.1), and for percent cover of tree species = 0.05 (Table 4.2). There were no clear patterns of distribution of rare species as a group in relation to retention level in any post-harvest cover types (Fig. 4.4o). Higher percent cover of low shrubs positively influenced overall abundance of rare species while rare species were more commonly encountered in compartments with lower tree density (Table 4.1). Interestingly and somewhat contrary to expectation, rare species were more common in early successional habitats as presence of *P. glauca* negatively affected their overall abundance (Table 4.2).

Summary

Data from controls suggest that populations of *C. frigidum*, *S. haematopus*, *C. ingratus*, *A. retractum*, *P. foveocollis*, *P. pensylvanicus*, *S.impunctatus* and *P. punctatissimus* would maintain relatively stable abundance on un-harvested landscapes. However, *T.apicalis*, *T. chalybeus, P. adstrictus*, *C. advena*, *P. decentis* and *C. chamissonis* would apparently vary in abundance temporally even without harvesting (Table 4.3), likely in a way that depends on annual variation in weather. For the two *Trechus* species, *T.apicalis* and *T. chalybeus,* abundances were influenced by neither harvest treatment nor cover type, but were a matter of purely temporal variation in beetle activity-abundance. Influences of harvest intensity in addition to natural temporal variation shaped the dynamics of *P. adstrictus*, *C. advena*, *P. decentis* and *C. chamissonis*. Although my models made only weak predictions, it seems that overall abundance of 53 rare species would be more or less stable if there were no harvesting (Table 4.3).

In terms of habitat use, *P. adstrictus* and *T.apicalis* are associated with open-habitat. *P. decentis*, *A. retractum*, *P. foveocollis* and *P. pensylvanicus* are associated with deciduous stands while *C. advena*, *S. haematopus* and *C. chamissonis* are conifer-associated species. The data about overall abundance of 53 rare species suggests that populations of rare species were not concentrated in any particular cover type.

Except for *P. foveocollis,* patterns in actual abundance for the seven key carabid species could be reasonably predicted by both Models (R^2=0.16-0.41 in Model1 and R^2=0.12-0.30 in Model 2). Abundance of the seven common carabid species, was also significantly explained by Model 1 (R^2=0.17-0.33), but abundance of only a few was weakly predicted by Model 2 (R^2=0.06-0.18). The total abundance of 53 rare species was poorly explained by either Model (R^2=0.06 in Model 1 and R^2=0.05 in Model 2), suggesting that rare species in general are not associated with particular habitat elements defined by vegetation.

4.4 Discussion

Our results strongly support our first hypothesis, i.e., habitat variability strongly influenced the spatial patterns of ground beetle abundance through species-specific matches to habitat characteristics reflected in vegetation. Distributions of all seven key ground beetle species that drove observed changes in beta-diversity and an additional seven common species were significantly explained (R^2=0.16-0.41) by Model 1, which included percent cover of bryophytes, forbs, graminoids, lichens, low-shrubs, tall-shrubs and trees. However, the distribution pattern was not well predicted for any species by particular vegetation variables alone. Therefore, we suggest that complex combinations of habitat characteristics, as partly reflected in aspects of vegetation, significantly affect patterns of species abundance, and that these in turn translate into carabid distribution patterns.

Interestingly, relationships between the abundance of particular ground beetle species and habitat variability were also strong when data about relative cover of tree species alone were used as habitat variables in Model 2. Species-specific data about canopy composition may, in fact, better reflect the joint influence of both forest cover-type and green tree retention levels than does the broader combination of variables used in Model 1. Distributions of several key beetle species such as *C. advena* and *S. haematopus* were actually more tightly linked to percent cover of different tree species (R^2=0.30 and 0.25, respectively by Model 2), suggesting that the match of species-specific habitat requirements with canopy composition drives the influence of habitat variability, supporting our second hypothesis. These results also corroborate previous findings of Bergeron et al. (2011, 2012), suggesting that beetle species are associated with particular tree species, and that a well-developed forest tree inventory provides a reasonable surrogate for arthropod biodiversity. Therefore, understanding such habitat associations may be highly relevant to planning sustainable retention harvest scenarios that are sensitive to conserving biodiversity.

The seven key species and additional seven common species considered in this study differ with respect to use of forest habitats as defined by tree cover on the mixedwood landscape at EMEND. *P. adstrictus*, is in fact strongly associated with open-habitat, although it is common in forest environments in western Canada (Niemalä and Spence 1992, Niemalä et al. 1993). Three species, *C. advena*, *S. haematopus* and *C.chamissonis* were all negatively influenced by deciduous tree cover and reached their abundances under high percent cover of conifer trees. In contrast, abundances of

P. decentis, *A. retractum, P. foveocollis* and *P. pensylvanicus* were strongly associated with deciduous trees. These results may be used to characterize the carabid fauna of boreal mixedwood landscapes and are generally consistent with findings of previous studies (Niemalä et al. 1993, Gandhi et al. 2001, Buddle et al. 2006).

The pattern of species abundance in compartments harvested to higher retention prescriptions was closer to that found in controls than it was in low retention stands and clear-cuts. This supports our 3rd hypothesis and suggests that relatively high levels of retention would be required to preserve healthy populations of local forest assemblages *in situ*. Nonetheless, retention harvest apparently maintains populations and conserves forest biodiversity, much better than does traditional clear-cutting up to 10 years post-harvest, after which we can expect positive effects of forest regeneration to become increasingly stronger. For *P. decentis*, *A. retractum* and *P. foveocollis* abundance in all compartments harvested with retention were more similar to controls 10 years post-harvest than they were to clear-cuts, showing especially strong recovery of deciduous associated species in deciduous stands. However, for *C. advena*, *S. haematopus* and *C.chamissonis,* abundance was higher and closer to that in controls only in compartments with the highest (50%-75%) retention. Therefore, higher and presently impractical green retention levels would likely be needed to conserve populations of species typical of mature coniferous forest after harvest. This result is also consistent with findings of the previous chapter and previous work (e.g., Work et al. 2010, Bergeron et al. 2017), showing that conifer associated assemblages are less resistant and resilient to harvesting.

The deciduous forest specialist *A. retractum*, became more abundant 10 years post-harvest in stands that were originally mixed and conifer forest. This suggests that, in addition to driving loss of conifer-associated carabid species, low retention harvests in late successional stands also promote development of populations of deciduous associated species (year × treatment × cover type interaction was highly significant

($F_{30, 144}=2.47$; $P<0.001$ from Table 13, Appendix) as predicted by Spence et al. (1996). Thus beetle assemblages of such post-harvest stands become more similar to those of deciduous stands, moving them further away from the pre-harvest condition as represented by the controls. Given these natural tendencies, reserving significantly large stands from harvest in conifer dominated areas, appears to be necessary to prevent local assemblages of coniferous dominated species from shifting to those characteristic of deciduous stands. Under the latter circumstances we can expect that assemblages of mature late-successional forest will require a lengthy post-harvest period to develop.

Harvesting had an important effect on ground beetle abundance in each forest cover type through 10 years post-harvest. For eight of the 14 key and common species and combined numbers of 53 rare species, overall abundance likely would remain stable in each forest cover type if there was no harvesting. Thus harvest intensity appears to be the main factor that shapes species abundance patterns for these species, and the benefits of retention harvest as discussed above should promote stability and conservation of their populations. In contrast, populations of *P. adstrictus*, *C. advena*, *P. decentis* and *C. chamissonis* fluctuated in controls and temporal variation was exaggerated with higher harvest intensity. Therefore, retention harvest should also provide advantages for conserving these species by holding their temporal variation in a more natural range.

Unfortunately, the pattern of distribution of the group of rare species at EMEND was not well explained by either of our models, suggesting that faunal conservation strategies based on setting particular habitats aside based on vegetation structure will not be useful for this most vulnerable portion of the fauna. There are at least three possible scenarios that might be further investigated in relation to effects of habitat and contribute to solving this problem. First, a binomial model may better predict presence and absence of rare species than can be achieved by modeling the total abundance in a GLM approach following a negative binomial distribution. Second, the data about tree species used in our models may be insufficient, especially if uncommon beetle species are strongly associated with uncommon tree species as suggested by Bergeron et al. (2011). Thus, our model may fail to predict rare species distributions due to lack sufficient data about specific habitat defined by presence of uncommon tree species. Third, although habitats of common species may be defined by general vegetation characteristics, those of rare species may need to be described in more detail, reflecting characteristics not well encompassed by the vegetation.

Our results underscore that habitat variability shaped by both cover-type and harvest intensity plays an important role in structuring the relative abundance and, ultimately, the distribution of the most common forest species on managed landscapes in northern Alberta. There are two important implications for forest management. First, variable retention harvests will maintain biodiversity better than clear-cutting, and higher retention levels will more rapidly generate species distributions similar to those present before harvest. Second, high retention levels better accommodate species-specific habitat requirements, and thus may lifeboat mature forests specialists in situ well into post-harvest recovery.

In addition, our results emphasize the importance of retaining key elements of stand structural complexity to conserve forest biodiversity as has been emphasized by Lindenmayer, Franklin and Fischer (2006) and Thomas et al. (2006). In the boreal mixedwood, conifer stands will require extra attention because regeneration of deciduous trees post-harvest leads to stand structure that is more similar to that of a deciduous forest. As emphasized by Bergeron et al. (2017), management of forest structure to conserve post-disturbance ecosystem memory will increase overall resilience of the biotic elements in mixedwood forests, and assist in meeting the modern concept of sustainability. The present work suggests that insufficient attention to the coniferous component of the mixedwood will lead to loss or reduction of populations that are key elements of forest biodiversity, and slow recovery of at least carabid biodiversity on harvested landscapes. Other taxa that have habitat affinities based on forest structural characteristics and only limited dispersal ability should follow similar patterns. Therefore, I suggest that development of retention strategies should consider differences among forest cover types in the quest for more sustainable management of forest biodiversity. Toward this end, I propose that 1) more aggregated and higher overall retention levels should be left after harvest in conifer stands, and that 2) old trees and patches of especially old forest should be incorporated into retention as often as is practical.

From a broader perspective, it seems apparent from my results that harvesting will negatively affect post-harvest abundance of species in groups like carabid beetles, thus, will largely alter their temporal variation after harvest. Retention harvest may serve as a practical way to minimize this variation, and bring species biodiversity back to or close to its own level of natural variation driven mainly by natural disturbance.

Table 4.1 Effects of understory vegetation cover percentage on abundance of carabid beetles (Model1).

Variable	Estimate	z value	R^2
Abundance			
Key Species			
Pterostichus adstrictus			0.37
Intercept	4.04^{***}	26.97	
Bryophyte	$-1.08E\text{-}02^{**}$	−3.04	
Forb	$-1.39E\text{-}02^{**}$	−2.08	
LShrub	$4.56E\text{-}02^{***}$	5.35	

Tree	$-1.21\text{E-}02^{***}$	−3.83	
TShrub	$-3.80\text{E-}02^{***}$	−9.91	
Calathus advena			0.28
Intercept	3.31^{***}	11.06	
Forb	$-5.89\text{E-}02^{***}$	−3.82	
TShrub	$-4.82\text{E-}02^{***}$	−5.02	
Stereocerus haematopus			0.40
Intercept	3.92^{***}	18.58	
Graminoid	$-2.51\text{E-}02^{*}$	−2.05	

LShrub	−5.48E-02***	−4.15	
TShrub	−3.81E-02***	−5.74	
Calosoma frigidum			0.41
Intercept	2.85***	4.33	
Bryophyte	−1.12E-02***	−3.56	
Forb	−1.07E-02***	−3.03	
Lichen	−7.66*	−2.57	
Tree	5.94E-02***	3.95	
TShrub	5.83E-02**	−3.02	

Platynus decentis			0.26
Intercept	2.89***	10.35	
Bryophyte	−2.47E-02***	−4.05	
Forb	−5.03E-02***	−4.30	
LShrub	−1.09E-01***	7.31	
TShrub	−2.57E-02***	−3.73	
Calathus ingratus			0.16
Intercept	3.56***	19.49	
Forb	−2.16E-02**	−2.84	

Graminoid	−2.02E-02*	−2.26	
LShrub	2.57E-02***	2.67	
TShrub	−1.44E-02**	−3.20	
Agonum retractum			0.38
Intercept	2.80***	10.42	
Bryophyte	−5.06E-02***	−7.66	
Forb	−3.81E-02***	−3.37	
Graminoid	−3.31E-02*	−2.52	
LShrub	9.52E-02***	6.69	

Common Species			
Patrobus foveocollis			0.17
Intercept	1.48^{***}	9.15	
Bryophyte	$-1.35\mathrm{E}\text{-}02^{**}$	−3.16	
LShrub	$4.20\mathrm{E}\text{-}02^{***}$	5.07	
Pterostichus pensylvanicus			0.22
Intercept	2.02^{***}	8.03	
Bryophyte	$-3.86\mathrm{E}\text{-}02^{***}$	−4.59	
Lichen	-2.67^{***}	−3.43	

TShrub	−1.95E-02**	−2.92	
Trechus chalybeus			0.30
Intercept	-2.43***	-5.78	
Bryophyte	2.22E-02**	2.66	
Forb	6.84E-02***	4.63	
Lichen	2.00**	2.73	
LShrub	5.43E-02**	2.90	
TShrub	3.28E-02***	3.92	
Carabus chamissonis			0.26

Intercept	2.34***	8.89	
Bryophyte	-1.94E-02**	-2.97	
Graminoid	-4.53E-02**	-2.78	
Tree	1.59E-02**	2.83	
TShrub	-3.97E-02**	-4.75	
Synuchus impunctatus			0.33
Intercept	-3.05***	-6.97	
Forb	8.57E-02***	5.18	
Graminoid	1.00E-01***	5.92	

LShrub	5.24E-02***	2.83	
Trechus apicalis			0.21
Intercept	1.37***	6.36	
Graminoid	3.85E-02*	2.23	
Tree	-2.35E-02**	-3.28	
TShrub	-5.07E-02***	-5.76	
Pterostichus punctatissimus			0.23
Intercept	0.62*	2.13	
Forb	3.54E-02*	2.41	

Graminoid	5.10E-02**	3.01	
LShrub	-4.51E-02*	-2.32	
TShrub	-6.27E-02***	-5.27	
Rare species			0.06
Intercept	1.53***	7.70	
LShrub	2.40E-02*	2.21	
Tree	-1.48E-02**	-3.29	

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 4.2 Effects of percent cover of tree species on abundance of carabid beetles (Model 2).

Variable	**Estimate**	***z* value**	**R^2**
Abundance			
Key Species			
Pterostichus adstrictus			0.28
Intercept	4.29^{***}	42.114	
Betula papyrifera	$-2.11E\text{-}02^{**}$	−2.63	
Picea mariana	$-8.06E\text{-}02^{**}$	−2.58	
Populus tremuloides	$-3.08E\text{-}02^{***}$	−8.33	

Calathus advena			0.30
Intercept	1.97***	8.92	
Abies balsamea	1.20E-01*	2.08	
Picea glauca	6.68E-02***	4.97	
Populus balsamifera	−4.53E-02*	−2.33	
Populus tremuloides	−6.70E-02***	−7.28	
Stereocerus haematopus			0.25
Intercept	2.75***	17.55	
Betula papyrifera	−3.00E-01*	−2.35	

Picea glauca	3.70E-02***	3.87	
Populus balsamifera	−7.73E-02***	−5.58	
Populus tremuloides	−2.80E-02***	−4.82	
Calosoma frigidum			NA
NA	NA	NA	
Platynus decentis			0.12
Intercept	3.45***	18.78	
Picea glauca	−2.24E-02*	−1.99	
Picea mariana	−2.38E-01***	−3.76	

Populus balsamifera	3.21E-02*	2.27	
Populus tremuloides	−2.50E-02***	−3.76	
Calathus ingratus			0.13
Intercept	3.38***	33.59	
Picea mariana	−9.56E-02**	−2.72	
Populus tremuloides	−2.34E-02***	−5.82	
Agonum retractum			0.18
Intercept	3.45***	20.56	
Picea glauca	−7.14E-02***	−6.25	

Picea mariana	−1.60E-01**	−2.67	
Populus tremuloides	1.30E-02*	1.98	
Common Species			
Patrobus foveocollis			0.10
Intercept	2.03***	19.712	
Picea glauca	−2.23E-02**	−2.93	
Populus balsamifera	3.08E-02**	3.40	
Pterostichus pensylvanicus			0.14
Intercept	1.88***	9.89	

Picea glauca	−5.84E-02***	−4.75	
Picea mariana	−3.04E-01**	−3.27	
Populus tremuloides	2.05E-02**	3.06	
Trechus chalybeus			0.11
Intercept	0.51***	2.43	
Betula papyrifera	3.66E-01*	2.14	
Populus balsamifera	8.38E-02***	4.66	
Carabus chamissonis			0.10
Intercept	1.34***	8.03	

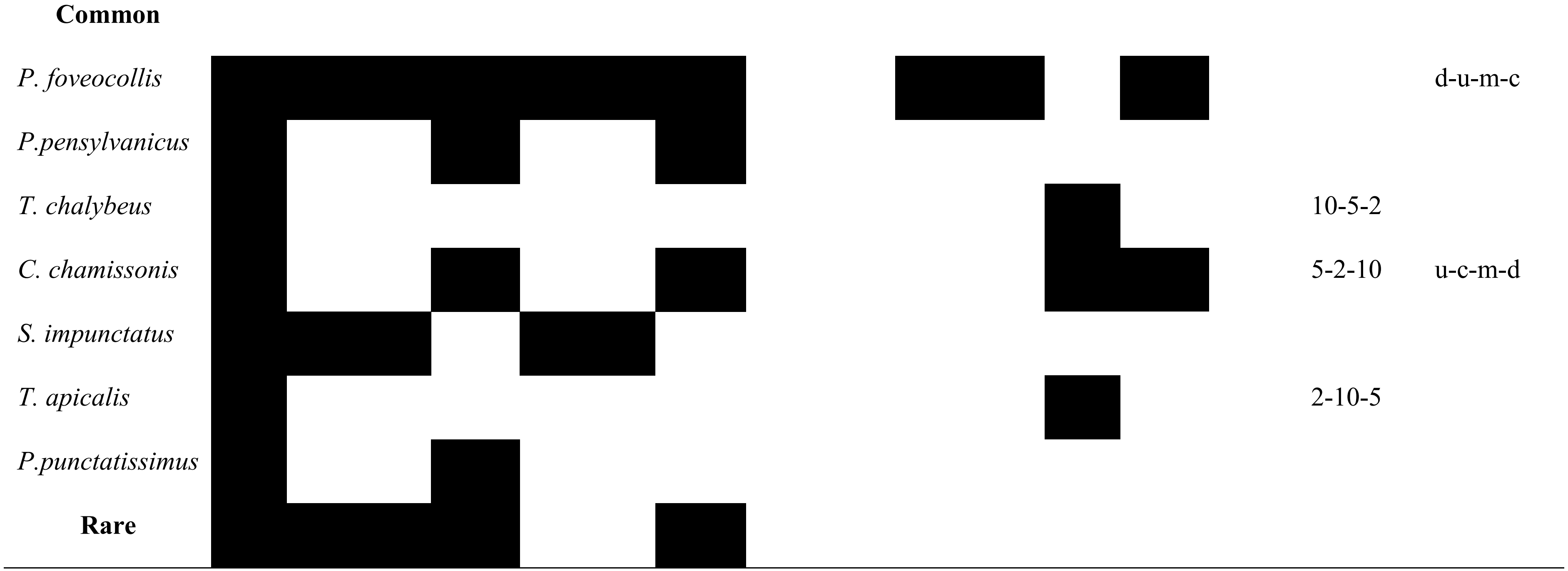
Betula papyrifera	−1.05*	−2.53	
Picea glauca	2.84E-02*	2.54	
Synuchus impunctatus			0.06
Intercept	−2.89E-02	-0.13	
Picea mariana	3.49E-02***	3.56	
Trechus apicalis			0.14
Intercept	1.40***	6.63	
Picea glauca	−3.49E-02*	−2.44	
Populus balsamifera	−6.13E-02**	−3.17	

Populus tremuloides	−2.95E-02***	−3.52	
Pterostichus punctatissimus			0.18
Intercept	0.78***	5.88	
Populus balsamifera	−1.14E-01***	−5.00	
Rare species			0.05
Intercept	1.53***	15.61	
Picea glauca	-2.27E-02**	−2.62	

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 4.3 Summary of ANOVA outcomes for effects of Year, Treatment and Cover type on abundance of carabid species

	Three-way ANOVA							Two-way ANOVA			Controls	
Species	**Year**	**Treatment**	**Cover type**	**Year× Treatment**	**Year× Cover type**	**Treatment× Cover type**	**Year× Treatment× Cover type**	**Year**	**Cover type**	**Year× Cover type**	**Years (highest -lowest catch)**	**Cover type (highest -lowest catch)**
Key												
P. adstrictus	■	■	■	■	■			■			5-2-10	
C. advena	■	■	■	■	■			■	■		5-10-2	c-m-u-d
S. haematopus	■	■	■	■					■			c-u-m-d
C. frigidum	■		■									
P. decentis	■	■	■	■	■		■	■	■		10-2-5	d-u-m-c
C. ingratus	■	■	■	■	■		■					
A.retractum	■	■	■	■	■	■	■		■			d-u-m-c



■ Significant d=deciduous u=deciduous with conifer understory

□ Not significant m=mixed c=conifer

Order of catch (highest to lowest) is given under controls if year or cover type is significant in two-way ANOVA.

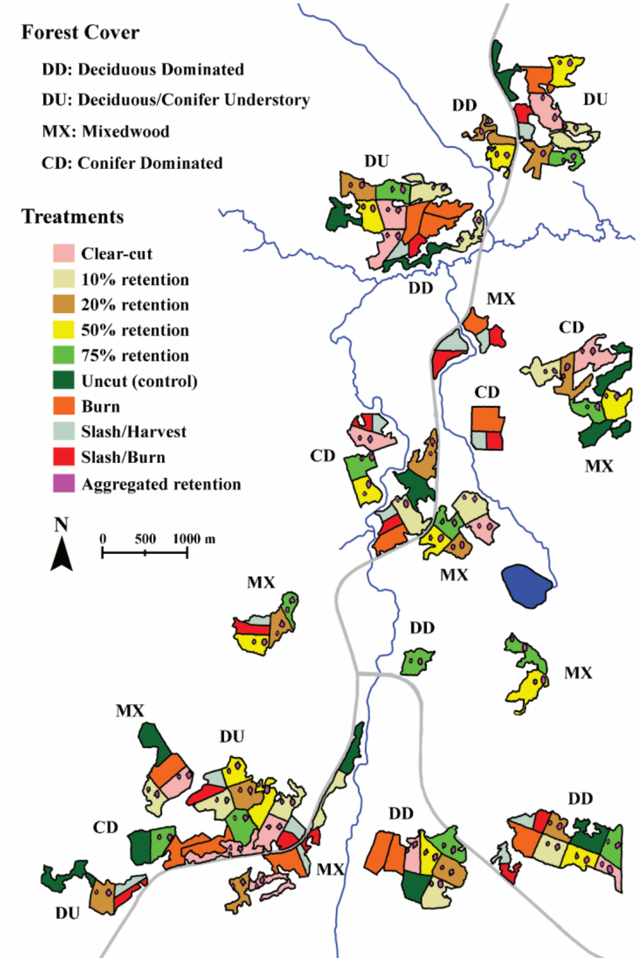
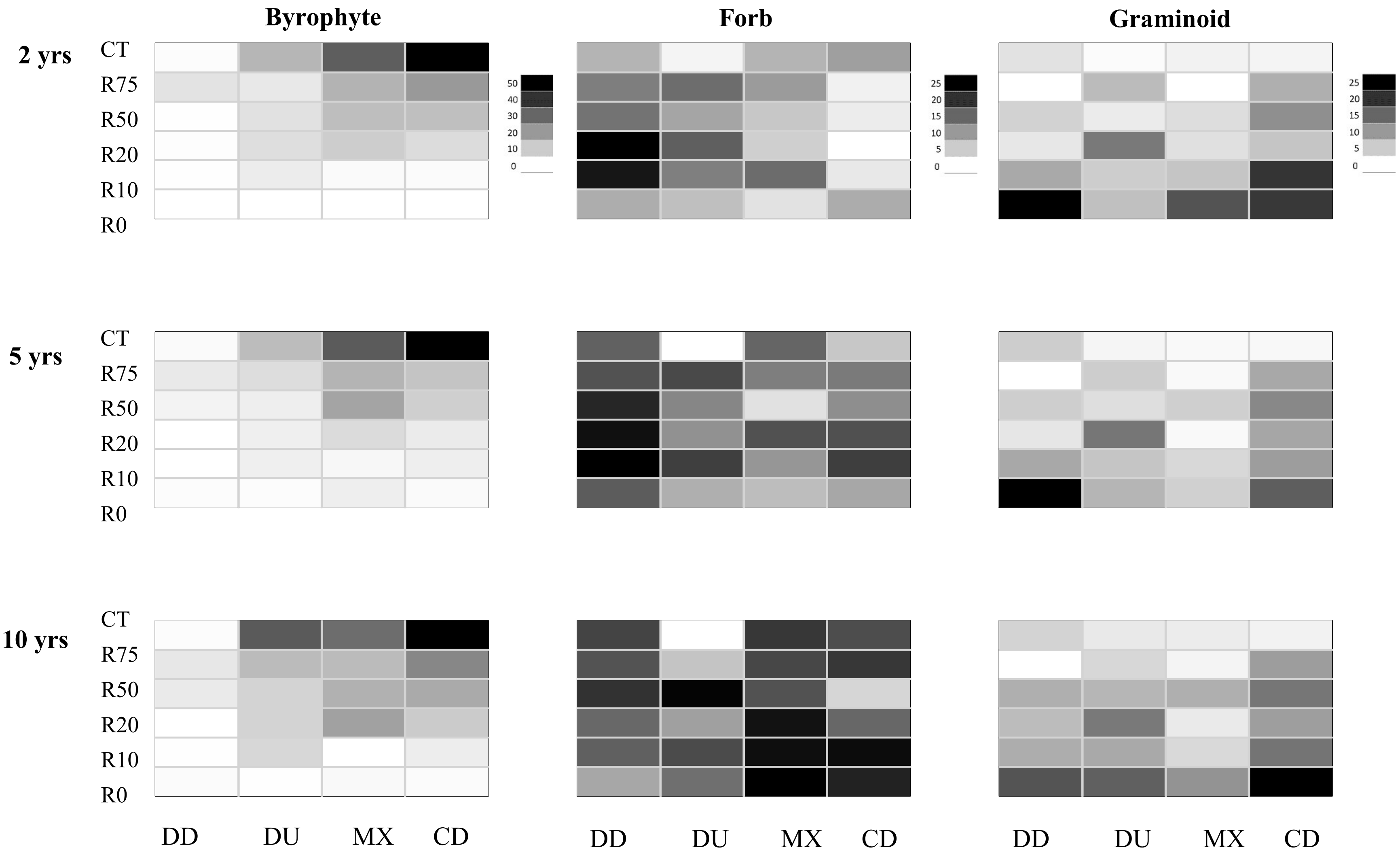


Fig. 4.1. Map of the EMEND (Ecosystem Management by Emulating Natural Disturbance) experimental site. Compartments of harvesting treatments and un-harvested controls in four forest cover-types.


Byrophyte
Forb
Graminoid
2 yrs
5 yrs
10 yrs
CT
R75
R50
R20
R10
R0
DD
DU
MX
CD
50
40
30
20
10
0
25
20
15
10
5
0

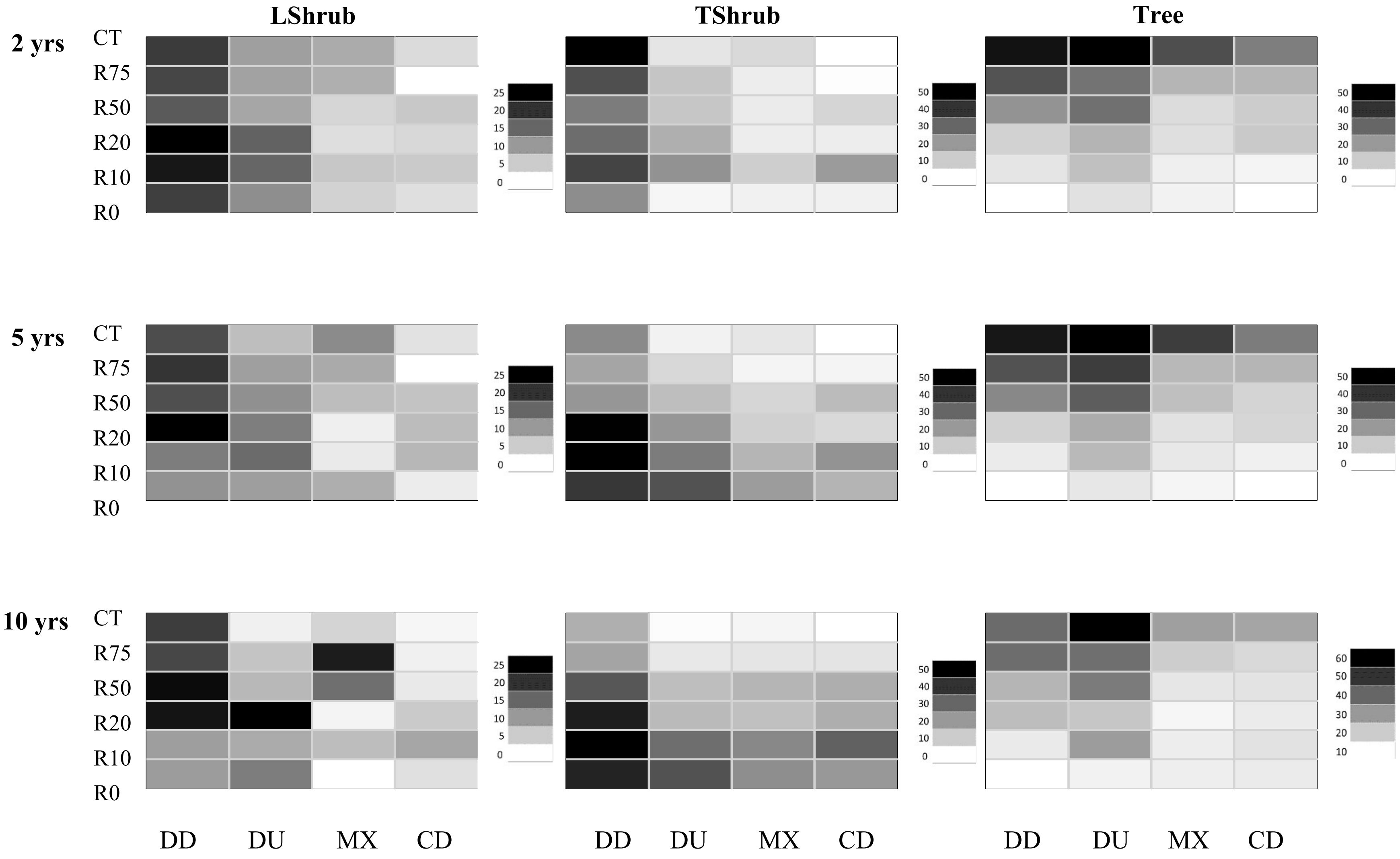

LShrub
TShrub
Tree
2 yrs
5 yrs
10 yrs
CT
R75
R50
R20
R10
R0
25
20
15
10
5
0
50
40
30
20
10
0
60
50
40
30
20
10
DD
DU
MX
CD

Fig. 4.2. Distribution of bryophytes, forbs, graminoids, lichens, low-shrubs (LShrub), tall-shrubs (TShrub) and trees in Deciduous-dominated stands (CD), Deciduous-dominated stands with spruce understory (DU), Mixed stands (MX) and conifer-dominated stands (CD) with increasing retention level (R0, R10, R20, R50, R75 and CT). Darker color means higher percent of cover, as indicated in the legend associated with each figure.

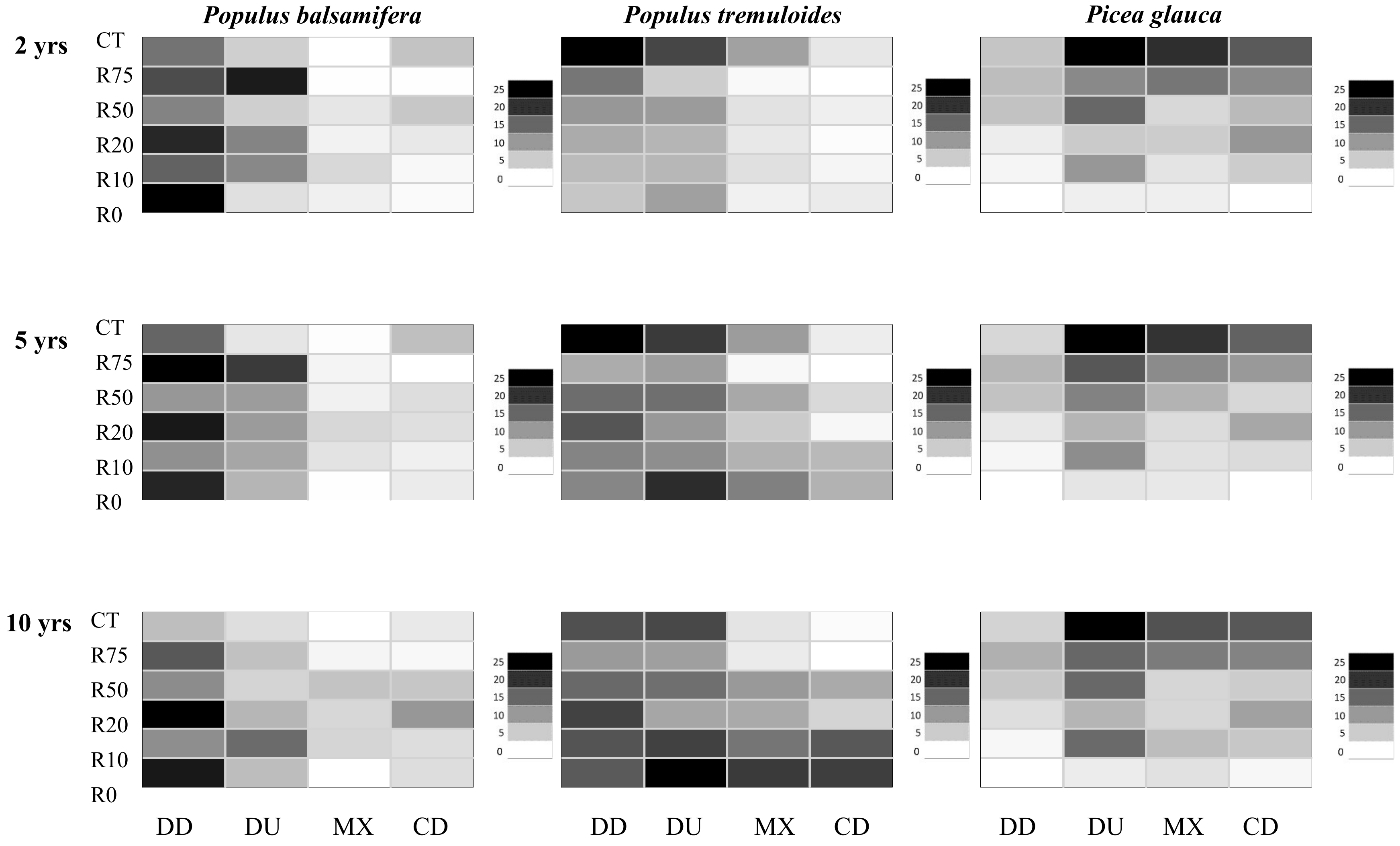
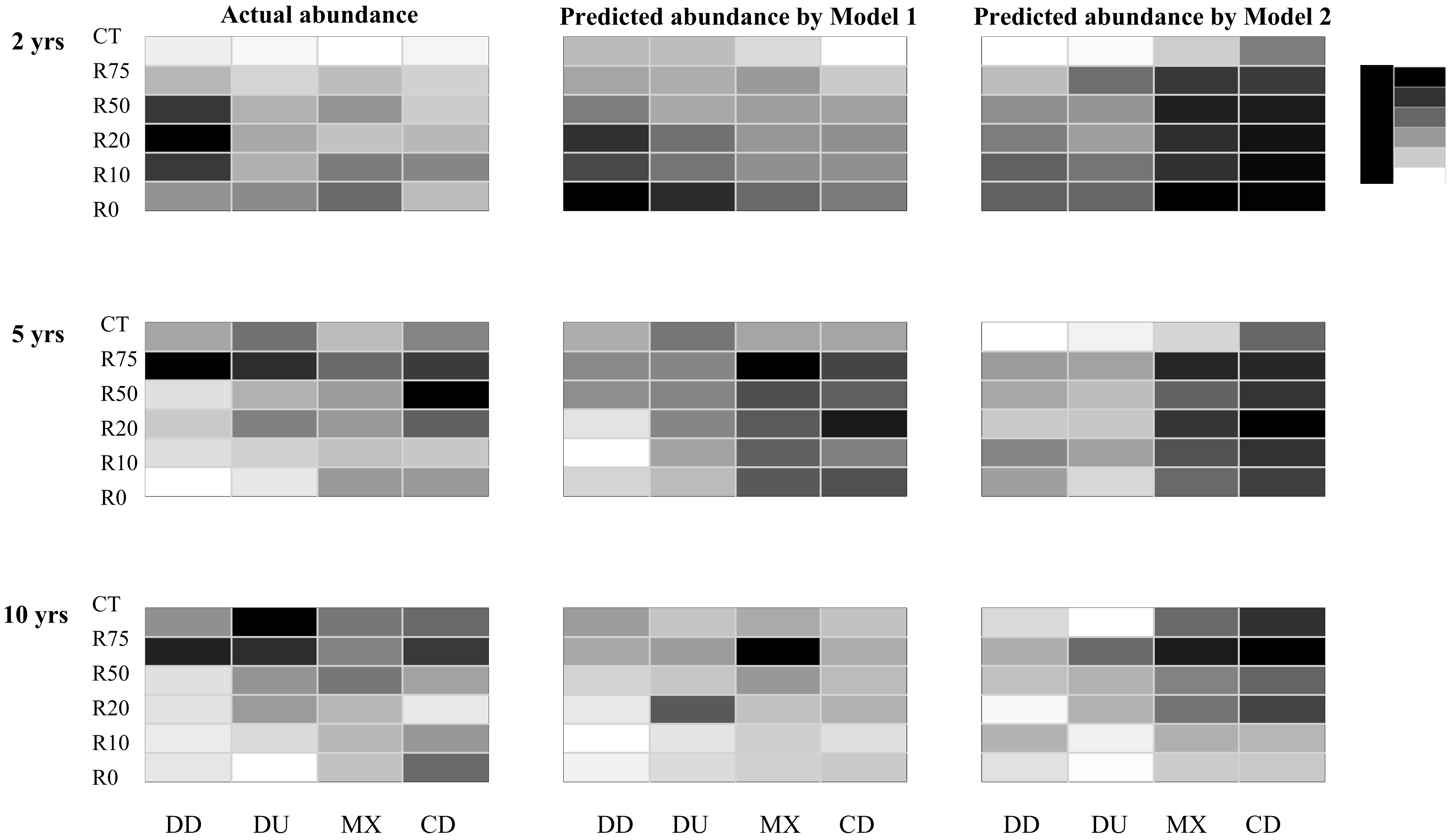
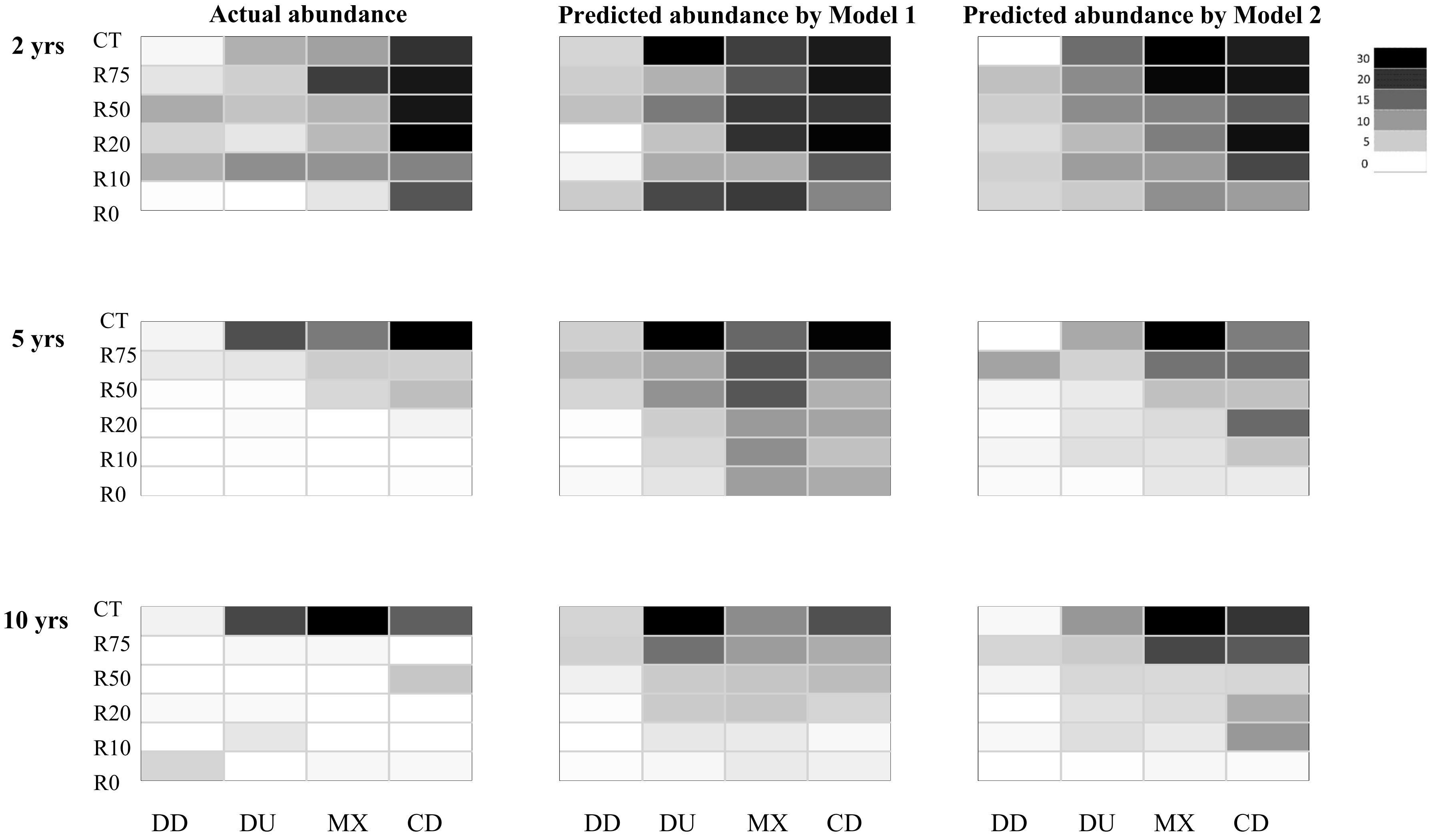

Populus balsamifera
Populus tremuloides
Picea glauca
2 yrs
5 yrs
10 yrs
CT
R75
R50
R20
R10
R0
25
20
15
10
5
0
DD
DU
MX
CD

Fig. 4.3. Distribution of *Populus balsamifera*, *Populus tremuloides* and *Picea glauca* in Deciduous-dominated stands (CD), Deciduous-dominated stands with spruce understory (DU), Mixed stands (MX) and conifer-dominated stands (CD) with increasing retention level (R0, R10, R20, R50, R75 and CT). Darker color means higher percent of cover, as indicated in the legend associated with each figure.

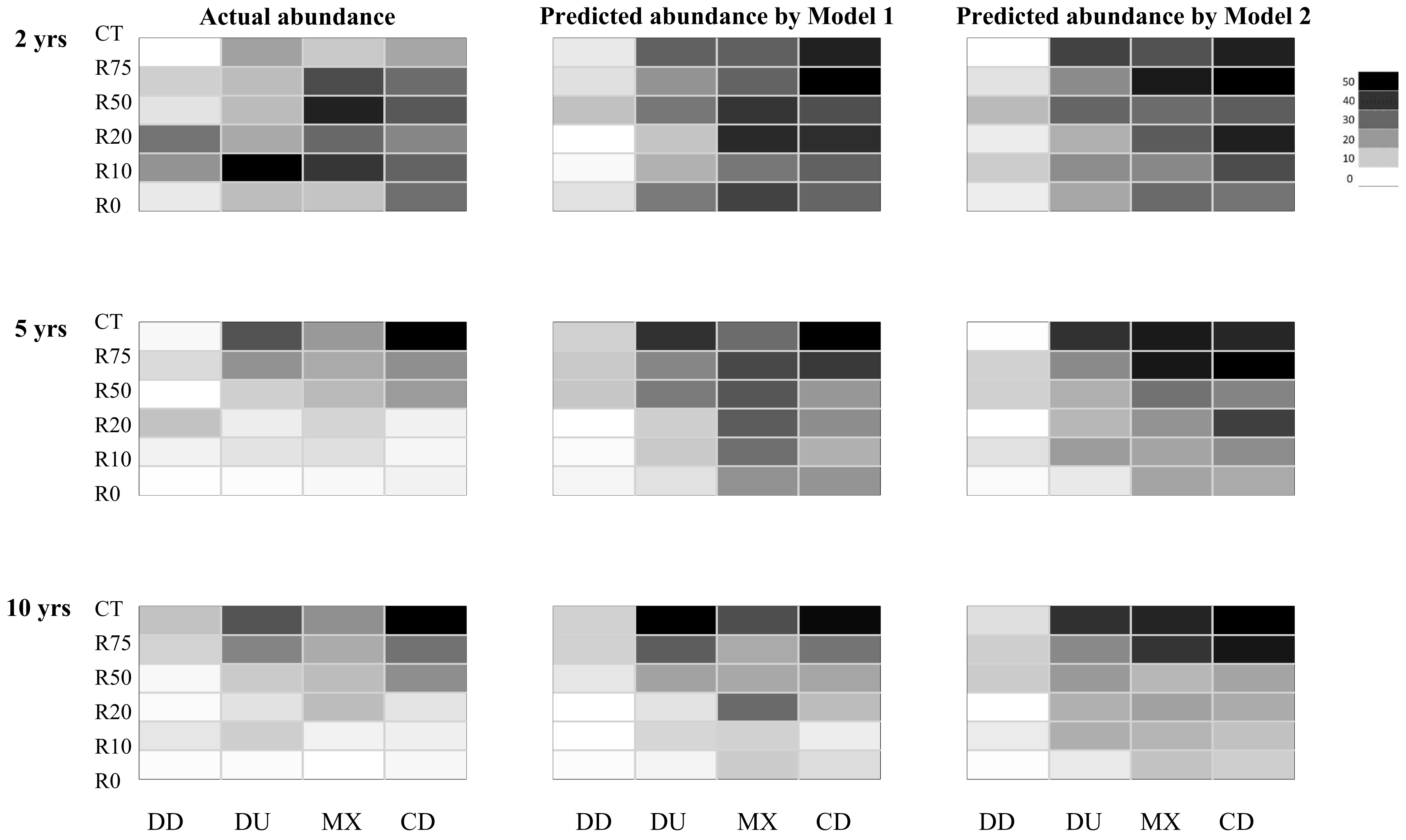
(a) Pterostichus adstrictus



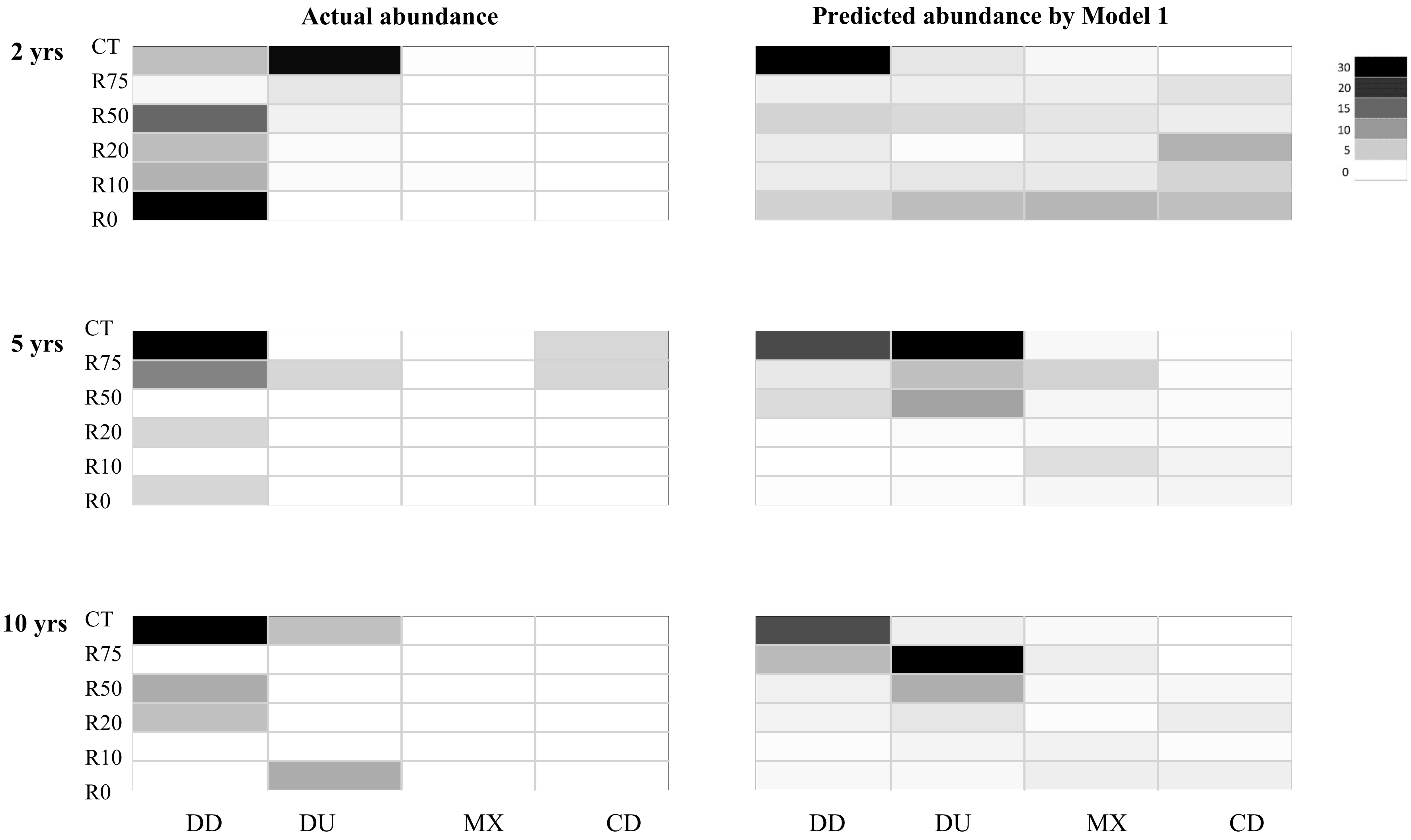
(b) Calathus advena



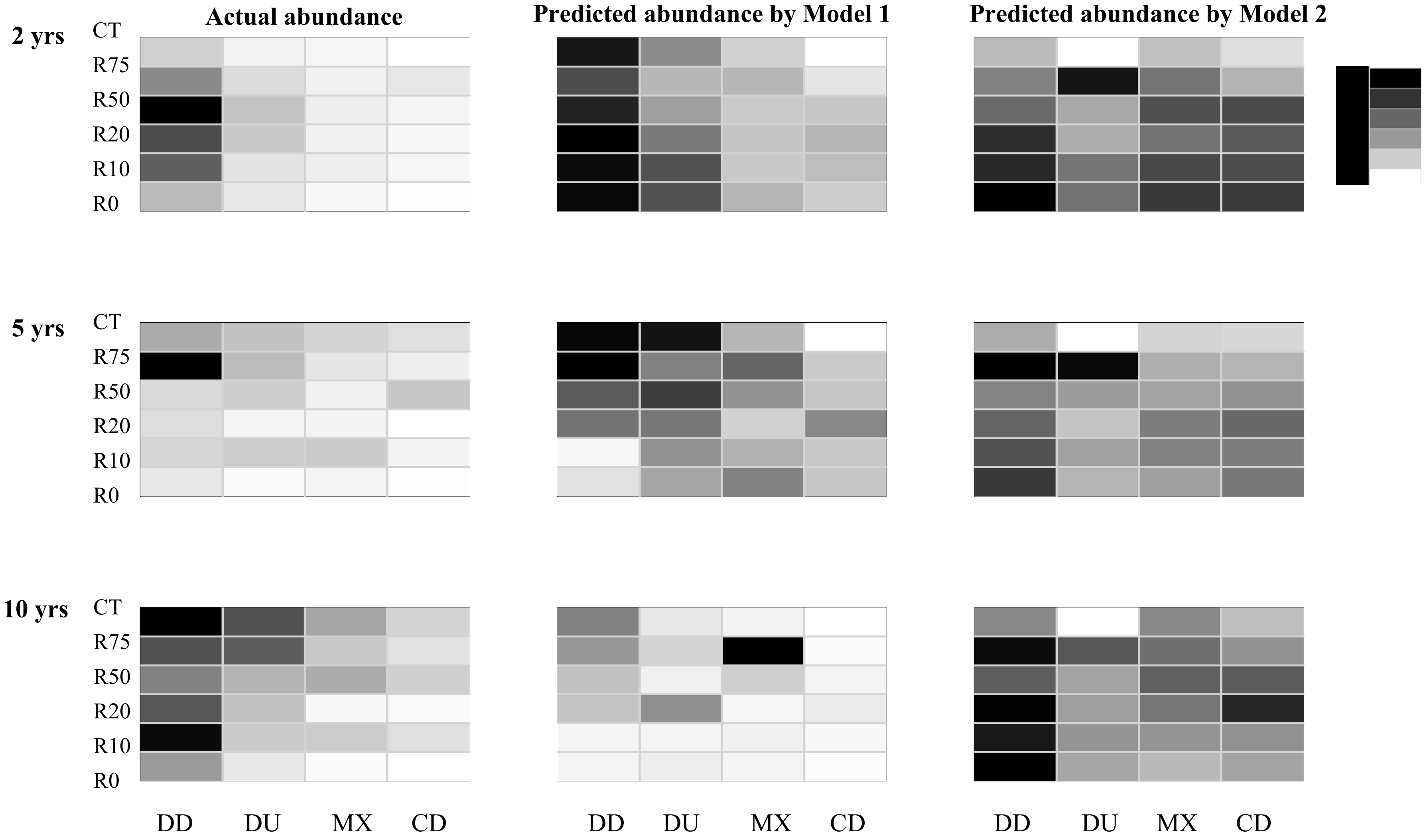
(c) Stereocerus haematopus



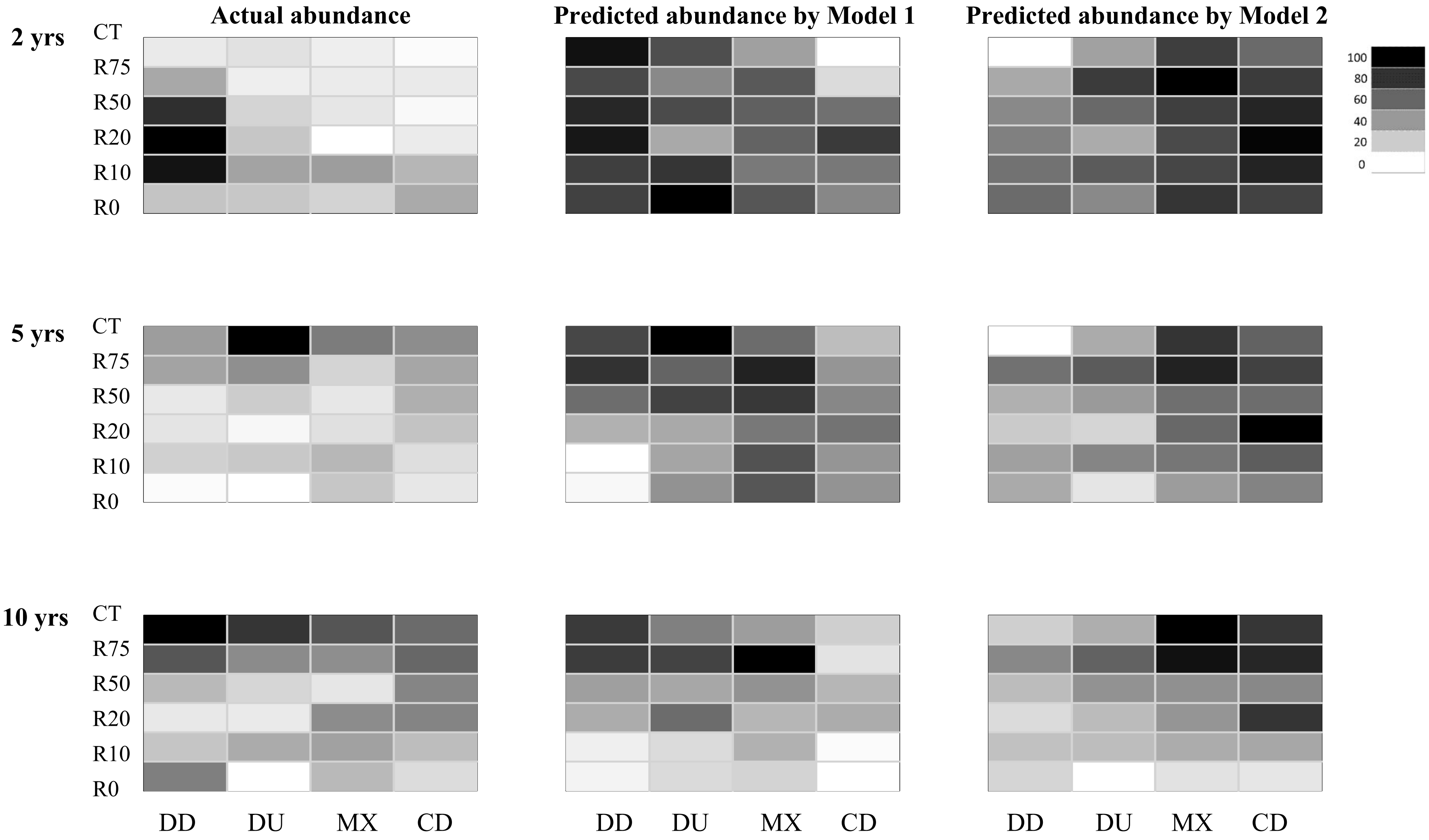
(d) Calosoma frigidum



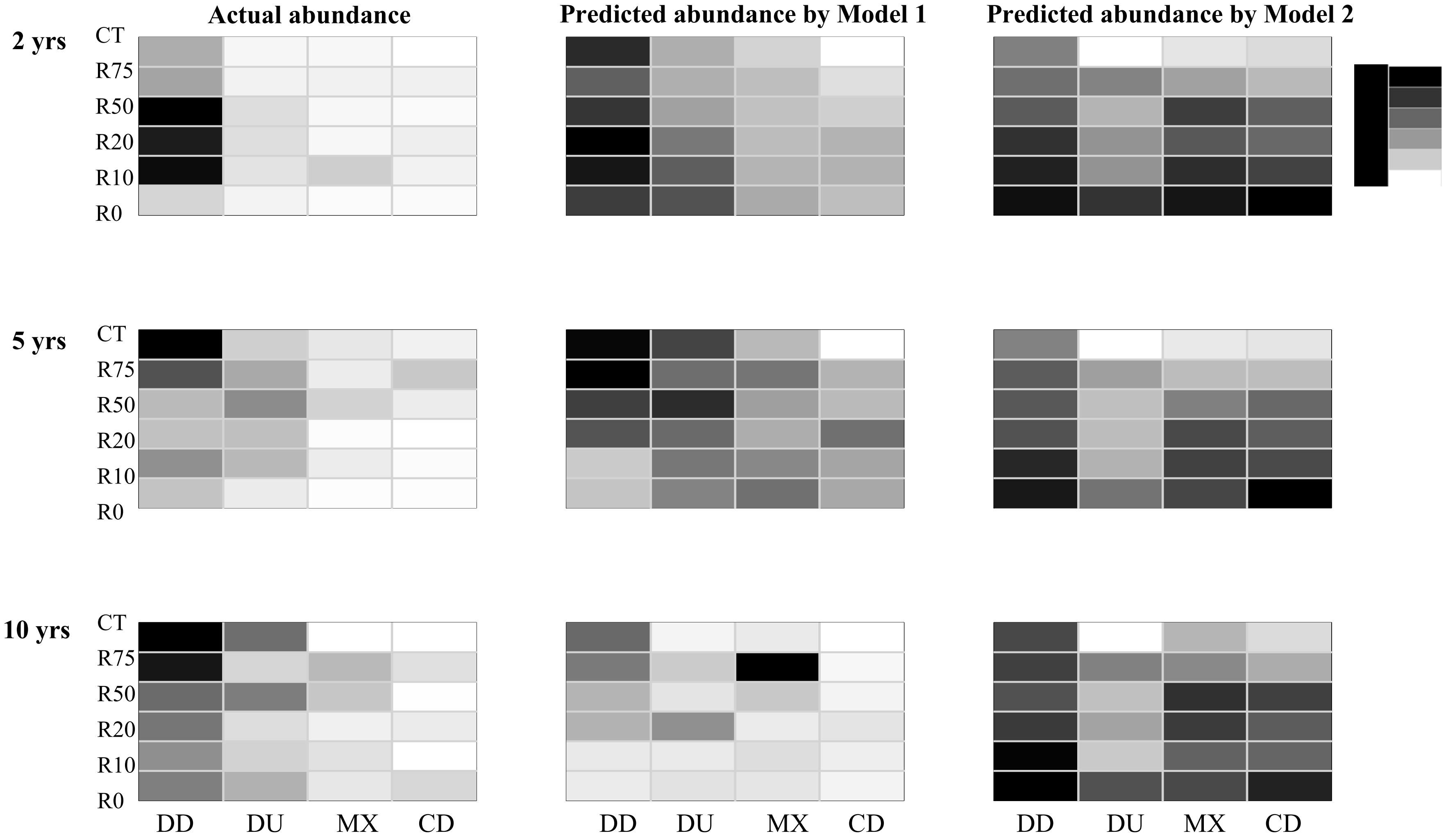
(e) Platynus decentis



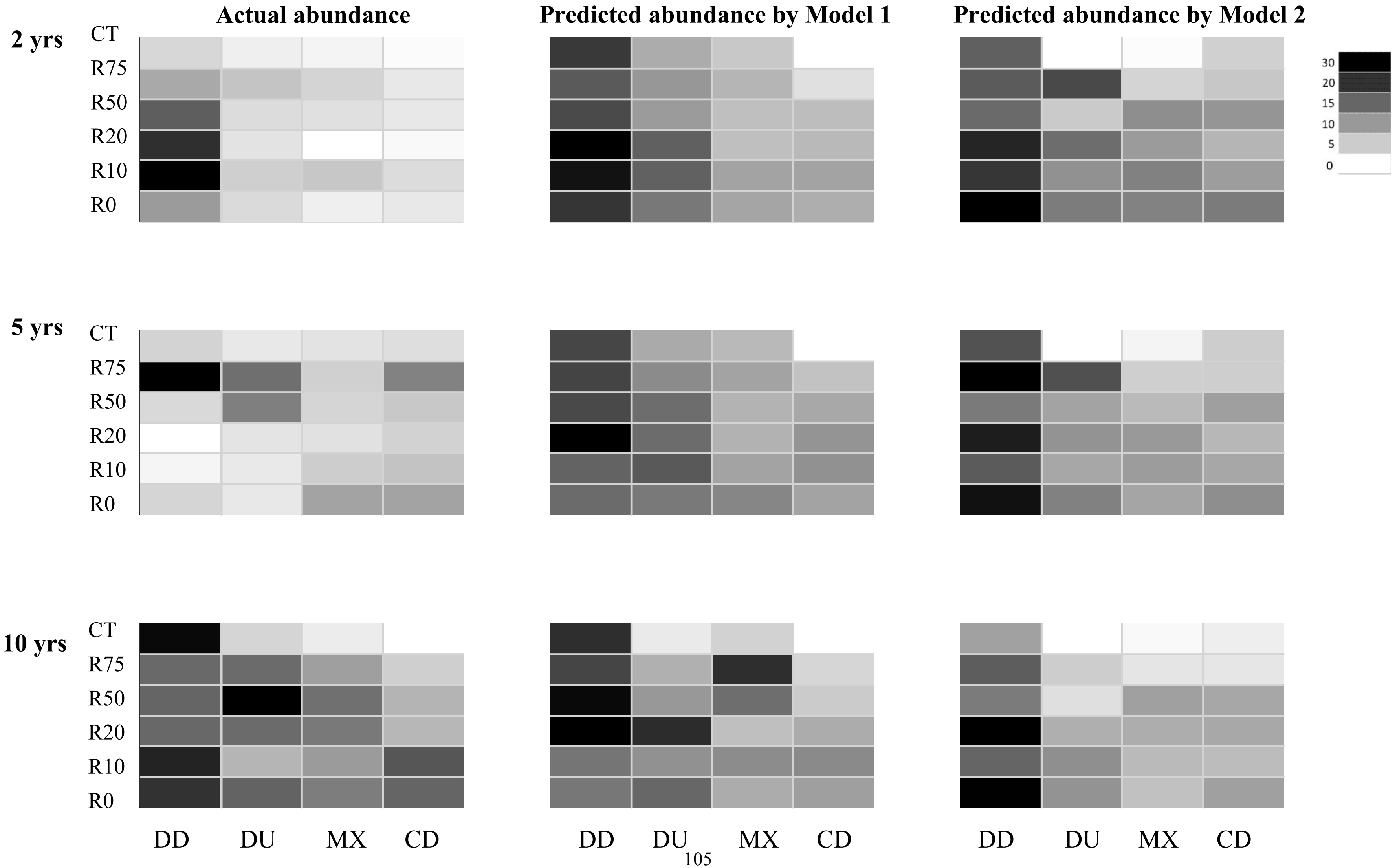
(f) Calathus ingratus



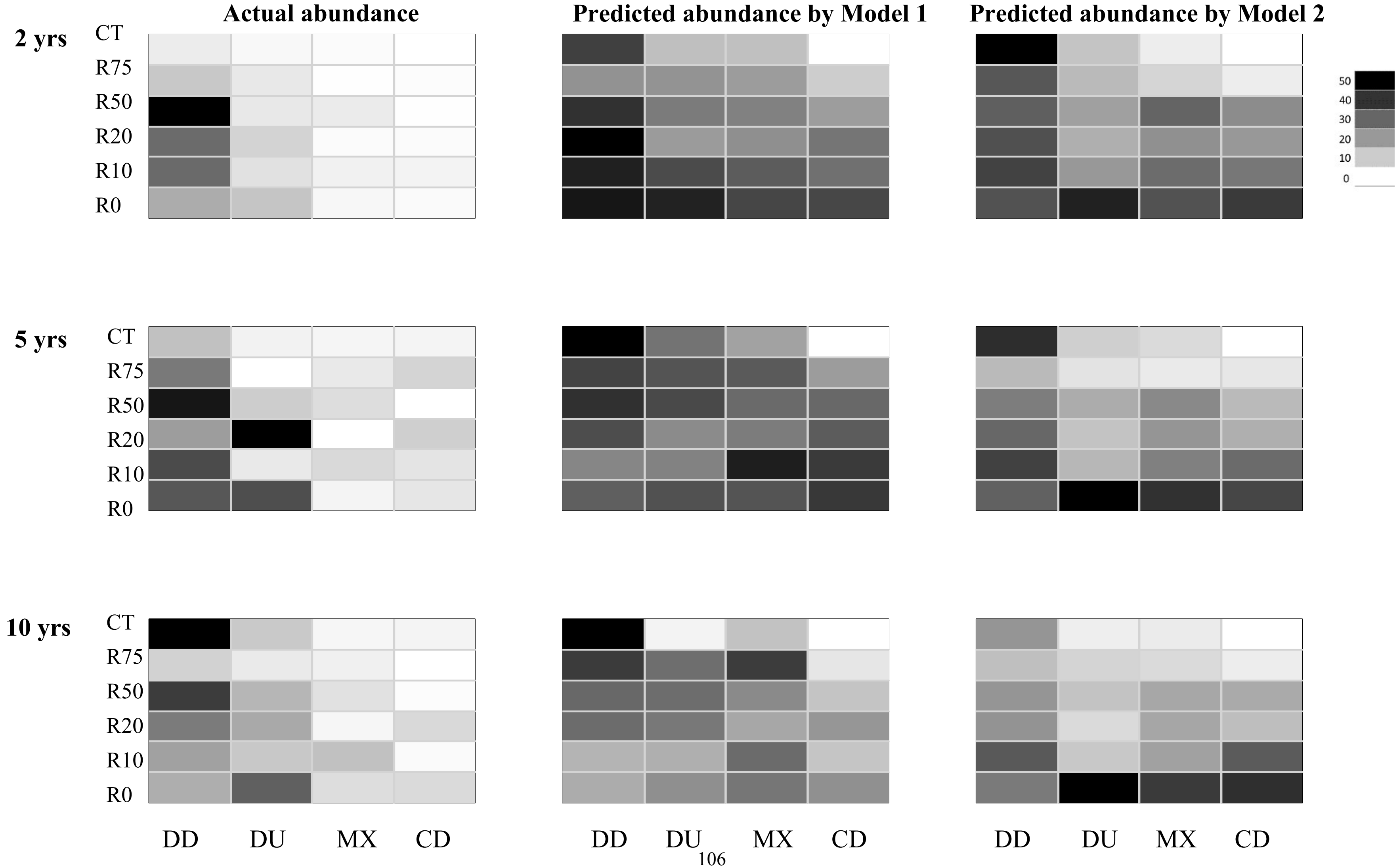
(g) Agonum retractum



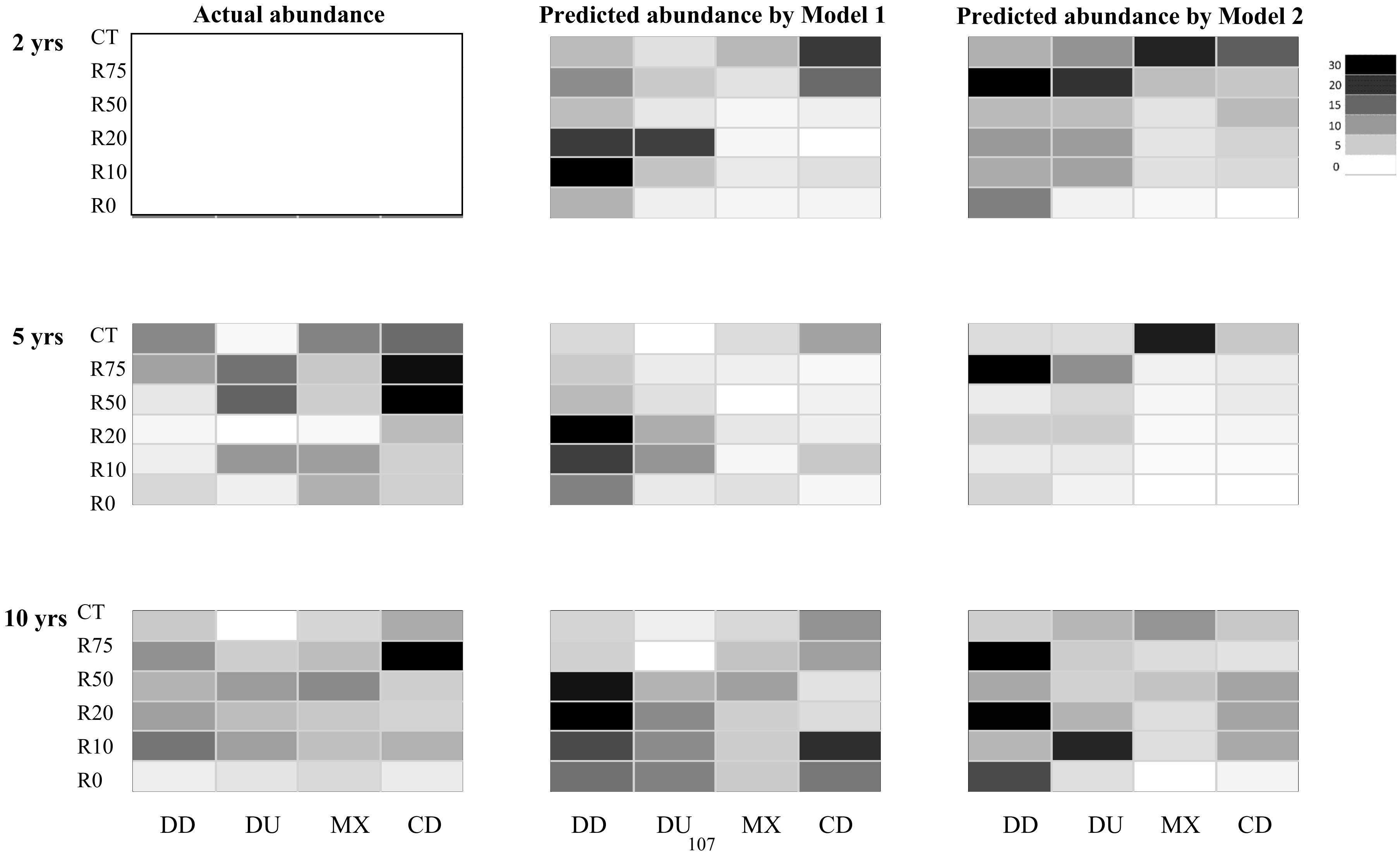
(h) Patrobus foveocollis



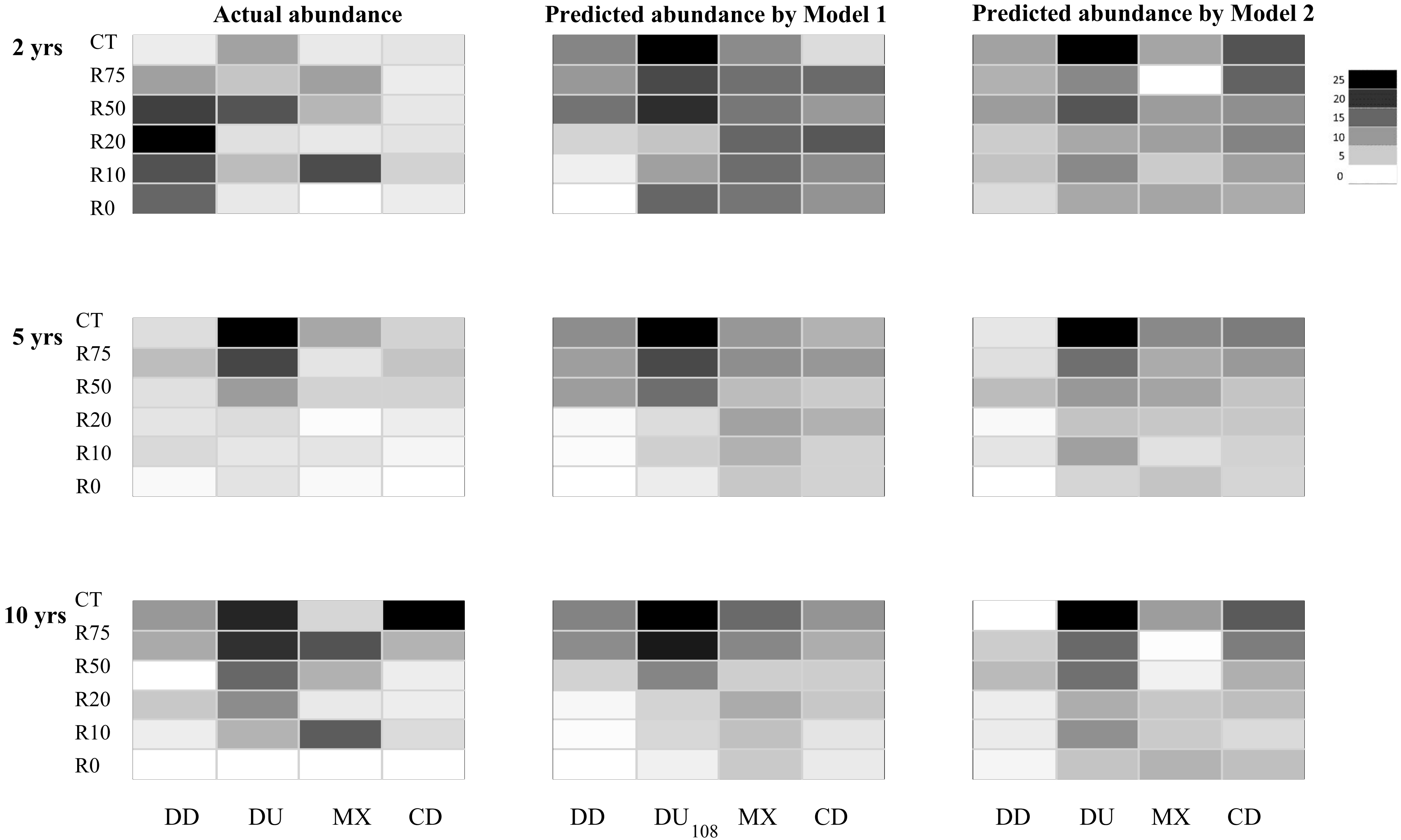
(i) Pterostichus pensylvanicus



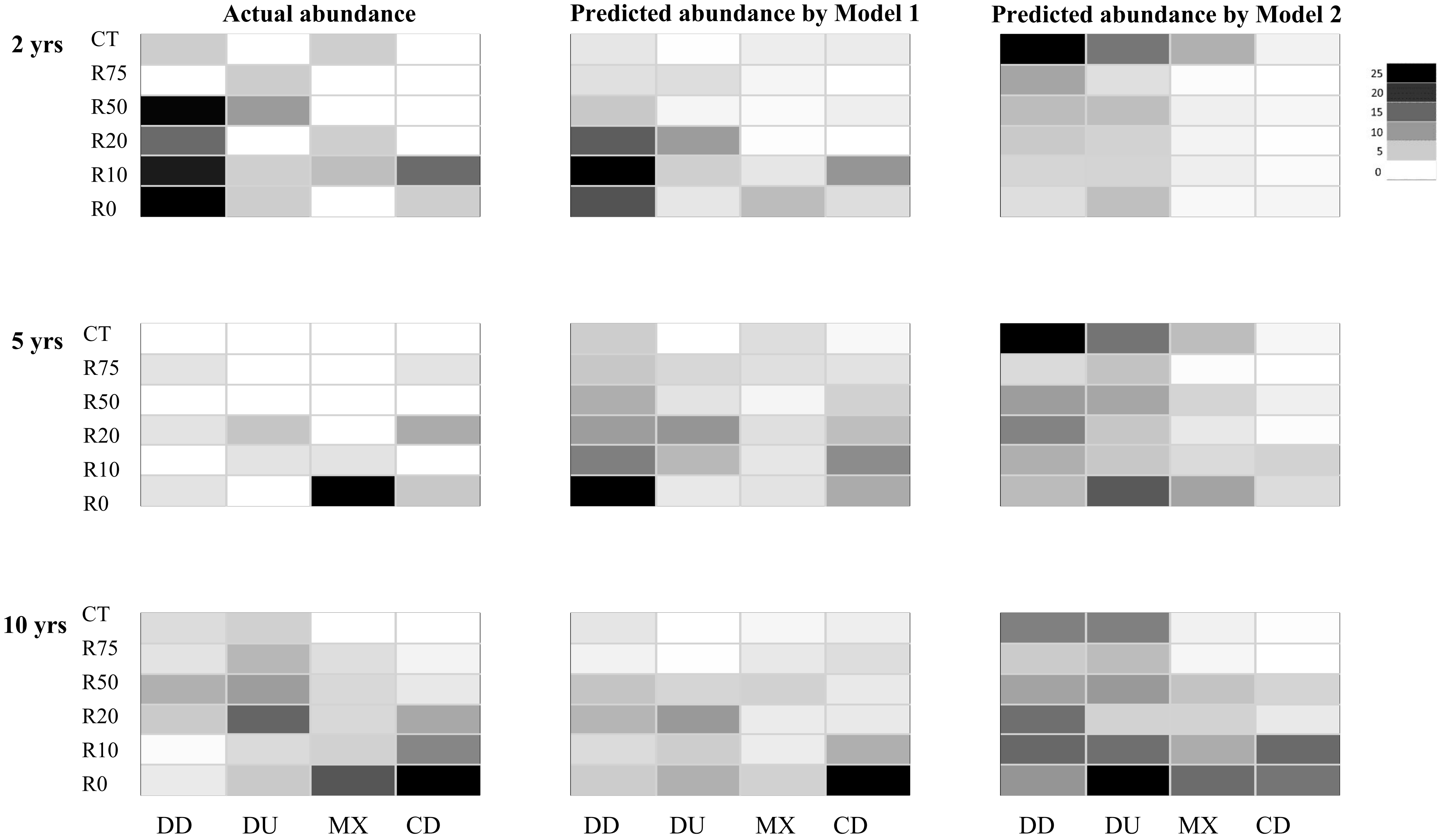
(j) Trechus chalybeus



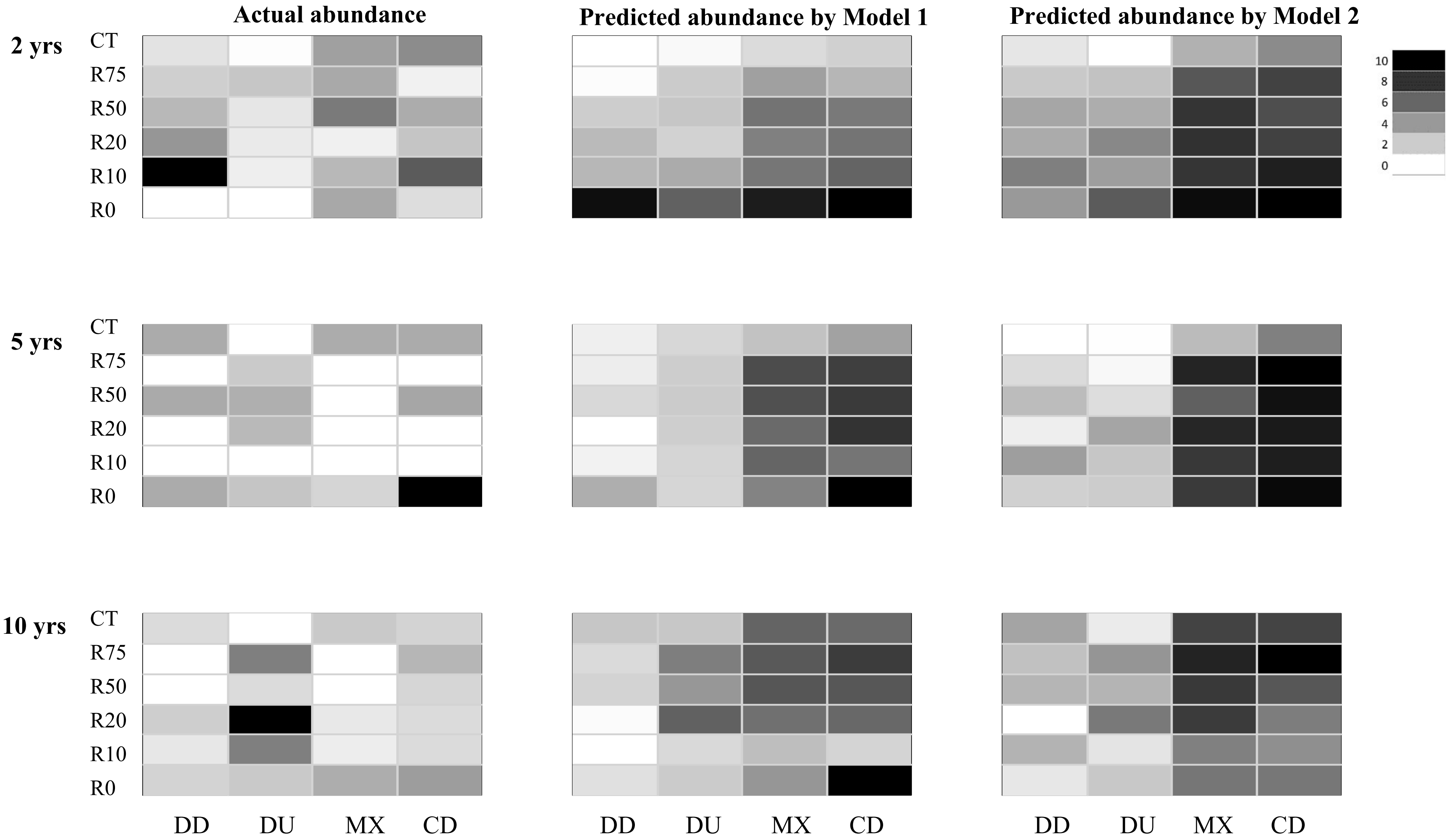
(k) Carabus chamissonis



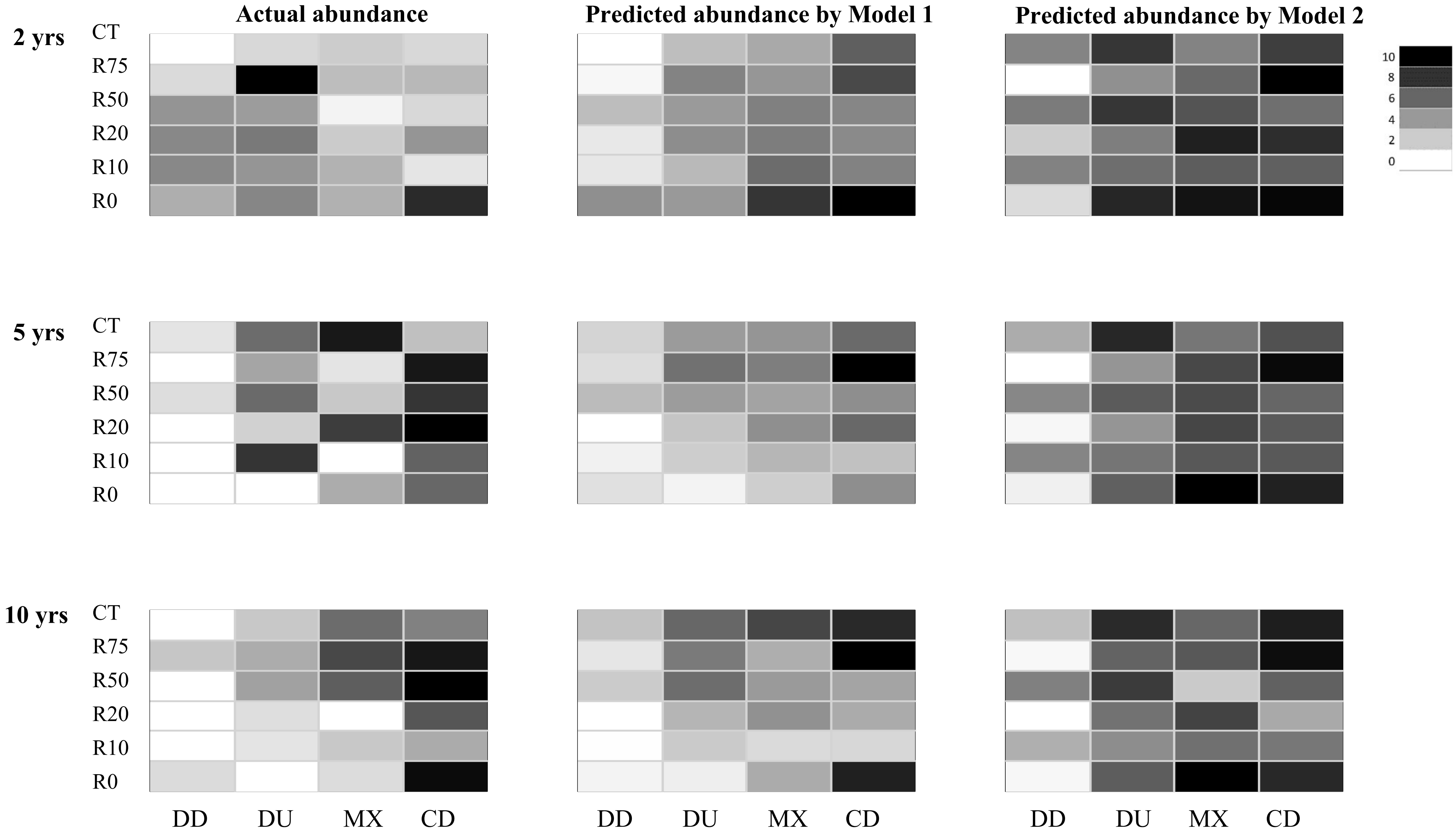
(l) Synuchus impunctatus



(m) Trechus apicalis



(n) Pterostichus punctatissimus



(o) Rare Species

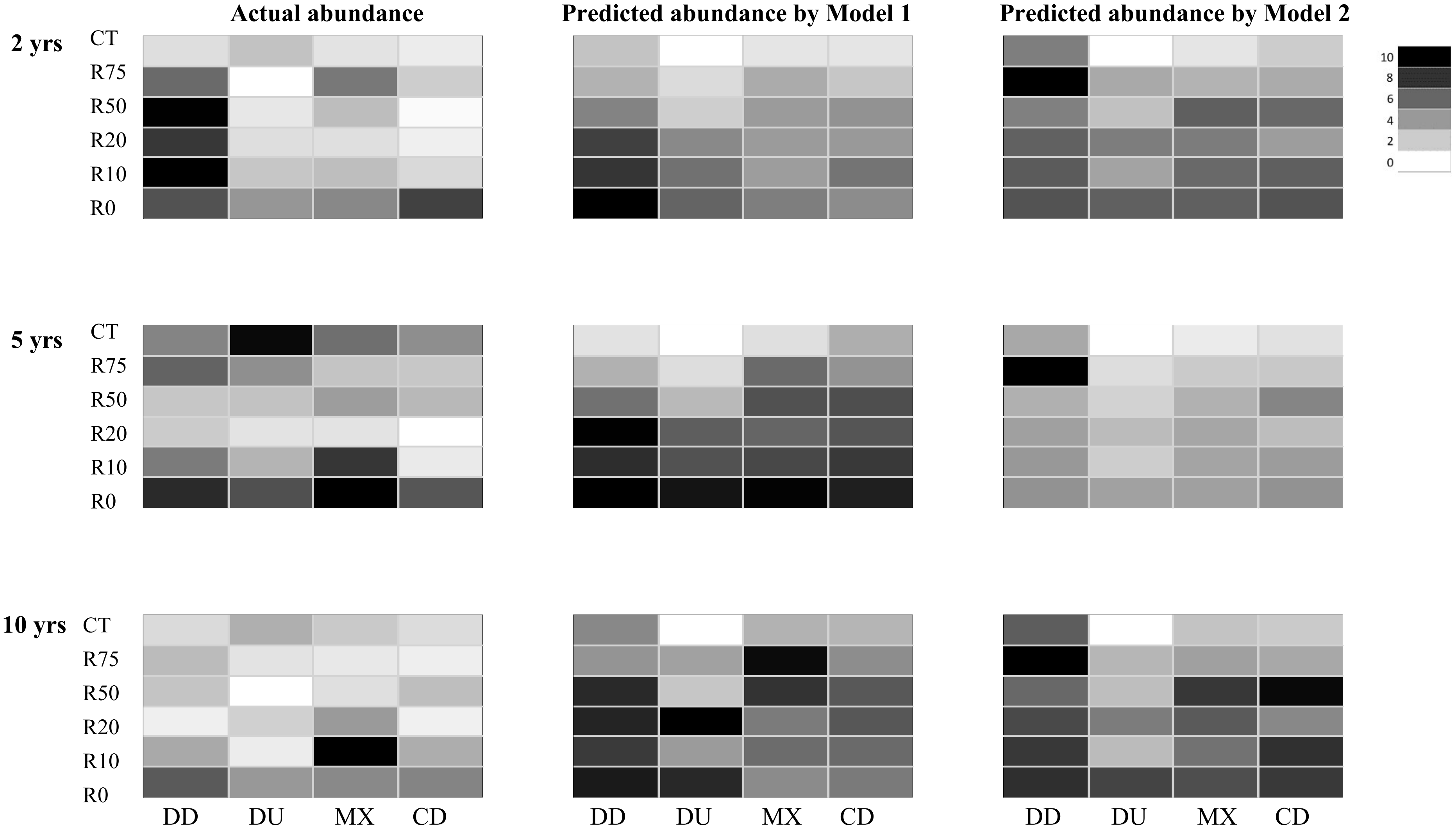


Fig. 4.4. Distribution of (a) *Pterostichus adstrictus,*(b) *Calathus advena,* (c) *Stereocerus haematopus,*(d) *Calosoma frigidum,*(e) *Platynus decentis,* (f) *Calathus ingratus,* (g) *Agonum retractum,* (h) *Patrobus foveocollis,* (i) *Pterostichus pensylvanicus*, (j) *Trechus chalybeus,* (k) *Carabus chamissonis,* (l) *Synuchus impunctatus,* (m) *Trechus apicalis,* (n) *Pterostichus punctatissimus,* and (o) Rare species in Deciduous-dominated stands (CD), Deciduous-dominated stands with spruce understory (DU), Mixed stands (MX) and conifer-dominated stands (CD) with increasing retention level (R0, R10, R20, R50, R75 and CT). Darker color means relatively more number of individuals of carabid beetle in each panel, however, absolute number of individuals represented by darkness varies among species, as legends showed in each panel. For example, abundance of *Pterostichus adstrictus* ranges from 0-150 individuals in panel (a) while abundance of *Pterostichus punctatissimus* ranges from 0-10 individuals in panel (n). Legends are associated with all the nine plots in each panel.

Chapter 5

General Discussion

This dissertation is focused on understanding variation of ground beetle assemblages in time and space, in relation to the joint influences of forest cover type and disturbances caused by forest harvest. I explored turnover of ground beetle species on a northern mixedwood landscape in response to variable retention harvest and subsequent natural forest recovery. In addition, I explored how habitat variability is linked to distribution of ground beetle species over a 15 year post-harvest period. My main findings are summarized below and discussed in relation to forest management strategies to improve conservation of biodiversity. Finally, I offer a few suggestions for future work that would expand on what I have achieved.

5.1 Disturbance, succession of forest habitats and biodiversity recovery

Disturbance drives the dynamics in many ecosystems, and variation in disturbance regimes can affect both structure and function of ecosystems and the included communities. The intermediate disturbance hypothesis (IDH) is a leading idea about how disturbances and other environmental fluctuations affect species diversity (Roxburgh et al. 2004, Catford et al. 2012). The IDH posits that diversity of competing species will be maximized at intermediate frequencies or intensities of disturbance because the associated environmental change opens up space for colonizing species that are subsequently eliminated over time by more competitive species (Connell, 1978).

Although retention harvest appears to maintain forest biodiversity better than traditional clear-cutting, our results do not clearly support the application of the IDH to the system studies here because we can identify no general retention threshold that better conserves boreal ground beetle assemblages. In another word, compartments at intermediate disturbance (with 50% retention) do not conserve beetle diversity better than controls because removal of canopy at an intermediate level does not prevent substantial loss of forest-associated species even though it does open up space for open-habitat associated species. Variation in harvest intensity promotes recovery for the ground beetle fauna along different trajectories on post-harvest landscapes, and collectively this variation contributes to conservation of assemblages on a landscape scale. Few other empirical studies have actually demonstrated the predicted peak in diversity at intermediate disturbance levels. Mackey and Currie (2001), for example, concluded that less than 20% of published studies that they reviewed support the IDH, and this failure of the IDH was also identified by Hughes (2007).

Ground beetle assemblages at EMEND showed clear recovery toward the pre-harvest condition, a target established by data from un-harvested control compartments, 15 years after harvest, instead of continuing to diverge from it. However, I have shown in the dissertation that the extent of their recovery after 15 years differed across forest cover types. Assemblages in stands that were deciduous-dominated or deciduous-dominated with spruce understories before harvest converged strongly 15 years post-harvest toward the pre-harvest condition of stands with deciduous canopies. However, by that time beetle assemblages in stands characterized as coniferous-dominated or as having mixed canopies before harvest, had also became more similar to those originally with deciduous-dominated canopies, and species strongly associated with coniferous forest were gone or significantly reduced in number.

This result emphasizes the strong effects of forest succession on habitats used by animals like ground beetle. Harvested stands of boreal mixed wood forest generally regenerate through a deciduous phase, regardless of pre-harvest cover type. Therefore, following harvest of mixed and conifer stands the regenerating forest becomes similar to that of originally deciduous stands through a strong pulse of deciduous trees regeneration, in turn, providing habitat highly suitable for ground beetle species associated with deciduous forest.

Overall, a spatially variable mix of harvest intensities (variable retention), sensitive to pre-harvest conditions and mindful of the habitat dependencies of particular species, seems to offer a fruitful approach to conserving biodiversity in managed forest.

5.2 Disturbance, species turnover and conservation of biodiversity

Most conservation studies focus on how management practices affect α-diversity, and little attention is paid to β-diversity. This oversight is serious because β-diversity associated with habitat variation across the mixedwood is a significant part of boreal diversity. Anthropogenic disturbance such as forest harvesting can impact biodiversity and lead to large species turnover across habitat, even at relatively small scales. β-diversity reflecting faunal differences between harvested stands and uncut controls also reflect the influence of harvest intensity on the extent of faunal recovery toward the un-harvested condition. In addition, β-diversity can change as a result of local gains and losses of species in response to harvesting. Thus, determining which species are key drivers of changes in β-diversity is essential for understanding, evaluating and managing conservation efforts on landscapes managed for forestry.

In this study, β-diversity arises mainly from the combination of forest harvest and the changes that reflect successional sequence. Compartments harvested to retention prescriptions at EMEND were associated with lower species turnover than those subjected to traditional clear-cuts. Responses of the 'key species' that I designated accounted for most of the observed faunal turnover, and those changes were mediated by cover type. In particular, species turnover in stands harvested with mixed and conifer canopies were mainly driven by the loss of forest specialists.

β-diversity on landscapes is most threatened by the extent of forest harvest, especially in relation to successional sequence as showed in this study. Thus different forestry approach should be applied in stands with different forest cover type, to ensure that post-harvest landscape are structured to best maintain the pre-harvest biota. Because harvesting homogenized the biota toward assemblages characteristic of early successional phases regardless of the pre-harvest cover types (Gradowski et al. 2010, Pinzon et al. 2012), low retention levels in late successional stands were not only insufficient to conserve mature conifer associated species, but also promoted development of carabid assemblages dominated by species associated with deciduous forest.

In summary, it seems apparent from my results that β-diversity could be very useful for assessing responses of species to disturbance, and that determination of key species could contribute to conservation efforts. Understanding which species contribute to turnover would allow us to prioritize efforts to retain α-diversity in harvested compartments. Perhaps we should manage to conserve more habitat required by key species, i.e., by leaving more green tree retention in coniferous stands. This should contribute to more rapid and effective restoration of biodiversity in those stands, and thus, to conserving a more natural pre-harvest condition across managed landscapes in a region (γ-diversity).

5.3 Disturbance, habitat variability and species spatio-temporal distribution

Evolution of species niches in the context of habitat differentiation permits many species to exist together in communities, even as partial competitors, with distributions broadly and continuously overlapping to form many intergrading communities on landscapes (Whittaker, 1965). Because of niche differentiation, each species occupies habitat in different ways, and thus habitat variability must be critical to explaining species diversity. In this dissertation, I show that variability in forest habitats, shaped by both cover-type and harvest intensity influences distribution of carabid species.

Habitat variability strongly influences ground beetle distributions through species-specific matches to habitat characteristics that are at least partially reflected by characteristics of the vegetation. Such associations are complex, however, as the distribution of species was not generally well explained by any of the vegetation variables alone. Nonetheless, distribution of specific beetle species, especially some of the key species that drove turnover, was more tightly linked to percent cover of different tree species than to variables associated with understory vegetation.

Intensity of harvest strongly affected ground beetle abundance in each forest cover type through 10 years post-harvest. Relative abundance of the carabid species in stands with higher retention was closer to that in controls than to low retention stands and clear-cuts. And thus, retention harvest apparently maintains forest biodiversity, much better than does traditional clear-cutting, at least up to 10 years post-harvest.

In the big picture, high retention levels better accommodate species-specific habitat requirements for the biota, and thus may lifeboat mature forests specialists in situ well into post-harvest recovery. Of course, these residual populations provide a seed for efficient re-colonization of stands as the included habitats become more similar to those of un-harvested forest. In this way, retention harvest may serve as a practical way to minimize temporal variation caused by harvesting, and also to speed recovery of biodiversity towards its own range of natural variation.

5.4 Suggestions for forest management and future work

The range of forest cover types in a potential harvest area should be carefully considered before retention harvest is applied. In the boreal mixedwood, a relevant consideration flowing from work in this thesis is that higher retention level will more effectively conserve species associated with mature forest, but that without significant un-harvested reserves, harvest will simply promote recovery of assemblages to the pre-harvest condition of deciduous stands. Thus, if regional conservation of the natural fauna is important, extra attention must be given to conifer stands. More aggregated reserves and higher retention harvest strategies should be applied in coniferous forest to accelerate recovery of species specializing in late-successional coniferous forest.

Given the clear associations between particular beetle and tree species suggested by Bergeron et al. ((2011, 2012) and corroborated here, pre-harvest forest inventories should be well developed and documented especially for uncommon tree species because their presence seems to be related to the distribution of also uncommon beetle species.

Although the present 15 year study is of longer duration that most other published work about forest invertebrates from single locations, further long-term studies are required to rigorously evaluate the lasting effects of retention harvesting on recovery of biodiversity in the boreal mixedwood forest. Studies like EMEND are especially well suited to better understand relationships between forest succession and changes in other biotic elements. Temporal changes in forest biodiversity at single sites after disturbance reflect some combination of inter-annul variation based on prevailing weather and forest succession as shown in this study. However, the extent to which inter-annual variation obscures efforts to track successional processes remains unclear. Therefore, it would be very useful to partition variation of beetle assemblages into those driven by annual temporal variation and those affected by harvesting to track recovery of this fauna across managed landscape. Given that EMEND is projected run for 80-100 years, the progressive signals of climate change also will likely influence recovery of beetle assemblages, along with the year-to-year variation in weather. Thus, unraveling and understanding the variation caused by climate change will present a problem in for those interested in conservation. Will biodiversity in low-retention stands be more vulnerable compared to that in high-retention stands and un-harvested forest as effects of climate change become more pronounced? Will the apparent stability of species in the control compartments lessen over time reflecting the changing climate? Answering such questions will require that we partition, analyze and quantify successional change and climate change.

We know that β-diversity also arises from dispersal ability and spatial effects in addition to habitat variation as explored in this study. Blanchet et al. (2012) explored how a spatially sensitive hierarchy of effects can account for variation in ground dwelling beetle assemblages. As these hierarchies change, changes in β-diversity should also affect interspecific variation in dispersal ability, and of course, understanding such relationships will provide better ability to predict how forest faunas will change over time. Some relevant questions include: How do forest specialist species that escape post-harvest conditions affect β-diversity right after harvest? How mature forest faunas recovery through succession when their dispersal ability become stronger with the close of canopy?

Finally, multi-taxa studies will offer more comprehensive idea about how biodiversity, as such, recovers after harvest, the topic of largest concern. Various taxa data have been well studied at EMEND including songbirds, spiders, ground beetles, regenerated trees, shrubs, etc., which support solid multi-taxa analyses over a 15 year period. Bergeron et al. (2017) examined how ecosystem memory of wildfires affects resilience of boreal mixedwood biodiversity after retention harvest by using data about seven different taxa at EMEND, and found that influence of ecosystem memory varies among biotic assemblages. Pinzon et al. (2016) studied ten-year responses of dwelling spiders to retention harvest at EMEND. It will be very interesting to apply same analysis in this thesis to different taxa to explore how other fauna diversity recovers after harvest? Will they follow the same recovery pattern or not? And, of course, 15 years, as presently encompassed by the EMEND data, represents only about 16.7% of a projected boreal forest rotation of 90 year. Therefore, although this dissertation must now be brought to an end, it finished only a single graduate program, but opens a door to interesting but undeveloped possibilities for research that may be applied to improve the sustainability of forest management in the boreal mixedwood.

References

Anderson M. J., et al. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecology Letters*, 14: 19–28.

Baker, S.C., Spies, T.A., Wardlaw, T.J., Balmer, J., Franklin, J.F. & Jordan, G.J. 2013. The harvested side of edges: effect of retained forests on the re-establishment of biodiversity in adjacent harvested areas. *Forest Ecology and Management*, 302, 107–121.

Baker, S.C., et al. 2016. A cross-continental comparisons of plant and beetle responses to retention of forest patches during timber harvest. *Ecological Applications*, 26 (8): 2495-2506.

Bell, Susan S.; McCoy, Earl D.; and Mushinsky, H R. 1991. Habitat Structure: The Physical Arrangement of Objects in Space. *Integrative Biology Faculty and Staff Publications*. 217.

Bergeron, J.A.C. et al. 2011 Landscape patterns of species-level associations between ground-beetles (Coleoptera: Carabidae) and overstory trees in boreal forests of western Canada (Coleoptera: Carabidae).*Zookeys* 147: 577-600.

Bergeron, J.A.C, FG Blanchet, JR Spence & WJA Volney. 2012. Ecosystem classification and inventory maps as surrogates for ground beetle assemblages in boreal forest. *Journal of Plant Ecology* 5: 97-108.

Bergeron, J.A.C, JR Spence. WJA Volney, J Pinzon & DJ Hartley. 2013. Effect of habitat type and pitfall trap installation on captures of eipgaeic arthropod assemblages in the boreal forest. *The Canadian Entomologist* 145: 547-565.

Bergeron, J.A.C., J. Pinzon, S. Odsen, S. Bartels, E. Macdonald & J. R. Spence. 2017. Ecosystem memory of wildfires affects resilience of boreal mixedwood biodiversity after retention harvest. *Oikos* 126: 1738-1747.

Blanchet, F.G., J. A. Colin Bergeron, John R. Spence & Fangliang He. 2013. Landscape effects of disturbance, habitat heterogeneity and spatial autocorrelation for a ground beetle (Carabidae) assemblage in mature boreal forest. *Ecography* 36: 636-647.

Bousquet, Y., and A. Larochelle. 1993. Catalogue of the Geadephaga (Coleoptera: Trachypachidae, Rhysodidae, Carabidae including Cicindelini) of America North of Mexico. *Memoirs of the Entomological Society of Canada*, No. 167; 397 pp.

Buddle, C. M., D. W. Langor, G. R. Pohl, and J. R. Spence. 2006. Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. Biological Conservation 128:346 – 357.Devictor, V et al. 2008 Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, 117: 507-514.

Cameron, E.A. & Reeves, R.M. (1990). Carabidae (Coleoptera) associated with gypsy moth, Lymantria dispar (L.) (Lepidoptera: Lymantriidae), populations subjected to *Bacillus thuringiensis* Berliner treatments in Pennsylvania. Canadian Entomologist 122: 123-129.

Catford, J. A., Daehler, C. C., Murphy, H. T., Sheppard, A. W., Hardesty, B. D., Westcott, D. A., ... Hulme, P. E. 2012. The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics*, 14(3), 231-241

Chao, A. and L. Jost. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, 93(12): 2533-2547.

Cleland, Elsa E., Scott L. Collins, Timothy L. Dickson, Emily C. Farrer, Katherine L. Gross, Laureano A. Gherardi, Lauren M. Hallett, et al. 2013. “Sensitivity of Grassland Plant Community Composition to Spatial Vs. Temporal Variation in Precipitation.” *Ecology*, 94 (8): 1687–96.

Collins, Scott L., Katharine N. Suding, Elsa E. Cleland, Michael Batty, Steven C. Pennings, Katherine L. Gross, James B. Grace, Laura Gough, Joe E. Fargione, and Christopher M. Clark. 2008. “Rank Clocks and Plant Community Dynamics.” Article. *Ecology*, 89 (12): 3534–41.

Condit, R., et al. 2002. Beta-diversity in tropical forest trees. *Science* 295:666 – 669.

Connell, J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310.

Diamond, J. M. 1969. “Avifaunal Equilibria and Species Turnover Rates on the Channel Islands of California.” *Proceedings of the National Academy of Sciences* 64: 57–63.

Franklin, J. F., D. R. Berg, D. A. Thornburgh, and J. C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. Pages 111–139 *in* K. A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, D.C., USA.

Gandhi, KJK, JR Spence, DW Langor & LE Morgantini. 2001. Fire-residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). *Biological Conservation* 102: 131-141.

Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* 405 (6783): 220-227.

Gradowski, T., V. J. Lieffers, S. M. Landhasser, D. Sidders, J. Volney, and J. R. Spence. 2010. Regeneration of *Populus* nine years after variable retention harvest in boreal mixedwood forests. *Forest Ecology and Management*, 259:383–389.

Guisan, A., and N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135(2–3):147-186.

Gustafsson, L., Jari Kouki & Anne Sverdrup-Thygeson. 2010 Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences, Scandinavian Journal of Forest Research, 25:4, 295-308.

Gustafsson, L., et al. 2012. Retention forestry to maintain multifunctional forests: a world perspective. *BioScience*, 62:633.

Hallett, L., et al. 2016. Codyn: community dynamics metrics. R Package.

Harrison, S., S. J. Ross, and J. H. Lawton. 1992. Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology* 61:151 – 158.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *American Naturalist* 163:192 – 211.

Holt, R.D. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proc. Natl. Acad. Sci*. U. S. A. 106(Supplement 2):19659-19665.

Hsieh, T. C., and A. Chao. 2016. iNEXT: an R package for interpolation and extrapolation in measuring species diversity. R Package.

Hughes, A.R. et al. (2007) Reciprocal relationships and potential feedbacks between diversity and disturbance. *Ecol. Lett* 10, 849–864.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.

Hyvarinen, E., J. Kouki, and P. Martikainen. 2006. Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forests. *Conservation Biology*, 20:1710-1719.

Jacobs, J., T. T. Work, and J. R. Spence. 2008. Influences of succession and harvest intensity on ground beetle (Coleoptera:Carabidae) populations in the boreal mixedwood forests of Alberta, Canada: species matter. In: Back to the Roots and Back to the Future? Towards a new synthesis between taxonomic, ecological and biogeographical approaches in carabidology: Proceedings of the XIII European Carabidologists Meeting, Blagoevrgard, August 20-24, 2007, eds. L. Penev, T. Erwin, and T. Assmann. Pensoft, Sophia-Moscow.

Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology*, 88, 2427–2439.

Keenan, R. J., and J. P. Kimmins. 1993. The ecological effects of clear-cutting. *Environmental Reviews 1*: 121-144.

Koleff, P., J. J. Lennon, and K. J. Gaston. 2003. Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography* 12:483 – 498.

Koivula, M., P. Punttila, Y. Haila, and J. Niemelä. 1999. Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography* 22(4):424-435.

Koivula, M. 2002. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). *Forest Ecology and Management*, 167, 103-121.

Koivula, M. J. 2011. Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. *ZooKeys* 100: 287-317.

Legendre, P., and L. Legendre. 2012. Numerical ecology. Third English edition. Elsevier, Amsterdam, the Netherlands.

Lengyel S, Déri E, Magura T (2016) Species Richness Responses to Structural or Compositional Habitat Diversity between and within Grassland Patches: A Multi-Taxon Approach. *PLoS ONE* 11(2): e0149662.

Lennon, J. J., P. Koleff, J. J. D. Greenwood, and K. J. Gaston. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70:966 – 979.

Lindenmayer, D.B et al. 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology*,14: 941-950.

Lindenmayer, D. B., and Franklin J. F.. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington, D.C., USA.

Lindenmayer, D. B., J. F. Franklin, and J. Fischer. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation* 131(3): 433-445.

Lindenmayer, D. B., et al. 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters*, 5:421–431.

Lindroth, C. H. 1961. The ground beetles (Carabidae, excl. Cincindelinae) of Canada and Alaska Part 2. Opuscula Entomologica Supplentum 20:1–200.

Lindroth, C. H. 1963. The ground beetles (Carabidae, excl. Cincindelinae) of Canada and Alaska Part 3. Opuscula Entomologica Supplentum 24:201–408.

Lindroth, C. H. 1966. The ground beetles (Carabidae, excl. Cincindelinae) of Canada and Alaska Part 4. Opuscula Entomologica Supplentum 29:409–648.

Lindroth, C. H. 1968. The ground beetles (Carabidae, excl. Cincindelinae) of Canada and Alaska Part 5. Opuscula Entomologica Supplentum 33:649–944.

Lindroth, C. H. 1969a. The ground beetles (Carabidae, excl. Cincindelinae) of Canada and Alaska Part 1. Opuscula Entomologica Supplentum 35:I–XLVII.

Lindroth, C. H. 1969b. The ground beetles (Carabidae, excl. Cincindelinae) of Canada and Alaska Part 6. Opuscula Entomologica Supplentum 34:945–1192.

MacArthur, R.H. &MacArthur, J.W. 1961. On bird species diversity. *Ecology*, 42: 594-598.

MacArthur, Robert H., and Edward O. Wilson. 1963. “An Equilibrium Theory of Insular Zoogeography.” *Evolution*. 17 (4). Society for the Study of Evolution: 373–87.

Mackey, R.L. and Currie, D.J. (2001) The diversity–disturbance relationship: is it generally strong and peaked? *Ecology* 82, 3479–3492.

McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. P. 105-142 in Frontiers in Econometrics, Zarembka, P. (ed.). Academic Press, New York.

McClain, CR. & Barry, JP. 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* 91: 964-976.

Moreno-Rueda, G. & Pizzaro, M. 2009. Relative influences of habitat heterogeneity, climate, human disturbance, and spatial structure on vertebrate species richness in Spain. *Ecological Research* 24, 335-344.

Muotka, T. & Virtanen, R. 1995. The stream as a habitat templet for bryophytes-species distributions along gradients in disturbance and substratum heterogeneity. *Freshwater Biology*, 33:141-160.

Nash, Kirsty L.; Allen, Craig R.; Barichievy, Chris; Nyström, Magnus; and Graham, Nicholas A.J., 2014. Habitat structure and body size distributions: cross-ecosystem comparison for taxa with determinate and indeterminate growth. *Nebraska Cooperative Fish &Wildlife Research Unit -- Staff Publications*. 167.

Niemelä J., Spence J.R. and Spence D.H. 1992. Habitat associated and seasonal activity of ground-beetle (Coleoptera, Carabidae) in central alberta. *Can.Ent.* 124: 521-540.

Niemelä, J., Y. Haila, E. Halme, T. Pajunen, and P. Punttila. 1992. Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish Taiga. *Journal of Biogeography* 19(2):173-181.

Niemelä, J., D.W. Langor & J.R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conservation Biology* 7: 551-561.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, B. O’ Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. vegan: Community Ecology Package. R Package.

Rowe, J. S. 1972. Forest regions of Canada. Canadian Forestry Service Publication No. 1300, Publishing Division, Information Canada, Ottawa, Onrario. Canada.

Roxburgh, S. H., Shea, K. and Wilson, J. B. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology*, 85: 359–371.

Parisien, M.A. & Moritz, M.A. (2009) Envionmental controls on the distribution of wildfire at multiple spatial scales. *Ecol. Monogr*. 79: 127-154.

Perhans, K., et al. 2009. Retention patches as potential refugia for bryophytes and lichens in managed forest landscapes. *Biological Conservations*, 142, 1125-1133.

Peterson, A.T. 2001. Predicting species' geographic distributions based on ecological niche modeling. *The Condor* 103(3):599-605.

Pickett STA, White PS. 1985. Natural disturbance and patch dynamics: an introduction. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, pp 3-13.

Pinzon, J., J. R. Spence, and D. W. Langor. 2012. Responses of ground-dwelling spiders (Araneae) to variable retention harvesting practices in the boreal forest. *Forest Ecology and Management* 266:42-53.

Pinzon, J., J. R. Spence, D. W. Langor and D. P. Shorthouse. 2016. Ten-year reponses of dwelling spiders to retention harvest in the boreal forest. *Ecological applications*, 26 (8): 2581-2599.

Qian, H., R. E. Ricklefs, and P. S. White. 2005. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters* 8:15-22.

Rainio, J. & Niemela, J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biological Conservation* 12: 487-506.

Roberts, M. W. et al. 2016. Long-term impacts of variable retention harvesting on ground-layer plant communities in Pinus resinosa forests. *Journal of Applied Ecology*, 53, 1106-1116.

Soininen, J., Lennon, J.J. and Hillebrand H. 2007. A multivariate analysis of beta diversity across organisms and environments. *Ecology*, 88(11), 2830-2838.

Spence, J. R., and J. K. Niemela. 1994. Sampling carabid assemblages

with pitfall traps—the madness and the method. *Canadian Entomologist* 126:881–894.

Spence, JR, DW Langor, J Niemelä, HA Cárcamo & CR Currie. 1996. Northern forestry and carabids: the case for concern about old-growth species. *Annales Zoologici Fennici* 33: 173-184.

Spence, J.R. et al. 1999. The Alberta EMEND project: recipe and cooks' argument.-In: Veeman, T.S. et al. (eds), The Sustainable Forest Management Network Conference- Science and Practice: Sustaining the Boreal Forest, Edmonton, Canada, 14-17 February 1999, pp. 583-590.

Sullivan, T. P., D. S. Sullivan, and P. M. F. Lindgren. 2001. Influence of variable retention harvests on forest ecosystems. I. Diversity of stand structure. *Journal of Applied Ecology*, 38:1221–1233.

Sullivan, T. P., D. S. Sullivan, and P. M. F. Lindgren. 2008. Influence of variable retention harvests on forest ecosystems: plant and mammal responses up to 8 years post-harvest. *Forest Ecology and Management* 254:239-254.

Thomas, J. W., J. F. Franklin, J. Gordon, and K. N. Johnson. 2006. The Northwest forest plan: origins, components, implementation experience, and suggestions for change. *Conservation Biology* 20(2):277-287.

Tscharntke, T. et al. 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biol. Rev.* 87 (3): 661-685.

Vellend, M. 2010. Conceptual synthesis in community ecology. *Q. Rev. Biol.*, 85, 183–206.

Venables, W. N. and Ripley, B. D. 2002. Modern applied statistics with S. – Springer.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.*,30, 279–338.

Whittaker, R.H. (1965). Dominance and diversity in land plant communities. Science, 147, 250-260.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon*, 21, 213–251.

Work, T.T et al. 2004. Stand composition and structure of the boreal mixed wood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. *Can.J.For.Res* 34: 417-430.

Work, T.T et al. 2008. Evaluation of carabid beetles as indicators of forest change in Canada. *Can Ent* 140: 393-414.

Work, T. T., J. M. Jacobs, J. R. Spence, and W. J. A. Volney. 2010. High levels of green-tree retention are required to preserve ground beetle biodiversity in boreal mixedwood forests. *Ecological Applications* 20:741–751.

Work, T.T et al. 2013. Initial response of rove and ground beetle (Cole) (Coleoptera, Staphylinidae, Carabidae) to removal of logging residues following clearcut harvesting in the boreal forest of Quebec, Canada. *Zookey* 258: 31-52.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed effects Models and extensions in ecology with R. Springer, New York. 574 p.

Appendix

Table 1. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Pterostichus adstrictus*.

	Df	SS	MS	F	Pr(>F)
Year	2	119147	59574	86.71	<2.2E-16***
Treatment	5	11108	2222	3.23	8.5E-03**
Cover type	3	6258	2086	3.04	0.03*
Year:Treatment	10	65872	6587	9.59	3.93E-12***
Year:Cover type	6	31266	5211	7.59	4.34E-07***
Treatment:Cover type	15	12495	833	1.21	0.27
Year:Treatment:Cover type	30	30593	1020	1.48	0.07
Residuals	144	98931	687		

Number of obs=216

Adjusted R^2=0.61

$F_{71, 144}$=5.67

$P < 0.001$

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 2. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Pterostichus adstrictus* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	2807.1	1403.55	5.91	8.2E-03**	Number of obs=36
Cover type	3	739.5	246.52	1.04	0.39	Adjusted R^2=0.18
Year:Cover type	6	796.5	132.75	0.56	0.75	$F_{11, 24}$=1.66
Residuals	24	5696.9	237.37			P =0.14

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 3. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Calathus advena.*

	Df	SS	MS	F	Pr(>F)	
Year	2	3709.7	1854.87	24.27	8.29E-10***	
Treatment	5	2233.2	446.63	5.84	6.05E-05***	Number of obs=216
Cover type	3	2406.3	802.11	10.49	2.76E-06***	Adjusted R^2=0.36
Year:Treatment	10	1883.0	188.30	2.46	0.0095**	$F_{71,\,144}$=2.70
Year:Cover type	6	1855.4	309.23	4.05	8.90E-04***	$P < 0.001$
Treatment:Cover type	15	1351.1	90.08	1.18	0.29	
Year:Treatment:Cover type	30	1189.5	39.65	0.52	0.98	
Residuals	144	11008.0	76.44			

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 4. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Calathus advena* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	888.7	444.33	3.85	0.036^{*}	Number of obs=36
Cover type	3	1904.4	635.15	5.50	0.0051^{**}	Adjusted R^2=0.35
Year:Cover type	6	668.7	111.45	0.96	0.47	$F_{11, 24}$=2.73
Residuals	24	2772.1	115.50			P =0.019

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 5. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Stereocerus haematopus*.

	Df	SS	MS	F	Pr(>F)	
Year	2	7996.9	3998.4	20.20	1.85E-08***	
Treatment	5	2362.9	472.6	2.39	0.041*	Number of obs=216
Cover type	3	2871.1	957.0	4.84	0.0031**	Adjusted R^2=0.21
Year:Treatment	10	5469.3	546.9	2.76	0.0038**	$F_{71,\ 144}$=1.80
Year:Cover type	6	755.9	126.0	0.64	0.70	P =0.002
Treatment:Cover type	15	3439.1	229.3	1.16	0.31	
Year:Treatment:Cover type	30	2414.4	80.5	0.41	0.99	
Residuals	144	28501.6	197.9			

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 6. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Stereocerus haematopus* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	913.4	456.70	1.60	0.22	Number of obs=36
Cover type	3	2865.5	955.15	3.34	0.036*	Adjusted R^2=0.12
Year:Cover type	6	766.0	127.67	0.45	0.84	$F_{11, 24}$=1.45
Residuals	24	6860.2	285.84			P =0.21

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 7. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Calosoma frigidum.*

	Df	SS	MS	F	Pr(>F)
Year	2	797.2	398.61	5.63	0.0044^{**}
Treatment	5	208.7	41.75	0.59	0.71
Cover type	3	606.0	202.00	2.86	0.0040^{*}
Year:Treatment	10	342.2	34.22	0.48	0.90
Year:Cover type	6	976.3	162.71	2.30	0.038
Treatment:Cover type	15	768.8	51.26	0.72	0.76
Year:Treatment:Cover type	30	1697.5	56.58	0.80	0.76
Residuals	144	10186.9	70.74		

Number of obs=216

Adjusted R^2=0.02

$F_{71, 144}$=1.08

P =0.35

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 8. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Calosoma frigidum* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	518.7	259.37	1.45	0.26	Number of obs=36
Cover type	3	475.1	158.37	0.88	0.47	Adjusted R^2=-0.005
Year:Cover type	6	949.5	158.25	0.88	0.52	$F_{11, 24}$=0.98
Residuals	24	4307.5	179.48			P =0.49

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 9. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Platynus decentis*.

	Df	SS	MS	F	Pr(>F)
Year	2	53877	26938.4	53.80	<2.2E-16***
Treatment	5	9744	1948.8	3.89	0.025**
Cover type	3	79298	26432.7	52.76	<2.2E-16***
Year:Treatment	10	21217	2121.7	4.23	3.61E-05***
Year:Cover type	6	71091	11848.5	23.65	<2.2E-16***
Treatment:Cover type	15	11624	775.0	1.55	0.096
Year:Treatment:Cover type	30	32.35	1067.8	2.13	0.0017**
Residuals	144	72144	501.0		

Number of obs=216

Adjusted R^2=0.69

$F_{71, 144}=7.84$

$P < 0.001$

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 10. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Platynus decentis* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	2088.1	1044.07	6.50	0.0056^{**}	Number of obs=36
Cover type	3	4080.6	1360.21	8.47	$5.16E-04^{***}$	Adjusted R^2=0.51
Year:Cover type	6	1400.0	233.33	1.45	0.24	$F_{11, 24}$=4.29
Residuals	24	3853.9	160.58			P =0.0014

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 11. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Calathus ingratus*.

	Df	SS	MS	F	Pr(>F)
Year	2	15226	7613.0	34.32	6.49E-13***
Treatment	5	2648	529.7	2.39	0.041*
Cover type	3	4555	1518.3	6.84	2.42E-04***
Year:Treatment	10	13926	1392.6	6.27	6.02E-08***
Year:Cover type	6	11103	1850.5	8.34	9.14E-08***
Treatment:Cover type	15	4491	299.4	1.35	0.18
Year:Treatment:Cover type	30	10903	363.4	1.64	0.030**
Residuals	144	31944	221.8		

Number of obs=216

Adjusted R^2=0.50

$F_{71, 144}$=3.99

P < 0.001

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 12. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Calathus ingratus* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	1617.9	808.94	2.92	0.07	Number of obs=36
Cover type	3	1094.9	364.97	1.32	0.29	Adjusted R^2=0.10
Year:Cover type	6	1359.5	226.59	0.82	0.57	$F_{11, 24}$=1.33
Residuals	24	6659.5	277.48			P =0.27

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 13. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Agonum retractum.*

	Df	SS	MS	F	Pr(>F)
Year	2	46707	23353.4	47.94	<2.2E-16***
Treatment	5	8335	1667.0	3.42	0.0059**
Cover type	3	70089	23363.1	47.96	<2.2E-16***
Year:Treatment	10	19943	1994.3	4.09	5.64E-05***
Year:Cover type	6	77770	12961.7	26.61	<2.2E-16***
Treatment:Cover type	15	13700	913.3	1.88	0.030*
Year:Treatment:Cover type	30	36133	1204.4	2.47	1.98E-04***
Residuals	144	70141	487.1		

Number of obs=216

Adjusted R^2=0.69

$F_{71,\ 144}$=7.89

$P < 0.001$

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 14. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Agonum retractum* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	714.2	357.09	1.39	0.27	Number of obs=36
Cover type	3	7614.3	2538.11	9.86	2.00E-04***	Adjusted R^2=0.45
Year:Cover type	6	1976.6	329.43	1.28	0.30	$F_{11, 24}$=3.64
Residuals	24	6175.6	257.31			P =0.004

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 15. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Patrobus foveocollis*.

	Df	SS	MS	F	Pr(>F)	
Year	2	1714.1	857.05	23.75	1.22E-09***	
Treatment	5	581.7	116.33	3.22	0.0087**	Number of obs=216
Cover type	3	2016.2	672.06	18.62	2.91E-10***	Adjusted R^2=0.44
Year:Treatment	10	715.9	71.59	1.98	0.039*	$F_{71,\ 144}$=3.39
Year:Cover type	6	1553.4	258.89	7.17	1.04E-06***	P < 0.001
Treatment:Cover type	15	438.4	29.23	0.81	0.67	
Year:Treatment:Cover type	30	1674.5	55.82	1.55	0.048*	
Residuals	144	5197.2	36.09			

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 16. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Patrobus foveocollis* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	158.9	79.45	2.84	0.08	Number of obs=36
Cover type	3	317.6	105.87	3.78	0.024^{*}	Adjusted R^2=0.32
Year:Cover type	6	286.8	47.80	1.71	0.16	$F_{11, 24}$=2.48
Residuals	24	672.2	28.01			P =0.031

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 17. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Pterostichus pensylvanicus*.

	Df	SS	MS	F	Pr(>F)	
Year	2	2092.6	1046.28	13.43	4.50E-06***	
Treatment	5	842.3	168.45	2.16	0.062	Number of obs=216
Cover type	3	5117.2	1705.74	21.89	9.75E-012***	Adjusted R^2=0.41
Year:Treatment	10	1093.2	109.32	1.40	0.18	$F_{71, 144}$=3.07
Year:Cover type	6	3359.7	559.94	7.19	1.02E-06***	P < 0.001
Treatment:Cover type	15	1885.3	125.69	1.61	0.077	
Year:Treatment:Cover type	30	2607.0	86.90	1.12	0.33	
Residuals	144	11220.6	77.92			

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 18. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Pterostichus pensylvanicus* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	167.3	83.64	1.37	0.27	Number of obs=36
Cover type	3	293.7	97.89	1.60	0.22	Adjusted R^2=0.006
Year:Cover type	6	225.2	37.53	0.61	0.72	$F_{11, 24}$=1.02
Residuals	24	1467.3	61.14			P =0.46

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 19. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Trechus chalybeus*.

	Df	SS	MS	F	Pr(>F)	
Year	2	3475.6	1737.80	41.65	5.35E-15***	
Treatment	5	432.4	86.48	2.07	0.072	Number of obs=216
Cover type	3	119.9	39.97	0.96	0.41	Adjusted R^2=0.24
Year:Treatment	10	459.7	45.97	1.10	0.36	$F_{71, 144}$=1.98
Year:Cover type	6	119.2	19.87	0.48	0.82	$P < 0.001$
Treatment:Cover type	15	449.3	33.29	0.80	0.68	
Year:Treatment:Cover type	30	743.2	24.77	0.59	0.95	
Residuals	144	6008.9	41.73			

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 20. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Trechus chalybeus* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	287.3	143.65	7.50	0.0029^{***}	Number of obs=36
Cover type	3	104.8	39.94	1.83	0.17	Adjusted R^2=0.27
Year:Cover type	6	62.1	10.36	0.54	0.77	$F_{11, 24}$=2.16
Residuals	24	459.5	19.15			P =0.056

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 21. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Carabus chamissonis*.

	Df	SS	MS	F	Pr(>F)
Year	2	916.2	458.12	9.87	9.63E-05***
Treatment	5	384.4	76.89	1.66	0.14
Cover type	3	533.1	177.71	3.83	0.011*
Year:Treatment	10	848.9	84.89	1.83	0.061
Year:Cover type	6	997.8	166.30	3.58	0.0024**
Treatment:Cover type	15	870.0	58.00	1.25	0.24
Year:Treatment:Cover type	30	818.5	27.28	0.59	0.96
Residuals	144	6684.7	46.42		

Number of obs=216

Adjusted R^2=0.17

$F_{71, 144}$=1.63

P =0.007

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 22. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Carabus chamissonis* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	382.6	191.29	4.29	0.026^{*}	Number of obs=36
Cover type	3	510.2	170.07	3.81	0.023^{*}	Adjusted R^2=0.34
Year:Cover type	6	413.9	69.00	1.55	1.55	$F_{11, 24}$=2.66
Residuals	24	1071.1	44.63			P =0.022

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 23. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Synuchus impunctatus*.

	Df	SS	MS	F	Pr(>F)	
Year	2	1151.8	575.92	38.41	4.28E-14***	
Treatment	5	225.2	45.04	3.00	0.013*	Number of obs=216
Cover type	3	34.0	11.34	0.76	0.52	Adjusted R^2=0.34
Year:Treatment	10	288.5	28.85	1.92	0.046*	$F_{71, 144}$=2.58
Year:Cover type	6	124.5	20.76	1.38	0.22	$P < 0.001$
Treatment:Cover type	15	330.5	22.03	1.47	0.12	
Year:Treatment:Cover type	30	587.9	19.60	1.31	0.15	
Residuals	144	2159.2	14.99			

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 24. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Synuchus impunctatus* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	28.1	14.08	2.76	0.08	Number of obs=36
Cover type	3	10.9	3.65	0.72	0.55	Adjusted R^2=0.03
Year:Cover type	6	22.7	3.79	0.74	0.62	$F_{11, 24}$=1.10
Residuals	24	122.3	5.09			P =0.40

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 25. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Trechus apicalis*.

	Df	SS	MS	F	Pr(>F)	
Year	2	524.1	262.07	39.48	2.14E-14***	
Treatment	5	30.0	6.01	0.91	0.48	Number of obs=216
Cover type	3	13.6	4.52	0.68	0.57	Adjusted R^2=0.31
Year:Treatment	10	124.3	12.43	1.87	0.054	$F_{71, 144}$=2.35
Year:Cover type	6	108.7	18.12	2.73	0.015*	$P < 0.001$
Treatment:Cover type	15	112.3	7.48	1.13	0.34	
Year:Treatment:Cover type	30	194.1	6.47	0.98	0.51	
Residuals	144	956.0	6.64			

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 26. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Trechus apicalis* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	76.5	38.26	4.50	0.022*	Number of obs=36
Cover type	3	27.2	9.07	1.07	0.38	Adjusted R^2=0.11
Year:Cover type	6	27.4	4.57	0.54	0.77	$F_{11, 24}$=1.40
Residuals	24	203.9	8.49			P =0.23

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 27. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on abundance of *Pterostichus punctatissimus*.

	Df	SS	MS	F	Pr(>F)	
Year	2	44.5	22.27	4.34	0.015*	
Treatment	5	11.1	2.22	0.43	0.83	Number of obs=216
Cover type	3	50.9	16.97	3.31	0.022*	Adjusted R^2=-0.05
Year:Treatment	10	41.4	4.14	0.81	0.62	$F_{71, 144}$=0.85
Year:Cover type	6	44.8	7.46	1.46	0.20	P =0.77
Treatment:Cover type	15	47.5	3.17	0.62	0.86	
Year:Treatment:Cover type	30	69.5	2.32	0.45	0.99	
Residuals	144	738.2	5.13			

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 28. Two-way ANOVA to examine the effects of Year and Cover type on abundance of *Pterostichus punctatissimus* in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	2.3	1.12	0.59	0.56	Number of obs=36
Cover type	3	13.6	4.53	2.40	0.09	Adjusted R^2=-0.01
Year:Cover type	6	3.9	0.65	0.34	0.91	$F_{11, 24}$=0.95
Residuals	24	45.4	1.89			P =0.51

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 29. Three-way ANOVA to examine the effects of Year, Treatment and Cover type on pooled abundance of rare species.

	Df	SS	MS	F	Pr(>F)	
Year	2	292.2	146.12	6.60	0.0018^{**}	
Treatment	5	495.8	99.16	4.48	$7.99E\text{-}04^{***}$	Number of obs=216
Cover type	3	334.4	111.48	5.04	0.0024^{**}	Adjusted R^2=0.17
Year:Treatment	10	184.6	18.46	0.83	0.60	$F_{71, 144}$=1.60
Year:Cover type	6	394.9	65.82	2.97	0.0091^{**}	P =0.009
Treatment:Cover type	15	293.7	19.58	0.88	0.58	
Year:Treatment:Cover type	30	521.1	17.37	0.78	0.78	
Residuals	144	3187.5	22.14			

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 30. Two-way ANOVA to examine the effects of Year and Cover type on abundance of rare species in controls.

	Df	SS	MS	F	Pr(>F)	
Year	2	12.8	6.43	1.09	0.35	Number of obs=36
Cover type	3	36.9	12.31	2.09	0.13	Adjusted R^2=-0.07
Year:Cover type	6	1.9	0.31	0.05	1.00	$F_{11, 24}$=0.80
Residuals	24	141.3	5.89			P =0.64

p-values: *** < 0.001; ** < 0.01; * < 0.05.

Table 31. Carabid beetle sampled on the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment landscape in northwestern Alberta (1998-2014).

Species	Abundance
Agonum affine Kirby	1
Agonum consimile (Gyllenhal)	1
Agonum corvus (LeConte)	1
Agonum cupreum Dejean	58
Agonum gratiosum (Mannerheim)	71
Agonum placidum (Say)	9
Agonum retractum Leconte	5518
Agonum sordens Kirby	97
Agonum superioris Lindroth	7
Agonum thoreyi thoreyi Dejean	1
Amara aeneopolita Casey	1
Amara apricaria (Paykull)	1

Amara cupreolate Putzeys	6
Amara erratica (Duftschmid)	9
Amara familiaris (Duftschmid)	1
Amara laevipennis Kirby	16
Amara latior (Kirby)	1
Amara littoralis Mannerheim	7
Amara lunicollis Schiodte	48
Amara patruelis Dejean	32
Amara pseudobrunnea Lindroth	1
Amara quenseli Schönherr	1
Amara sinuosa (Casey)	1
Amara torrida (Panzer)	2
Atranus pubescens (Dejean)	1
Badister obtusus (LeConte)	9

Bembidion graphicum Casey	68
Bembidion mutatum Gemminger & Harold	29
Bembidion nigripes Kirby	1
Bembidion quadrimaculatum dubitans (LeConte)	1
Bembidion rupicola (Kirby)	3
Bembidion transparens (Gebler)	1
Blethisa multipunctata aurata Fischer von Waldheim	6
Bradycellus lecontei Csiki	1
Calathus advena (LeConte)	2805
Calathus ingratus Dejean	7403
Calosoma frigidum Kirby	1173
Carabus chamissonis Fischer von Waldheim	1263
Carabus taedatus agassii LeConte	43

Chlaenius purpuricollis frostii Carr	1
Cymindis cribricollis Dejean	18
Diplocheila oregona (Hatch)	1
Elaphrus clairvillei Kirby	4
Elaphrus lapponicus lapponicus Gyllenhal	8
Elaphrus pallipes (Horn)	1
Harpalus amputatus amputatus Say	2
Harpalus egregious (Casey)	6
Harpalus fulvilabris Mannerheim	62
Harpalus lewisii LeConte	3
Loricera pilicornis pilicornis (Fabricius)	109
Miscodera arctica (Paykull)	2
Nebria gyllenhali castanipes (Kirby)	7
Notiophilus borealis T.W. Harris	2

Notiophilus directus Casey	1
Notiophilus semistriatus Say	2
Patrobus foveocollis (Eschscholtz)	2405
Patrobus septentrionis Dejean	12
Pelophila rudis (LeConte)	1
Platynus decentis (Say)	7953
Platynus mannerheimii (Dejean)	203
Poecilus lucublandus lucublandus (Say)	1
Pterostichus adstrictus Eschscholtz	13798
Pterostichus brevicornis (Kirby)	137
Stereocerus haematopus (Dejean)	4709
Pterostichus luctuosus (Dejean)	8
Pterostichus melanarius (Illiger)	1
Pterostichus pensylvanicus LeConte	1747

Pterostichus punctatissimus (Randall)	369
Pterostichus riparius (Dejean)	5
Sericoda bembidioides Kirby	1
Sericoda quadripunctata (DeGeer)	29
Synuchus impunctatus (Say)	461
Trechus apicalis Motschulsky	526
Trechus chalybeus Dejean	1078
Trechus oregonensis Hatch	17
Trechus spp.	9
Trichocellus cognatus (Gyllenhal)	40

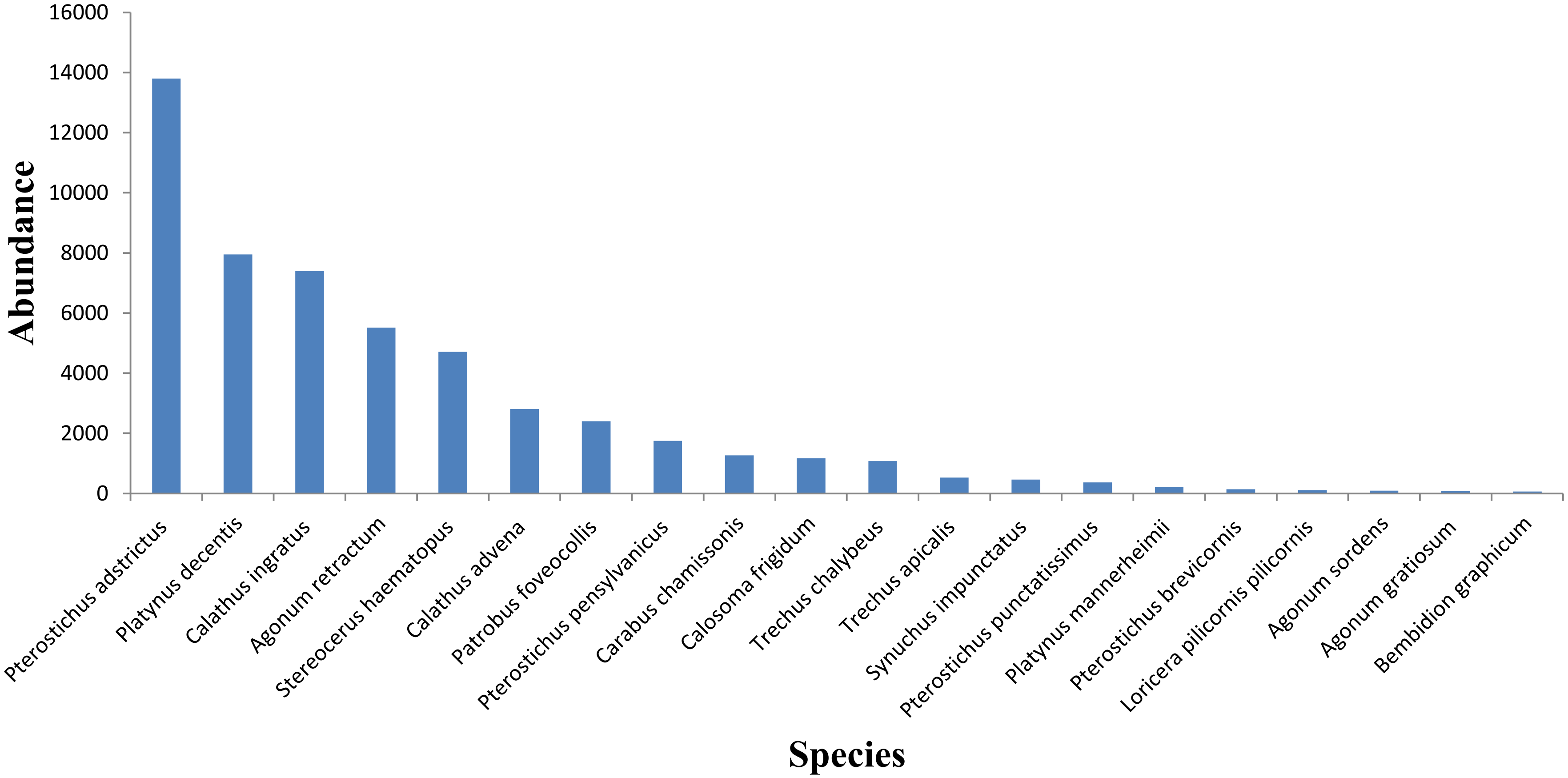


Fig. 1. Species abundance (rank-abundance) of twenty most abundant carabid species sampled on the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment landscape in northwestern Alberta (1998-2014).