UNIVERSITY OF QUEBEC IN MONTREAL

RECOVERY OF GROUND BEETLES FOLLOWING CLEAR-CUT AND PARTIAL-RETENTION HARVESTING IN BOREAL MIXEDWOOD FORESTS

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This thesis comprises three chapters written in the form of articles. As a PhD candidate, I collected a significant portion of the data, analyzed the results and led the writing of the manuscripts. As thesis adviser, Timothy Work is co-author for all three articles. In addition, each article notes contributions from specific individuals regarding sample or data collection in the acknowledgements and within the author contribution statements.

Each article has been submitted, or is planned for submission, to an academic journal and has been written to stand alone. The first article, "Twenty-year recovery of ground beetle communities after clear-cut and partial-retention harvests in boreal mixedwoods" is in preparation for submission to *Ecological Applications*. The second article "Increased retention after harvest better maintains carabid abundance in boreal mixedwood forests under two climate change scenarios" is under review for publication in the *Journal of Applied Ecology*. The third article "Forest harvest causes rapid changes of maternal investment strategies in ground beetles" was published by *Ecology* in 2024. The style of each article follows that of the scientific journal where it is published or for which it has been prepared.

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RÉSUME

La conservation de la biodiversité forestière à long terme dépendra des approches durables de la gestion forestière qui maintiennent l'hétérogénéité de l'habitat et qui ont la capacité d'atténuer les effets du changement climatique. Les pratiques sylvicoles qui maintiennent une rétention importante des peuplements devraient mieux conserver ou recréer des structures d'habitat conformes à celles que l'on trouve dans les peuplements maintenus par des perturbations naturelles comparativement aux coupes totales. Dans ce contexte, l'exploitation avec rétention partielle peut constituer une stratégie efficace et réalisable pour la conservation de la biodiversité.

Dans cette thèse, je teste l'efficacité de la coupe totale et de l'augmentation de l'intensité de la récolte par rétention partielle pour la conservation de la biodiversité des carabes, un groupe diversifié et omniprésent de prédateurs généralistes, sur une période de 20 ans après la récolte. Des traitements de récolte ont été appliqués dans le cadre de l'expérience SAFE dans trois types de couvert forestier représentatifs de la succession typique après incendie dans les forêts boréales mixtes du Québec (peuplements de feuillus, de résineux et mixtes). Les traitements sylvicoles comprennent la coupe totale avec des résidus d'exploitation laissés sur place ou traités par brûlage dirigé ou par récolte de l'arbre entier, la récolte avec rétention partielle où 34%, 60% ou 67% de la structure sur pied a été conservée et des témoins non récoltés. En utilisant des arbres de régression multivariés, j'ai constaté que la composition de carabes dans les coupes partielles de feuillus s'est rapprochée de celle des témoins dans les 10 ans suivant la récolte. Après 15 ans, les assemblages de coléoptères dans les coupes totales de résineux et de feuillus où les résidus d'exploitation ont été conservés se sont également rétablis. Après 20 ans, les carabes dans les coupes de feuillus avec brûlages dirigés ou récoltes d'arbres entiers s'étaient rétablis, mais les effets de la récolte dans les peuplements mixtes persistaient 20 ans après la récolte. Ces résultats indiquent que la récolte avec rétention partielle peut accélérer le rétablissement de la biodiversité résidente dans les peuplements dominés par les feuillus, alors que les options de gestion intensive devraient retarder le rétablissement.

J'ai ensuite prédit l'impact combiné à long terme de l'exploitation avec rétention partielle et du changement climatique sur l'abondance des carabes au cours des deux prochaines décennies, en combinant l'échantillonnage répété des carabes à SAFE avec des modèles de dynamique de peuplement forestier spécifiques aux sites et des données météorologiques dans le cadre du scénario de faibles émissions SSP1-2.6 et du scénario d'émissions élevées SSP5-8.5. Dans le cadre du scénario SSP1-2.6, la plupart des espèces de carabes devraient augmenter au cours des prochaines décennies, en particulier dans les peuplements ayant fait l'objet d'une rétention post-récolte importante. Les traitements à forte rétention ont également conféré un avantage numérique aux populations résidentes, augmentant la résistance aux périodes de stress à court terme, telles que les épidémies d'insectes. Dans le cadre du SSP5-8.5, de nombreuses espèces ont augmenté dans un premier temps, avant de décliner au fil du temps. Alors que l'abondance des carabes était la plus élevée dans les traitements à forte rétention, les populations de tous les traitements ont atteint une faible densité à la fin de la décennie dans le cadre du PAS5-8.5. Ces résultats suggèrent que l'exploitation avec rétention partielle peut contribuer à atténuer les effets du changement climatique et à préserver la biodiversité dans le cadre de scénarios d'émissions plus faibles, mais qu'elle sera probablement moins efficace dans le cadre de scénarios de changement climatique extrêmes.

Enfin, j’ai testé la façon dont les changements rapides des conditions environnementales après la récolte influencent la sélection des adaptations en matière de survie et de fécondité chez deux espèces de carabes, *Pterostichus pensylvanicus* et *Pterostichus coracinus*. En utilisant des parents issus de peuplements non récoltés ou ayant récemment subis une coupe totale, j'ai évalué le rendement reproductif des femelles et l'approvisionnement de la progéniture en élevant des descendants dans des expériences de jardin commun et de transplantation réciproque. J'ai constaté que les œufs pondus par des femelles de *P. pensylvanicus* provenant de coupes totales avaient plus de chances d'éclore et que la progéniture se développait plus rapidement, ce qui suggère un approvisionnement accru de la progéniture. Chez *P. coracinus*, les femelles provenant de coupes totales ont pondu plus d'œufs, ces derniers ont éclos plus rapidement et ont eu plus de succès à l'éclosion, ce qui suggère un investissement accru dans la production reproductive globale et un approvisionnement accru de la progéniture. Dans l'expérience de transplantation réciproque, j'ai observé des interactions significatives entre l'habitat et la lignée sur la survie de *P. coracinus*. La survie augmentait lorsque la progéniture était élevée dans de nouveaux habitats, ce qui indique que les zones adjacentes entre les habitats non exploités et les coupes totales peuvent être utiles pour maintenir la biodiversité pendant les périodes de stress. L'ensemble de ces résultats montre que les femelles provenant de coupes totales augmentent l'investissement dans la fécondité, compensant partiellement l'augmentation de la mortalité larvaire après la récolte, et peuvent améliorer la résilience des populations de coléoptères vivant dans des environnements physiologiquement stressants.

Dans l'ensemble, cette thèse contribue aux efforts de conservation en fournissant un calendrier pour les opérations forestières qui précise quand, ou si, les peuplements se sont complètement rétablis 20 ans après la coupe, en fournissant des lignes directrices sur les niveaux de rétention sur pied nécessaires pour préserver la biodiversité face aux futurs facteurs de stress climatique et en mettant en évidence des stratégies d’adaptation potentielles chez les carabes qui peuvent aider à compenser l'augmentation de la mortalité résultant de conditions environnementales stressantes.

Mots clés: conservation de la biodiversité; forêts mixtes boréales; Carabidae; changement climatique; sylviculture écologique; évolution du cycle de vie; coupe partielle; évolution rapide; rétention variable.

ABSTRACT

Conservation of forest biodiversity over long-term timeframes will depend on sustainable approaches to forest management that maintain habitat heterogeneity and have the capacity to mitigate climate change impacts. Silvicultural practices which maintain significant standing retention are expected to better conserve or recreate habitat structures consistent with those found in stands maintained by natural disturbances as compared to clear-cutting. In this context, partial-retention harvesting may provide an effective and achievable strategy for conservation of biodiversity.

In this dissertation, I test the efficacy of clear-cutting and variable-retention harvesting for conserving ground beetles, a diverse and ubiquitous group of generalist predators, over 20 years post-harvest. Harvesting treatments were applied as a part of the SAFE experiment in three forest cover-types representative of typical post-fire succession in Québec's boreal mixedwood forests (hardwood, mixedwood and softwood stands). Silvicultural treatments include clear-cutting with logging residues left *in situ* or further treated through prescribed burning or whole-tree harvest, partial-retention harvesting where 34%, 60%, 67% of the standing structure was retained and unharvested controls. Using multivariate regression trees, I found ground beetle composition in the hardwood partial harvests recovered to resemble those found within the controls within 10 years post-harvest. After 15 years, beetle assemblages in the softwood and hardwood clear-cuts where logging residues were retained had also recovered. After 20 years, ground beetles within hardwood clear-cuts with prescribed burns or whole-tree harvests had recovered, however, the effects of harvesting in mixedwood stands persisted 20 years post-harvest. These results indicate partial-retention harvesting can speed recovery of ground beetle species assemblages in hardwood stands, while intensive management options are expected to delay recovery.

I then predicted the long-term, combined impact of partial-retention harvesting and climate change on the abundance of ground beetles over the next two decades by combing repeated sampling of ground beetles at SAFE with site specific models of forest stand dynamics and meteorological data under low emissions scenario SSP1-2.6 and high emissions scenario SSP5-8.5. Under SSP1-2.6, most ground beetle species were expected to increase through the coming decades, particularly in stands with significant post-harvest retention. High-retention treatments also conferred a numerical advantage for ground beetle populations, increasing resilience to short-term periods of stress such as insect outbreaks. Under SSP5-8.5, many species increased initially but then declined over time. While ground beetle abundance was highest in high-retention treatments, populations within all treatments reached low density by the end of the decade under SSP5-8.5. These findings suggest that partial-retention harvesting can help mitigate the effects of climate change and conserve biodiversity under lower emissions scenarios but will likely be less effective under more extreme climate change scenarios.

Finally, I test how rapid changes in environmental conditions following harvest mediate selection for adaptations in survivorship and fecundity in two species of ground beetles, *Pterostichus pensylvanicus* and *Pterostichus coracinus.* Using parents drawn from recently clear-cut or unharvested stands, I evaluated female's reproductive output and among offspring provisioning by rearing progeny in both common garden and reciprocal transplant experiments. In *P. pensylvanicus*, I found eggs laid by females from clear-cuts were more likely to hatch and offspring developed more rapidly, suggesting increased offspring provisioning. In *P. coracinus,* females from clear-cuts laid more eggs, their eggs hatched more rapidly and had greater hatching success, suggesting increased investment in overall reproductive output and increased provisioning among offspring. In the reciprocal transplant experiment, I observed significant habitat by lineage interactions on survival in *P. coracinus*, with survivorship increasing when progeny was reared in novel habitats, indicating that adjacent areas between unharvested and clear-cut habitat may be useful in maintaining biodiversity under periods of stress. Together, these results show females from clear-cuts increase investment in fecundity, partially compensating for increased post-harvest larval mortality, and may improve resilience of beetle populations living in physiologically stressful environments.

As a whole, this dissertation contributes to conservation efforts by delivering a timetable for forest operations which specifies when, or if, stands have fully recovered from previous interventions 20 years post-harvest, by providing guidelines on the levels of standing retention necessary to preserve ground beetle populations under future climate stressors and by highlighting avenues for adaptation in ground beetles which may help offset increased mortality resulting from stressful environmental conditions.

Keywords: biodiversity conservation; boreal mixedwoods; Carabidae; climate change; ecological forestry; life-history evolution; partial-cut harvesting; rapid evolution; variable retention.

INTRODUCTION GÉNÉRALE

0.1 Stand dynamics and development patterns after natural disturbances

In Québec's boreal mixedwood forests, forest fires and insect outbreaks are two of the most prominent natural disturbances shaping stand dynamics. Following stand replacing fires or insect outbreaks, shade-intolerant hardwoods such as trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh.) are typically the first tree species to become established (Johnstone et al. 2004). As saplings grow, the stand enters the stem exclusion stage, a phase characterized by intense competition for growing space and resources which is then followed by rapid closure of the canopy (Chen and Popadiouk 2002). As the first cohort of hardwood trees senesce, a new cohort of hardwoods and softwood species enter the canopy, forming mixedwood stands. Given enough time, mixedwood stands transition to a softwood dominated composition as the second or even third cohort of shorter-lived hardwoods senesce, and the bud bank becomes skewed towards softwood species (Bergeron 2000; Bergeron and Harvey 1997; Lieffers et al. 1996).

Overlaying the effects of large, stand replacing disturbances are more localized compositional changes caused by small-scale disturbances. For example, mortality of hardwood trees caused by small-scale outbreaks of forest tent caterpillars (*Malacosoma disstria* Hübner) result in canopy openings which increase the growth rate of softwoods in the understory (Bergeron and Charron 1994). Alternatively, stands with a softwood dominated composition are more prone to damage from spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks which in turn can favor the return of hardwood species in the resulting gaps (Kneeshaw and Bergeron 1998). Finally, lower-intensity forest fires also influence stand composition and structure, as variations in terrain, moisture content and fuel type create uneven burn patterns (Franklin et al. 2002). At the landscape level, these large and small-scale natural disturbances work in concert to maintain heterogeneous forests, forming a mosaic of stands of differing age-classes and compositions (Bergeron and Fenton 2012).

0.2 Shifting paradigms in forest management

Most harvesting in Québec's boreal mixedwood forests occurs through clear-cutting, as clear-cutting maximizes yield and allows for an easy substitution of harvest for fire in public perception (Lieffers et al.

2003). However, it has now been clearly demonstrated that clear-cutting and forest fires are not ecologically analogous. Clear-cuts are often prescribed in regularly shaped patches which are larger than characteristic of most natural disturbances. Although clear-cutting larger areas increases the growth rate of regenerating stands, this practice converts a greater proportion of the landscape to homogenous, early successional hardwoods than would be found in forests shaped by natural disturbances alone (Bergeron et al. 2002; Work et al. 2004; Déchêne and Buddle 2009). Additionally, clear-cutting typically occurs on more frequent intervals than natural disturbances and removes biomass more uniformly, creating regenerating stands with a simplified structure and few biological legacies. For species which require complex stands with older-growth attributes, the combined impact of large-scale conversion of forest-cover to early successional hardwoods and the simplification of stand structure and age distributions across the boreal forest may represent a significant loss of suitable habitat (Virkkala et al. 2023; Bogdziewicz and Zwolak 2014; Venier et al. 2014).

0.2.1 Natural disturbance-based management model

Natural disturbance-based management (NDBM) has been proposed as a more sustainable harvesting approach which better maintains biodiversity as compared to conventional clear-cutting (Bergeron and Harvey 1997; Harvey et al. 2002; Kuuluvainen et al. 2021). Generally, NDBM approaches include: (1) partial-retention harvesting (*i.e.* retention of some proportion of standing green-trees dispersed throughout the stand or retained as grouped residuals around a gap cut); (2) maintenance of structural complexity by preserving biological legacies or managing for spatial heterogeneity; and (3) use of longer harvesting rotations. These silvicultural practices can be combined in an effort to mimic the effects of natural disturbances by manipulating stand structure, composition and age-classes (Mladenoff et al. 1993; Landres et al. 1999; Harvey et al. 2002). For example, thinning saplings can be used to emulate the stem exclusion phase of stand development, encouraging growth of larger, more vigorous trees (Harvey and Brais 2007). Alternatively, single-tree selection of large diameter trees can be used to emulate natural senescence or mortality of trees due to more minor insect outbreaks. When applied to hardwood or mixedwood dominated stands, partial-retention harvests can encourage growth of shade-tolerant fir or spruce species and may shift stand composition from hardwood dominated towards mixedwoods, or from mixedwoods towards a softwood dominated composition (O'Hara and Ramage 2013). In softwood dominated stands, partial-retention harvesting can be used in an effort to maintain softwood composition, or shift a stands composition towards mixedwoods, dependent on the intensity of the harvest employed (Maleki et al. 2020; Bergeron et al. 2002; Brais et al. 2004; Lieffers et al. 2003). Partial-retention harvesting also allows snags or coarse woody debris to develop over time, increasing presence of old-growth attributes within managed stands. In this way, NDBM may be capable of restoring/maintaining structural and compositional conditions more similar to those found in an unmanaged landscape (Mladenoff et al. 1993; Landres et al. 1999; Harvey et al. 2002).

0.2.2 Climate-smart forestry model

Climate-smart forest management typically emphasize the importance of developing stands which have improved resilience and an increased ability to respond adaptively to environmental conditions which are rapidly shifting outside of historical norms. This may be done by planting native or non-native tree species which are better suited for hotter or drier conditions (Guignabert et al. 2024; Messier et al. 2022). Alternatively, partial-retention harvesting may be used to improve resilience of a stand, as low-density stands with a high species diversity and increased size and age-class distributions allow for tree-level selection of individuals which are better adapted to heat and drought stress (Nolet et al. 2014) and can increase heterogeneity at the stand and landscape scale (D’Amato and Palik 2021).

0.3 Ground beetles as indicator taxa

Ground beetles (Coleoptera; Carabidae) are frequently used as indicator taxa, as they are taxonomically well known, have relatively stable systematics and the variations in their morphology, life-history strategies and abiotic and biotic requirements have been widely studied (Lövei and Sunderland 1996). In addition, shifts in ground beetle community composition generally occur more quickly than can be detected in plant or vertebrate species, as ground beetles have relatively rapid generational turnover (Thiele 1977). Thus, studies which monitor ground beetles can provide an early indication of the impacts of changing environmental conditions (Koivula 2011). Ground beetles have a well-documented history of use in detection of the impacts of disturbances such as forest harvesting, urbanization, agriculture and climate change across North America and Europe (for reviews, see Work et al. 2008; Koivula 2011; Lövei and Sunderland 1996; Kromp 1999; Niemelä et al. 2007; Kotze et al 2011). As ground beetle species assemblages are highly sensitive to changes in forest structure and composition at the stand-level (Bednarska and Laskowski 2009; Lovei and Sunderland 1996), ground beetles have been used in managed forests to reflect post-harvest recovery following clear-cutting (Heliölä et al. 2001; Niemelä et al. 1993; Werner and Raffa 2000) and partial-retention harvests (Lemieux and Lindgren 2004; Work et al. 2010; Wu et al. 2020; Klimaszewski at al. 2003, 2005) as well as natural disturbances such as wildfires (Buddle et al. 2006; Pihlaja et al. 2006; Saint-Germain et al. 2004, 2005).

0.3.1 Response of ground beetles to large-scale NDBM experiments in North America

Several large-scale forest manipulation experiments in North America have evaluated ground beetle response following NDBM. Of these projects, DEMO (Aubry et al. 2009), TRIAD (Graham-Sauvé et al. 2013), RECPA (Paradis and Work 2010) and SSAM (Klimaszewski et al. 2005) have published data spanning 0-7 years post-harvest, while EMEND (Wu et al. 2020) has published data spanning 15 years post-harvest. Generally, measurements of ground beetle recovery taken over the first 0-3 years post-harvest can be subject to the "lag effect", as most species are capable of surviving in suboptimal conditions for 2-3 years without producing offspring (Lovei and Sunderland 1996). When the lag effect is present, evaluations of the initial response of ground beetles to harvest may be skewed by non-viable remnant populations approaching local extinction (Saint-Germain et al. 2005; Work et al. 2010). However, by 5-10 years post-harvest community composition in harvested treatments typically has changed significantly as compared to the unharvested controls, as open habitat adapted species increase and forest generalist and closed-canopy specialists decline (Wu et al. 2020; Graham-Sauvé et al. 2013; Aubry et al. 2009; Klimaszewski et al. 2005). After 10 years post-harvest, recovery rates of ground beetle populations are expected to differ based on the initial stand composition as well as the intensity of the silvicultural treatment applied. Generally, the larger the proportion of standing structure removed, the slower the recovery. For example, clear-cuts at EMEND failed to recover within the 15-year timeframe of the published data (Wu et al. 2020). Recovery rates can also be impacted by the initial cover-type of the stand prior to harvest. At EMEND, high-retention partial harvests in the hardwood stands began to show signs of recovery 10-15 years post-harvest, however, community composition in mixedwood and softwood stands harvested with a similar intensity had yet to recover within this timeframe (Wu et al. 2020).

In this dissertation, I further develop this theme by evaluating the recovery and persistence of ground beetles following clear-cutting and partial-retention harvesting using a 20-year dataset collected as part of the SAFE (Silviculture et aménagement forestier écosystémique) project. While a mid-term study from the perspective of forest succession, this 20-year dataset ranks as one of the longest-term records of post-harvest ground beetle recovery available from anywhere in the world.

0.3.2 The SAFE project

The SAFE project, located within the Forêt d'enseignement et de recherche du lac Duparquet (FERLD) research site in northwestern Québec (48°30'14.8"N 79°16'15.6"W), is a large-scale experiment where a range of silvicultural treatments meant to emulate natural disturbances and forest succession were applied across replicated stands (Brais et al. 2004; Bergeron and Harvey 1997; Harvey et al. 2002; Bergeron et al. 2002). SAFE includes silvicultural treatments located within hardwood, mixedwood and softwood stands, as these cover-types are representative of typical post-disturbance patterns of succession in the boreal mixedwood forest (Lieffers et al. 1996).

The hardwood stands within SAFE originated from a fire in 1923 and are composed primarily of mature aspen with a sparse conifer understory. Harvests in the hardwoods occurred in 1998-1999 as clear-cuts or as partial-retention harvests, which retained 34% or 67% of the total basal area. In the 34% partial-retention harvest, large diameter marketable trees were harvested through single-tree selection, while non-vigorous small stems were selected for harvest in the 67% partial-retention. Clear-cuts within the hardwoods were further divided into three nested treatments; (1) slash retained on site, (2) residuals consumed in a prescribed burn, and (3) whole-tree harvest where all logging residuals were removed. Finally, unharvested stands were maintained as long-term experimental controls.

The mixedwood stands within SAFE originated following a fire in 1910 and are dominated by mature aspen, balsam fir (*Abies balsamea* (L.) Mill), black spruce (*Picea mariana* Mill.) and white spruce (*Picea glauca* (Moench) Voss). These stands were harvested in 2000-2001 through clear-cutting, where slash was retained on site, as well as through two partial-retention harvests both of which retained 60% of the total basal area. The first 60% partial-retention treatment occurred through single-tree selection where dispersed retention was maintained throughout the stand, while in the second 60% partial-retention treatment residuals were located around a gap cut of approximately 400 m². Unharvested stands were also maintained as long-term experimental controls.

The softwood stands with SAFE are composed primarily of balsam fir, white birch and white spruce. These stands have undergone damage from multiple spruce budworm outbreaks and dated back to the last stand replacing fire in 1760 (Dansereau and Bergeron 1993). Harvests in the softwoods occurred in 1999-2000 through clear-cutting where slash was retained on site. Additionally, unharvested stands were set aside to be used as experimental controls.

All harvesting treatments at SAFE were applied using manual felling and occurred while the ground was snow covered to minimize disturbances to the soil. In the partial-retention treatments, stems were generally bucked in 2.5, 5, or 7.5 m lengths before removal using small cable skidders to avoid damage to residuals or regeneration. Skid trails in the partial-retention treatments were approximately 4.5 m wide and space at 30 m. In the clear-cuts, stems were delimbed on site and hauled at their full length using larger sized cable skidders. Skid trails for the clear-cut treatments were approximately 5 m wide and spaced at 10 m. All of the silvicultural treatments at SAFE were replicated three times in a randomized complete block design, resulting in a total of 36 experimental stands which ranged from 1-3 hectares in size (Brais et al. 2004).

0.4 The role of evolutionary dynamics in post-harvest recovery of ground beetles

The state of remnant populations, which have survived *in situ,* is expected to directly impact the speed with which ground beetle populations recover post-harvest. Without the mediating effects of the canopy, low retention partial-harvests and clear-cuts cause increases in soil temperature and moisture extremes, as shading, interception and water uptake are reduced (Calogeropoulos et al. 2004; Ballard 2000). In insects, these rapid shifts in environmental conditions can increase mortality throughout juvenile life stages, as eggs and larvae passively exchange moisture with the surrounding environment and are at high risk for mortality due to evaporative water loss and heat stress (Buxton 1932). The magnitude of these impacts, however, may be offset by evolutionary forces such as maternal effects which can facilitate persistence of remnant populations throughout periods of rapid environmental change (Räsänen and Kruuk 2007).

Maternal effects occur when an offspring’s phenotype is affected by not only the genes contributed by the mother, but also the mother’s environmental conditions (Rossiter 1991, 1996; Mousseau and Fox 1998). This can impact a population’s evolutionary dynamics by affecting the rate or direction of genetic change in response to natural selection or by generating immediate phenotypic change through high levels of transgenerational phenotypic plasticity (Räsänen and Kruuk 2007). When remnant populations are exposed to rapid environmental change, one avenue through which maternal effects can shape the overall selection regime is through changes to female's maternal investment strategies (Beckerman et al. 2006).

At the time of producing offspring, females must allocate resources between their own physical growth and maintenance (*i.e.* absolute body size and associated metabolic demands), overall reproductive output (*i.e.* offspring quantity) and investment among individual offspring (*i.e.* offspring "quality"). Allocating more resources to any one of these categories can have consequences for the female or offspring's survival. For example, greater maternal investment per individual offspring can result in larger progeny with faster growth rates and decreased mortality (Einum and Fleming 1999; Fox and Mousseau 1996; Kyneb and Toft 2006). However, there is typically a trade-off between maternal investment in larger, better provisioned offspring, and the quantity of progeny a female can produce. Trade-offs between offspring quality and quantity are particularly detectible in females with a smaller absolute body size, as small females have limited resources to invest towards reproduction in addition to the potential for physiological constraints related to a smaller abdominal cavity (Smith and Fretwell 1974; Parker and Begon 1986; Einum and Fleming 2000).

Habitat conditions further impact trade-offs associated with maternal investment strategies. When environmental conditions are physiologically benign, maternal body size is expected to be positively correlated with increased offspring quantity, as larger females have more resources to invest in reproduction (Liao et al. 2014). However, when the environment is stressful, large females may be required to allocate a greater proportion of their resources towards meeting their more sizable metabolic demands. This can result in a decrease in the number of offspring larger females can produce as compared to small females (Shina 1988; Zera and Harshman 2001; Gibbs and van Dyck 2009). Additionally, increased investment per offspring is typically favored over producing a greater number of more poorly provisioned offspring when the habitat is stressful, as increased provisioning per offspring conveys a maximum benefit to progeny under stressful conditions (see examples in amphibians (Räsänen et al. 2008; Liao et al. 2014), reptiles (Sinervo 1999; Sinervo et al. 1992; Lovern and Adams

2008), fish (Einum and Fleming 1999; Hendry et al. 2001; Hutchings 1991) and invertebrates (Allen et al. 2008; Fox and Czesak 2000; García-Barros 2000)).

Given the significant and relatively abrupt impacts of forest harvesting on environmental conditions (Burton et al. 2010; Cyr et al. 2009), harvesting treatments such as clear-cutting or low retention partial harvesting are expected to impact maternal investment strategies in post-harvest remnant populations. For these remnant populations, increases in egg and larval mortality associated with drier or hotter habitat may be counterbalanced, at least to some degree, by increased maternal investment in higher quality offspring which are more likely to survive to maturity. As harvested areas continue to expand worldwide (Keenan et al. 2015; McEwan et al. 2020), understanding the effect of harvesting on remnant population's maternal investment strategies is necessary to predict how population dynamics and species distributions will shift throughout changing landscapes.

0.5 Thesis objectives

The overall goal of my thesis is to determine if ground beetle biodiversity will be preserved over long-term timeframes in boreal mixedwood forests which are harvested using clear-cutting or partial-retention harvesting. To do this, I address three main questions: (1) Within what timeframe do ground beetle species assemblages recover following clear-cutting and partial-retention harvesting? (2) Can increased retention after harvest improve survival/persistence of ground beetles under shifting temperature and precipitation regimes associated with climate change? and (3) How might rapid evolution of maternal investment strategies offset increased mortality in post-harvest remnant populations of ground beetles? I address these questions through three chapters, the specific objectives of which are described below.

In Chapter 1, I test the efficacy of clear-cutting and partial-retention harvesting (34%, 60% and 67% retentions) at preserving ground beetle biodiversity by comparing recovery across harvesting treatments and cover-types 5-, 10-, 15- and 20-years post-harvest. Additionally in this chapter, I examine how effective silvicultural treatments aimed at emulating natural disturbances are at transitioning ground beetle assemblages from those associated with early successional habitat towards those associated with stands with older growth attributes. The results from this chapter suggest partial-retention harvesting speeds recovery of ground beetles as compared to more intensive management options but is not effective at delaying or advancing the composition of ground beetle species assemblages between different successional stages. This work is in preparation for submission to *Ecological Applications*.

In Chapter 2, I examine the combined impacts of partial-retention harvesting and climate change on ground beetle abundance by combining repeated sampling of ground beetle communities over 20 years with site specific models of forest stand dynamics and meteorological data over the next two decades. The results from this chapter demonstrate that high-retention harvesting is likely to be an effective strategy to mitigate the effects of climate change under lower emissions scenarios but will likely be less effective under more extreme emissions scenarios. These results emphasize the value of prioritizing sustainable forest management practices under changing climatic conditions. This work is under review for publication in the *Journal of Applied Ecology*.

In Chapter 3, I investigate if habitat changes associated with recent clear-cutting elicits rapid evolution of maternal investment strategies in remnant populations of ground beetles and discuss how increased maternal investment into fecundity and offspring survivorship may influence remanent population's recovery post-harvest. This chapter explores the role of rapid evolution in the persistence of post-harvest communities in stressful environments and was published in *Ecology* (Egli and Work 2024).

In the final section of my thesis (Conclusion Générale) I summarize and integrate the major findings from the preceding chapters to produce a synthesis, use this information to recommend the most effective approaches to conservation of ground beetles over long-term timeframes in boreal mixedwood forests and suggest avenues for future research.

CHAPITRE 1

Twenty-year recovery of ground beetle communities after clear-cut and partial-retention harvests in boreal mixedwoods

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1.1 Abstract

Conservation of biodiversity in boreal forests depends on the development of sustainable approaches to forest management which go beyond conventional clear-cutting to preserve species assemblages over long-term timeframes. Natural disturbance-based management has been proposed as a more sustainable approach which aims to preserve biodiversity by reinitiating forest succession analogous to natural disturbances and creating/maintaining stands with older-growth attributes. We tested the efficacy of natural-disturbance based management at 1) conserving ground beetle biodiversity over 20 years post-harvest and 2) transitioning beetle assemblages from those associated with early successional habitat towards those associated with later successional forests. Between 1999 and 2001, we applied a series of experimental harvesting treatments across three forest cover-types representative of typical post-fire succession in eastern Canada's boreal forests (hardwood, mixedwood and softwood stands). Experimental harvests were part of the SAFE (Sylviculture et aménagement forestier écosystémique) experiment and included partial-retention harvests (34%, 60%, 67% retentions) and clear-cutting with logging residues left *in situ* or further treated through prescribed burns or whole-tree harvests. We collected ground beetles (70,877 individuals from 69 species) across replicated harvest treatments and cover-types ca. 5-, 10-, 15- and 20-years post-harvest and compared recovery of beetle assemblages using multivariate regression trees. In the initial 10 years post-harvest, beetle composition recovered in partial-retention harvests in the hardwood stands. After 15 years, beetle assemblages in the softwood and hardwood clear-cuts where logging residues were retained had also recovered. After 20 years, ground beetles within hardwood clear-cuts with prescribed burns or whole-tree harvests had recovered. However, the effects of harvesting in mixedwood stands continued to persist for 20 years post-harvest. While beetle assemblages in harvested hardwood and softwood stands were indistinguishable from the unharvested stands of their original cover-type, harvesting was not successful at either re-creating assemblages consistent with initial post-fire stand-types nor transitioning early successional species assemblages towards compositions consistent with later old-growth stands. However, maintaining significant standing retention was an effective strategy to speed recovery of ground beetles in hardwood stands, while intensive management options where logging residues were removed following clear-cutting delayed recovery.

Key Words: Alternative silviculture; biodiversity recovery; Carabidae; ecological resilience; ecosystem management; variable retention.

1.2 Introduction

In an effort to conserve biodiversity in managed forests, a natural disturbance-based approach to forest management has been suggested as a more sustainable alternative to clear-cutting (Bergeron et al. 2002; Kuuluvainen et al. 2021). In this approach, partial-retention harvesting (*i.e.* some proportion of residual trees left standing after harvest) can be used in an attempt to emulate small-scale natural disturbances to either maintain stand composition or advance forest composition towards older successional stages, depending on the intensity of the harvesting treatment applied (Fig. 1.1; Bergeron et al. 1999; 2002). Clear-cutting, implemented at intervals representative of the frequency of regional large-scale natural disturbances, may also be used in the NDBM approach in an attempt to shift stands of any cover-type to early successional hardwoods (Bergeron 2002). Used together, it is hoped that these strategies will maintain more heterogeneous habitat at the stand and landscape scale, which better reflect natural disturbance dynamics and maintains biodiversity which otherwise might be lost in areas managed solely through clear-cutting (Koivula et al. 2019; Klimaszewski et al. 2005).

Ground beetles (Coleoptera: Carabidae) are a highly diverse taxa that are effective indicators of the impacts of forest harvest on biodiversity (Work et al. 2008). In managed forests, species assemblages of ground beetles have been used to reflect changes associated with partial-retention harvesting (*e.g.* single-tree selection and gap-harvesting) as well as clear-cutting (Work et al. 2010; Klimaszewski et al. 2005; Wu et al. 2020). The large majority of these studies, however, lack frequent observations taken over long-term timeframes, as data was collected either from relatively newly established silvicultural experiments or through chronosequence comparisons of forest stands many years after harvesting occurred.

To evaluate the efficacy of NDBM at preserving biodiversity over longer timeframes, we measured the recovery of ground beetle assemblages through repeated sampling over 20 years following partial-retention harvesting (34%, 60% and 67% retentions) and clear-cutting in hardwood, mixedwood and softwood stands. We tested three main hypotheses. First, we predicted ground beetle assemblages would recover more quickly following partial-retention harvesting as compared to clear-cutting, as partial-retention harvesting provides continuous forest cover and minimizes post-harvest changes in soil temperature and moisture (Noualhaguet et al. 2023a; 2023b). Second, we predicted that maintaining significant standing retention (60% and 67% retentions) would advance ground beetle assemblages from species associated with early successional habitat, towards species compositions consistent with older, more structurally complex stands (Maleki et al. 2021). Finally, we predicted ground beetle assemblages in intermediate and late-successional stands would transition toward compositions consistent with early successional hardwood stands following lower retention harvesting (34% retention) or clear-cutting, as increased light reinitiates growth of shade intolerant hardwoods (Bergeron et al. 2014).

1.3 Methods

1.3.1 Study area

Harvesting treatments were applied in hardwood, mixedwood and softwood stands as part of the SAFE (Silviculture et aménagement forestier écosystémique) project located in the boreal forest of eastern Canada (Fig. 1.2). Hardwood stands originated after a fire in 1923 (Dansereau and Bergeron 1993) and are composed primarily of trembling aspen (*Populus tremuloides* Michx.) with a sparse conifer understory. Hardwood stands were harvested in 1998-1999 through single-tree selection harvests where 34% and 67% of the total basal area was retained and through clear-cutting. In the 34% partial-retention, large diameter marketable stems were removed, while non-vigorous small stems were cut in the 67% partial-retention (Brais et al. 2004). Clear-cuts were further divided into three nested treatments; (1) logging residues retained on site, (2) residues consumed in a prescribed burn and (3) whole-tree harvest where all logging residues were removed (Brais et al. 2004). Finally, unharvested hardwood stands were retained as long-term experimental controls.

Mixedwood stands originated following a fire in 1910 (Dansereau and Bergeron 1993) and are dominated by mature trembling aspen, balsam fir (*Abies balsamea* (L.) Mill), black spruce (*Picea mariana* Mill.) and white spruce (*Picea glauca* (Moench) Voss). Harvesting occurred in 2000-2001 through clear-cutting as well as two single-tree selection treatments which both retained 60% of the total basal area (Brais et al. 2013). In the first 60% partial-retention treatment, residuals were dispersed throughout the stand. In the second 60% partial-retention treatment, grouped islands of 400 m² were harvested with residuals retained around these islands. Unharvested mixedwood stands were also preserved as long-term experimental controls.

The late successional softwood stands are composed of balsam fir, white birch (*Betula papyrifera* Marshall) and white spruce. These stands have undergone damage from multiple spruce budworm outbreaks and date back to the last stand replacing fire in 1760 (Bergeron et al. 1995; Morin et al. 1993). Softwood stands were clear-cut in 1999-2000 (Strukelj et al. 2018). Additionally, unharvested softwood stands were retained as long-term experimental controls.

Within each cover-type, treatments were replicated three times in a randomized complete block design (Fig. 1.2). Experimental units (forest stand) ranged from 1-3 hectares in size. Within each experimental unit, five, 400 m^2 sized permanent sampling plots were established where changes in ground beetles and post-harvest shifts in stand structure and composition (*i.e.* live tree basal area (diameter at breast height (DBH) > 9cm), sapling abundance, etc.; Noualhaguet et al. 2023a; 2023b; Brais et al. 2004) were measured.

1.3.2 Ground beetle sampling

We sampled ground beetles within each permanent sampling plot using paired pitfall traps, set approximately 4 m apart. This resulted in 10 paired traps located within each treatment replicate (360 traps total). Pitfall traps were 7.5 cm in diameter and were filled with approximately 100 mL of propylene glycol as a killing agent and preservative (Niemelä and Spence 1994). We collected specimens from the pitfall traps at approximately 4-week intervals throughout the frost-free field season (late-May through August, >170,000 total trap days) in 2004-2006, 2010-2011, 2016 and 2018 (approximately 5-, 10-, 15- and 20-years post-harvest). We identified ground beetles to species using Larochelle (1976), Lindroth (1969) and Bousquet (2010).

1.3.3 Statistical analysis

We evaluated overall changes in ground beetle community composition using sum-of-squares multivariate regression tree (ssMRT) analysis (De'ath 2002). We square root transformed pooled catch rates of ground beetles within a stand (beetles/day) prior to analysis and used harvesting treatment and sample year as predictor variables. In the ssMRT analysis, sampling sites were successively divided based on explanatory variables to minimize differences within groups. The final tree ends in terminal nodes which represent sample units, in this case experimental stands, that differ in species composition. This approach has become increasingly used in ecological studies because it 1) directly relates species responses to explanatory variables without implicit assumptions about species responses across gradients, 2) is well suited for complex interactions or non-linear species responses and 3) outperforms commonly used ordination methods (De'ath 2002). We selected the final tree using cross-validation based on 1000 iterations and interpreted recovery to have occurred when species composition from the harvested stands and control were grouped into the same terminal node. We completed this analysis using package mvpart (Therneau and Atkinson 2014) in R studio (R version 4.2.3; R Core Team 2023).

1.4 Results

We identified a total of 70,877 ground beetles from 69 species collected over the 20 years sampled during this study. Changes in ground beetle assemblages were best characterized using a ssMRT with 13 terminal nodes. This model explained 59.7% of the total variance within the ground beetle assemblages (error = 0.403, CV error = 0.544, SE = 0.0355; Fig. 1.3). The initial split in the ssMRT accounted for 27.1% of the total variance (Fig. 1.4; for additional details see Appendix A: Table 1A) and separated the early response of species assemblages following harvest (2004-2010, *i.e.* ca. 5-10 years post-harvest) from responses in later years (2011-2018, *i.e.* ca. 11-20 years post-harvest; Fig. 1.3). This split was driven predominantly by significant increases in abundance of ground beetles over time in all silvicultural treatment by cover-type combinations (*e.g.* exponential rise in abundance of *Agonum retractum* LeConte, 1846*, Bembidion muscicola* Hayward, 1897*, Calathus ingratus* Dejean, 1828, *Harpalus fulvilabris* Mannerheim, 1853 and *Synuchus impunctatus* (Say, 1823) between 2004 and 2018) coupled with early reductions of closed canopy associated members of *Pterostichus* (Fig. 1.4) following harvest.

Within the early response to harvest (ca. 5-10 years post-harvest), beetle assemblages in clear-cuts in both hardwood and softwood stands differed from those found in the other treatments (Fig. 1.3, Split 2). Initially, assemblages in these clear-cuts were characterized by low abundances of the forest specialist *Platynus decentis* (Say, 1823) and closed-canopy associated species within the genera *Pterostichus* and *Sphaeroderus*, as well as increased abundance of open habitat associated members of *Agonum, Harpalus* and *Poecilus* (Figs. 1.4 and 1.5).

Throughout the same timeframe, beetle assemblages within the hardwood 34% and 67% partial-retentions recovered, as the community composition within these harvests was indistinguishable from those of the unharvested control (Fig. 1.3, Split 7). However, in the mixedwood stands, species assemblages in the partial-retention harvests (60% retention where residuals were dispersed throughout the stand or grouped around 400 m^2 gap-cuts) diverged from those in the unharvested stands and more strongly resembled assemblages found the mixedwood clear-cuts (Fig. 1.3, Split 4). In the mixedwoods, species assemblages in the partial-retention harvests and clear-cuts were characterized by the decreased abundance of forest specialist *P. decentis* and closed canopy associated members of *Pterostichus* (*Pterostichus adstrictus Eschscholtz, 1823*, *Pterostichus coracinus* (Newman, 1838) and *Pterostichus punctatissimus* (Randall, 1838)) as well as increased abundance of habitat generalist *Pterostichus pensylvanicus* LeConte, 1873 and open habitat associated *S. impunctatus* (Figs. 1.4 and 1.5).

In the decades following harvest, beetle assemblages differed between those collected ca. 10-15 years post-harvest (2011-2016), from those found ca. 20 years post-harvest (2018; Fig. 1.3, Split 3). Between 10-15 years post-harvest, all treatments applied in the softwood and mixedwood stands recovered and were indistinguishable from the uncut controls (Fig. 1.3, Split 12). During this period, beetle assemblages in the hardwood clear-cut where logging residues were retained and assemblages in the partial-retention harvests had recovered and were indistinguishable from those of the unharvested stands (Fig. 1.3, Split 8). However, prescribed burns and whole-tree harvests in the hardwood stands had yet to recover and continued to have species compositions which differed from those of the controls during this period (Fig. 1.3, Split 5). Beetle assemblages in these treatments were characterized by low abundances of species associated with closed canopies such as *P. decentis*, *P. adstrictus* and *P. coracinus* as well as high abundances of species associated with open canopy or early successional habitat, such as *A. retractum* and *S. impunctatus* (Figs. 1.4 and 1.5).

Twenty years post-harvest, beetle assemblages recovered across all hardwood treatments (Fig. 1.3, Split 9). Additionally, recovery of beetle assemblages in the harvested softwood stands, which initially occurred 10-15 years post-harvest, was persistent (Fig. 1.3, Split 9). In the mixedwood stands, however, recovery continued to change. During this period, the mixedwood partial-retention harvests and clear-cuts produced species assemblages which were more similar to each other and separate from that of the control (Fig. 1.3, Split 10). In these treatments, abundance of forest specialists such as *P. decentis, P. adstrictus* and *P. punctatissimus* and closed canopy associated species like *Platynus mannerheimii* (Dejean, 1828) and *Patrobus foveocollis* (Eschscholtz, 1823) remained low (Figs. 1.4 and 1.5). Additionally, open habitat associated species such as *Amerizus wingatei* (Bland, 1864), *Cymindis cribricollis* Dejean, 1831*, H. fulvilabris, Syntomus americanus* (Dejean, 1831) and invasive *Pterostichus melanarius* (Illiger, 1798), which were rarely caught in unharvested mixedwood stands, increased in abundance (Fig. 1.4).

1.5 Discussion

1.5.1 Speed of recovery following partial-retention harvesting

In the early successional hardwoods, ground beetle assemblages recovered within the initial 10 years after harvesting which retained as little as 34% of the standing basal area. This relatively rapid recovery comes in contrast to the findings in ongoing experiments in aspen-dominated boreal forests in western Canada, where ground beetle assemblages had yet to recover as of 15 years following comparable levels of partial-retention harvesting (Wu et al. 2020). Differences in the speed of recovery of ground beetle assemblages between these two study sites may be related, in part, to the size of the harvests. In our study, harvests were between 1-3 ha, whereas the ongoing recovery reported by Wu et al. (2020) was measured in larger harvested blocks (ca. 10 ha.). While localized effects of canopy removal on ground beetles (such as light penetration to the forest floor, accumulation of leaf-litter, etc.) are unlikely to differ between smaller and larger harvesting blocks, smaller-sized harvests may present a lower dispersal barrier for ground beetles, as individuals dispersing from neighboring stands are likely to reach the center of smaller-sized harvests more rapidly (Jopp and Reuter 2005). This may speed recovery, particularly in flightless species of ground beetles such as *P. coracinus* which have limited dispersal capabilities (Desender 2000).

Differing levels of fragmentation in the surrounding forested matrix may be an additional factor leading to more rapid recovery following harvests at our study site, as compared to ongoing recovery in western Canada reported by Wu et al. (2020). The forested landscape surrounding the experimental stands in our research site is, for the most part, intact (Appendix B, Fig. 1B(a)). In comparison, the landscape surrounding the partial-retention harvests in western Canada reported on by Wu et al. (2020) is significantly more fragmented, with additional clear-cuts neighboring, or in some cases surrounding, the experimental stands (Appendix B, Fig. 1B(b)). An intact forest matrix is likely to speed post-harvest recovery of ground beetle assemblages, as nearby source populations allow for a more consistent influx of forest specialist species into harvested areas, reduces intrusion of open canopy associated species from surrounding habitats and may result in a positive source/sink relationship between the surrounding unharvested habitat and the harvested site (Jopp and Reuter 2005; Desender 2000). Additionally, close proximity to source populations from unharvested habitat may also speed recovery of remnant populations by improving offspring survival, as eggs laid in harvested habitat by *P. coracinus* females originating from unharvested stands have an increased probability of survival (Egli and Work 2024).

Ground beetle assemblages in the 34% and 67% partial-retention harvests in the hardwood dominated stands recovered within the same timeframe. This was notable, as beetle assemblages in lower retention harvests measured in Europe and western Canada are typically slower to recover than assemblages in higher retention counterparts (Wu et al. 2020; Work et al. 2010; Toivanen et al. 2014; Koivula et al. 2019). The rapid recovery rate of ground beetles in the 34% retention in our study site could be related to variations in annual precipitation across the circumboreal forest. Over the past several decades, climate change has resulted in ongoing water deficits in much of Europe and central and western areas of North American boreal forests (Peng et al. 2011). Northeastern North America's boreal forest is projected to be the only area across the circumboreal forest with sufficient precipitation to fully compensate for increasing evaporative stress induced by warming temperatures, as this region receives more than twice the mean annual precipitation as its central and western counterparts (D'Orangeville et al. 2016). Ample precipitation may help equalize recovery speeds of ground beetles within low and high retention harvests by minimizing mortality of remaining mature trees, promoting more rapid growth of trees and minimizing the negative effects of increasing temperatures on saplings (Peng et al 2011; Boisvert-Marsh et al. 2019). Ample precipitation throughout the winter is also linked to high abundance of understory vegetation in boreal forests, as the insulating effects of persistent snow cover minimizes frost damage to roots and shoots, reduces pest outbreaks and facilitates synchronicity between plants and pollinators (Kreyling 2010). While understory vegetation is not measured as a part of basal area, increased shading of the forest floor from a robust understory layer contributes to increased retention of soil moisture and improves modulation of soil temperature extremes (Hart and

Chen 2006). Together, these impacts may have sped recovery of ground beetles within the low retention harvests, as the understory conditions associated with ample soil moisture improves survival of closed canopy associated species throughout the early phases of post-disturbance succession (Toivanen et al. 2014).

1.5.2 Shifts in species composition following partial-retention harvesting

The 67% partial-retention harvest in the hardwoods did not meet the NDBM aim of shifting ground beetle species compositions towards those associated with later successional stands but instead supported similar species compositions as the 34% retention throughout recovery. This ran counter to expectations, as ground beetle community composition measured following high retention partial harvests in Europe and western Canada have been found to shift towards later successional compositions post-harvest (Wu et al. 2020; Work et al. 2010; Toivanen et al. 2014; Koivula et al. 2019). Limitations of NDBM within our study site in transitioning species assemblages from hardwood associated towards later successional stages may have been linked to legacy effects in the hardwood stands minimizing changes to the post-harvest stand structure. In the years immediately following harvest, saplings were primarily composed of paper birch and spruce, as unharvested aspen stems maintain a supply of auxin in the root system, limiting aspen suckering and promoting growth of trees established prior to harvesting (Noualhaguet et al. 2023a). While the abundance of aspen saplings in the hardwood partial-retention harvests has increased over time, particularly in the 34% retention (Noualhaguet et al. 2023a), it's unlikely that this subtle shift in stand composition has led to changes in forest floor conditions (soil moisture, leaf litter accumulation, etc.) which are stark enough to directly impact ground beetle community composition (Thiele 1977). In future iterations of NDBM, it is possible that additional manipulations of stand structure (*e.g.* integration of seeding or planting to increase softwood regeneration following harvest; Lieffers et al. 2003) may be necessary to facilitate transitions of forest floor characteristics which would provide habitat for later successional compositions of ground beetles.

Consistent with ongoing studies in Europe and western Canada, beetle assemblages in the partial-retention harvests in the mixedwood stands had yet to recover as of 20 years post-harvest, retaining higher abundance of open-canopy associated species and fewer forest specialists than the control stands (Wu et al. 2020; Koivula et al. 2019). Delayed or lack of recovery in partial harvests may be linked to slowed growth of understory conifers in the mixedwood stands (Noualhaguet et al. 2023a; 2023b; Brais et al. 2013). While post-harvest recruitment of saplings was high in the mixedwood partial-retention harvests, legacy effects from the pre-existing bud/seed bank in the mixedwood stands resulted in regeneration of a second cohort of aspen which competed with the pre-established balsam fir saplings (Noualhaguet et al. 2023a; Brais et al. 2013). This slowed the transition of understory trees into the canopy, leading to a forest floor habitat which is more similar to clear-cuts due to prolonged increased light penetration (Noualhaguet et al. 2023b) and is likely to have favored open canopy associated species and limited species associated with mature mixedwoods (Thiele 1977).

1.5.3 Species composition following clear-cutting

Composition of ground beetles in the softwood clear-cuts did not shift towards assemblages consistent with early successional stands but instead recovered to assemblages consistent with uncut control stands. These results run counter to findings in western Canada, where clear-cutting is typically found to transition ground beetles towards species compositions associated with hardwoods (Wu et al. 2020; Work et al. 2010). Lack of a transition of ground beetle composition from softwood associated towards those associated with early successional hardwoods may be related to legacy effects in the softwoods hindering regeneration of saplings. Post-harvest regeneration of saplings in the clear-cut softwoods was much lower than anticipated, likely due to a combination of shade tolerant woody shrubs such as *Acer spictam* Lam. reducing conifer recruitment and growth, and low pre-harvest abundance of trembling aspen resulting in minimal regeneration of aspen saplings (Brais et al. 2004; Noualhaguet et al. 2023a). Throughout North America’s boreal forest, prevalence of aspen increases from east to west (Bergeron et al. 2014). Higher abundance of aspen in western Canada may account for ground beetles shifting towards hardwood dominated composition following clear-cutting (Wu et al. 2020; Work et al. 2010), as more significant aspen regeneration favors hardwood associated beetle species with higher tolerance ranges for increased seasonal variance in temperature and humidity associated with deciduous foliage (Koivula et al. 1999).

Another silvicultural practice utilized within SAFE, which may have contributed to beetle assemblages returning to their pre-harvest community composition following clear-cutting, is the prioritization of maintaining a relatively undisturbed soil and understory layer throughout harvest (Brais et al. 2004). This practice partially preserves habitat characteristics associated with pre-harvest canopy trees (*e.g.* sub-canopy light and microclimate, site moisture regime, etc.; Perry et al. 2008) and provides habitat for remnant populations of ground beetles to survive harvesting *in situ*. Many ground beetle species have highly localized populations and limited dispersal capabilities; therefore, a sizable portion of post-harvest recovery is likely to occur by rebuilding from remnant populations, rather than relying primarily on the slower process of colonization by individuals from neighboring stands (Jopp and Reuter 2005). While this is expected to speed post-harvest recovery, it also suggests that shifting ground beetle species composition is more complicated than simply creating conditions for the sought after species, as recovery driven by remnant populations is expected to advance along the pre-harvest ecological gradient rather than follow the anticipated trajectory of post-harvest succession (Bergeron et al. 2017).

To use clear-cutting to transition ground beetles towards early successional species compositions, harvesting in larger blocks may be required, as increased harvesting areas are frequently necessary to obtain significant regeneration of aspen (Rogers et al. 2014). Furthermore, more significant disruption of the soil/understory layer may be required to minimize recovery of ground beetle species assemblages driven by pre-existing remnant populations. Although these measures may more successfully transition species compositions, they are also likely to extend recovery time significantly given that colonization by individuals from neighboring stands can be a slow process, particularly if the distance required to reach the center of the harvesting block is large (Jopp and Reuter 2005; Desender 2000).

1.5.4 Impact of additional manipulations of logging residues

Additional manipulations of logging residues through prescribed burning or whole-tree harvest further increased abundance of open-habitat species and reduced forest specialists as compared to clear-cutting alone. For species which responded negatively to clear-cutting, such as *P. decentis* and *P. adstrictus*, these successive disturbances appeared to have additive effects which further reduce abundance and slowed recovery by an additional five years. Similar impacts were found in studies which investigated ground beetle response to whole-tree harvest and prescribed burning, as well as other intensive recuperations of biomass, such salvage logging and removal of residual deadwood (Work et al. 2014; 2023; Toivanen et al. 2014; Klimaszewski et al. 2005). These findings are noteworthy, as several international and national policies have been put in place which promote the removal of biomass post-harvest to help meet growing energy demands (Berch et al. 2011). However, given the additional impacts of biomass removal on the composition of ground beetle communities, efforts to avoid these compounding disturbances should be considered when developing forest management plans which aim to preserve biodiversity.

1.5.5 Conclusions and management implications

Our findings emphasize three principal implications for forest management and conservation of biodiversity: (1) Partial-retention harvesting in early successional, hardwood stands speeds recovery of ground beetles as compared to clear-cutting. Forest managers should therefore seek to balance these benefits with the trade-offs associated with increased total areas which must be harvested to meet economically sustainable timber volume requirements. (2) NDBM was not successful at reinitiating succession analogous to natural disturbances. As the current iteration of NDBM was unable to transition species assemblages associated with earlier successional stands towards those associated with stands with older-growth attributes, late successional stands should be preserved whenever possible to avoid future losses of biodiversity. Additionally, future iterations of NDBM may be more effective at transitioning fauna between successional stages through use of additional efforts, such as seeding or planting of softwood saplings to provide habitat for later successional compositions of ground beetles. (3) Additional manipulations of logging residues following clear-cutting further homogenizes species assemblages and delays recovery. This response was atypical to those observed following clear-cutting alone and likely falls outside the range of natural variability observed in this region. Thus, additional removals of biomass should be avoided when developing sustainable forest management practices.

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1.7 Contribution statement

All authors (both myself and Timothy Work) contributed to the conception of the study design, methodology and data collection for this chapter. Field collections of ground beetles at SAFE were led by Timothy Work and the following individuals: Elise Bolduc (2004), Kit O'Connor (2006), Simon Paradis (2010), Samuel Gladu (2016-2018) and me (Lauren Egli; 2018). Identifications of ground beetles to species was led by Timothy Work and the following individuals: Kit O'Connor (specimens collected in 2004-2006), Simon Paradis (specimens collected in 2010), Samuel Gladu (specimens collected in hardwood stands in 2016) and me (Lauren Egli; specimens collected in the hardwood, mixedwood and softwood stands in 2016 and all specimens collected in 2018). In total, I identified approximately 63% of the ground beetle specimens used in this study (~45000/71000). Timothy Work and I co-analyzed the data for this chapter, I led the writing of the manuscript, and Timothy Work revised the manuscript critically for important intellectual content.

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1.9 Figures

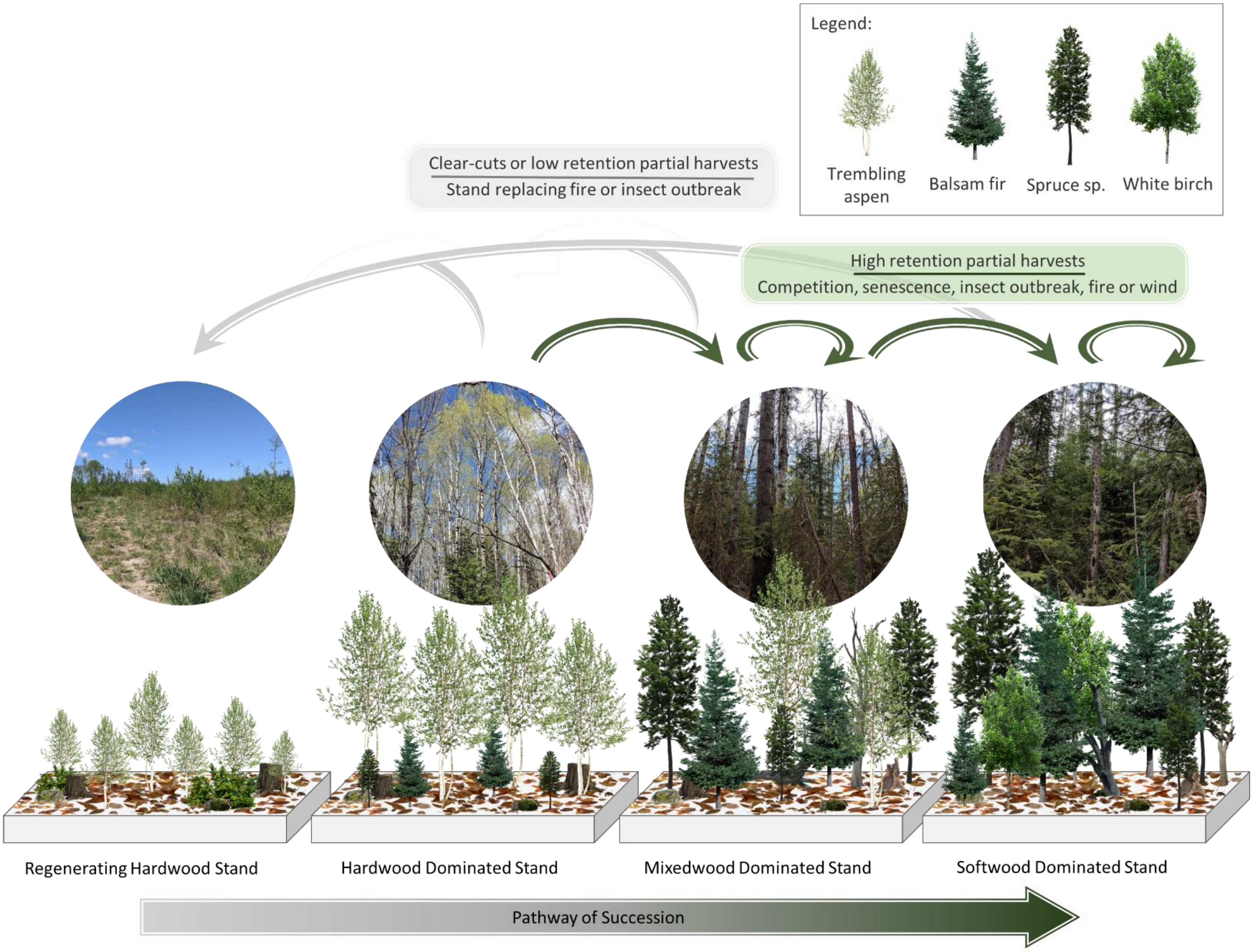
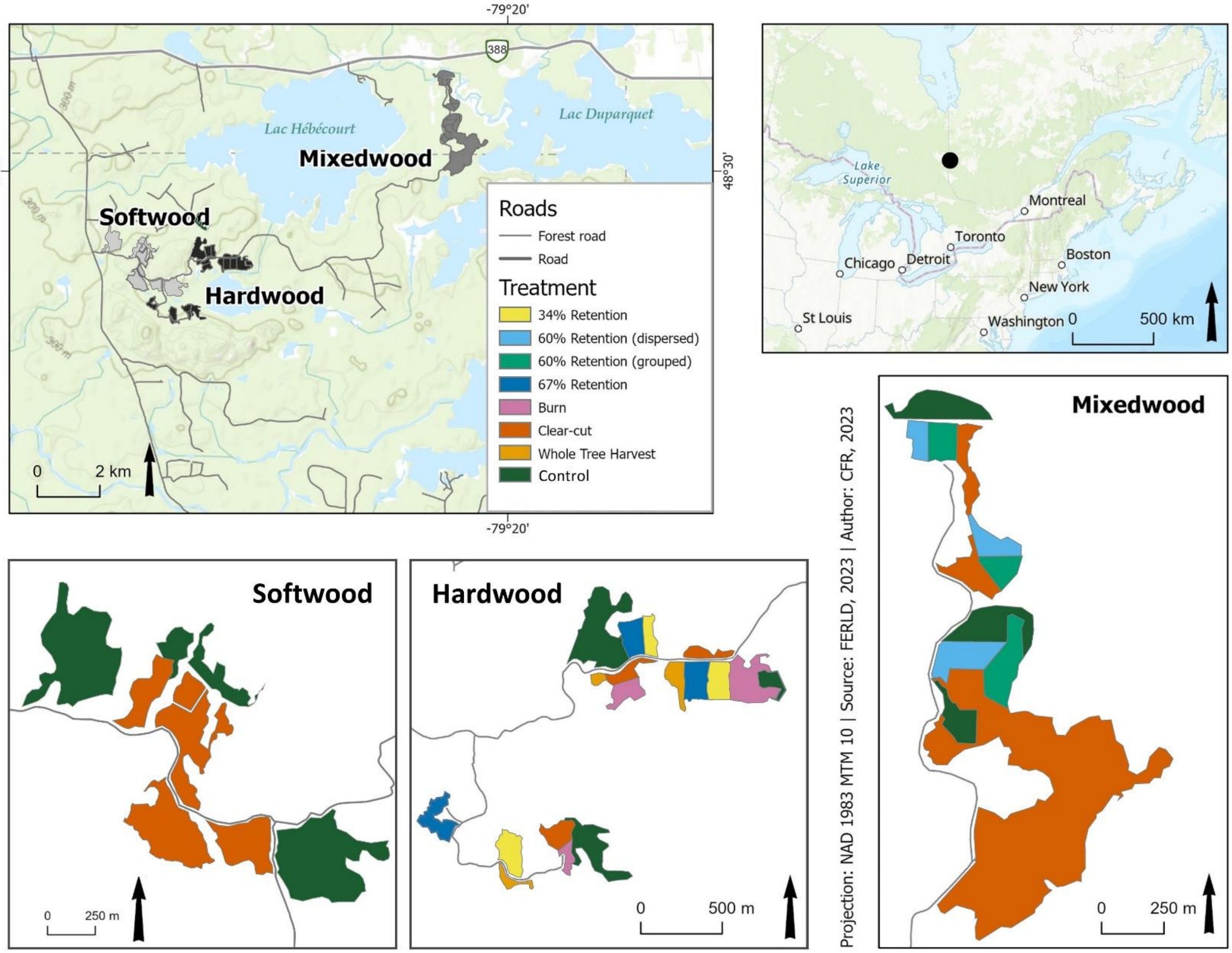


Figure 1.1. Classic stand dynamics in boreal mixedwood forests of eastern Canada following a stand replacing disturbance. Dominant cover-types correspond to the various post-fire stand successional stages, while arrows represent the effect of natural disturbances on a stand's movement between successional stages and the intended outcomes of natural disturbance-based silvicultural treatments (Bergeron et al. 1999, 2002; photographs of field site by L. Egli).



Projection: NAD 1983 MTM 10 | Source: FERLD, 2023 | Author: CFR, 2023

Figure 1.2. Map of the study area showing the location in northwestern Quebec (top right), the location of each forest cover-type within the Lake Duparquet Research and Teaching Forest research site (top left) and the experimental design within each cover-type (bottom).

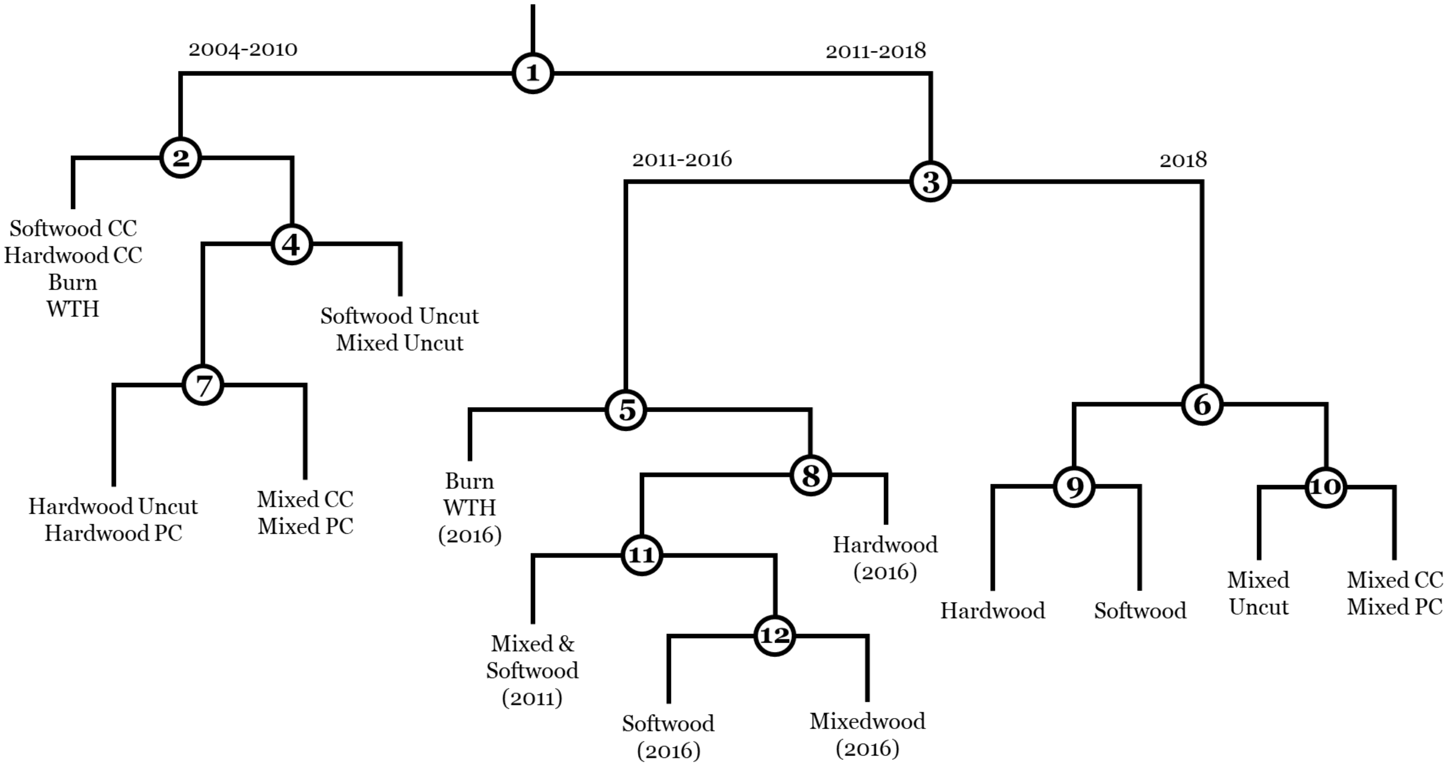
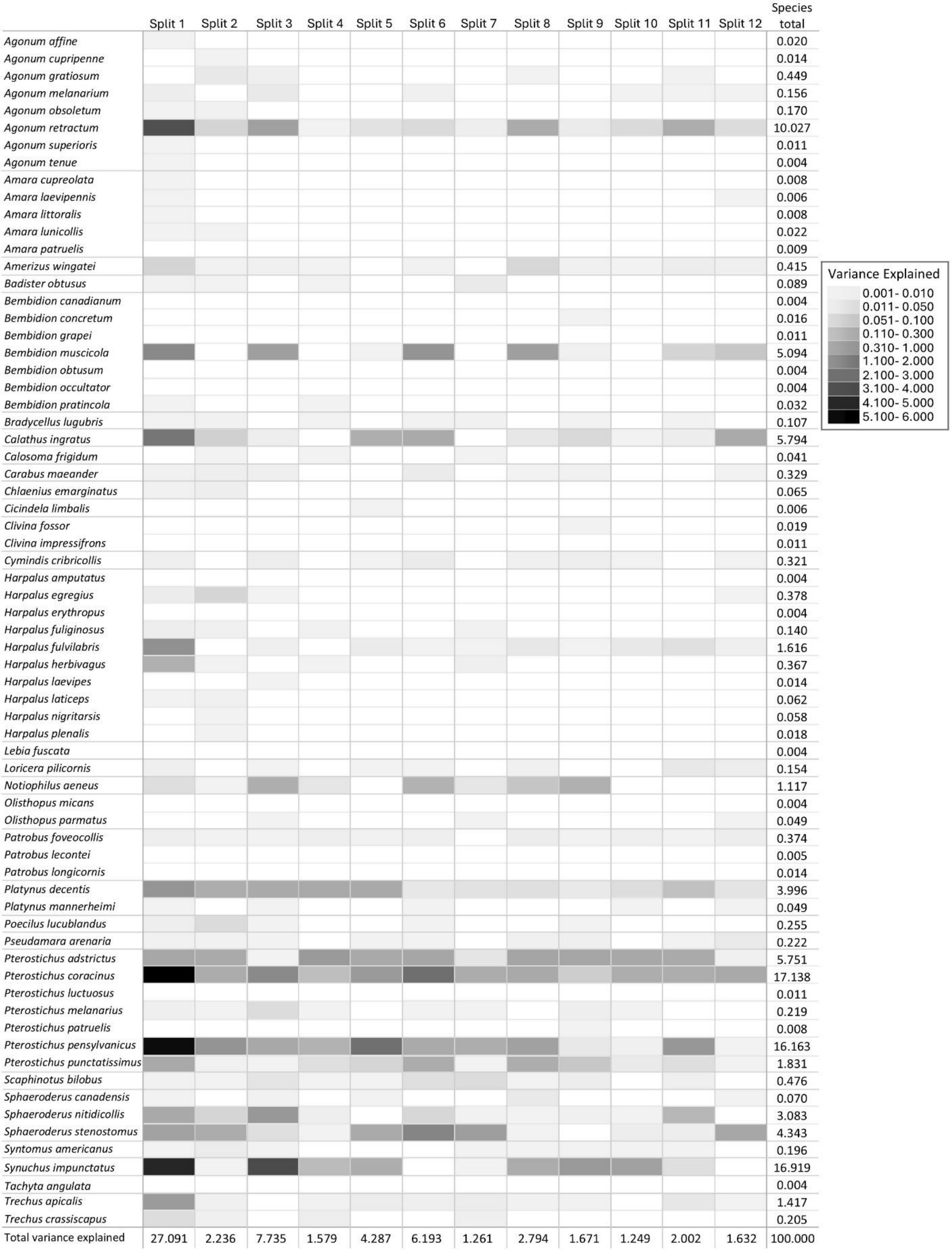


Figure 1.3. Sum of squares multivariate regression tree (ssMRT) depicting changes in ground beetle community compositing based on differences in harvesting treatment and time-since-harvest. This analysis explained 59.7% of the total variance and the final tree was based on 821/1000 iterations. Harvest treatments: CC, clear-cuts; Burn, prescribed burns of logging residues; WTH, whole-tree harvests; PR, partial-retention harvests; Uncut, unharvested controls.



	Split 1	Split 2	Split 3	Split 4	Split 5	Split 6	Split 7	Split 8	Split 9	Split 10	Split 11	Split 12	Species total
Agonum affine													0.020
Agonum cupripenne													0.014
Agonum gratiosum													0.449
Agonum melanarium													0.156
Agonum obsoletum													0.170
Agonum retractum													10.027
Agonum superioris													0.011
Agonum tenue													0.004
Amara cupreolata													0.008
Amara laevipennis													0.006
Amara littoralis													0.008
Amara lunicollis													0.022
Amara patruelis													0.009
Amerizus wingatei													0.415
Badister obtusus													0.089
Bembidion canadianum													0.004
Bembidion concretum													0.016
Bembidion grapei													0.011
Bembidion muscicola													5.094
Bembidion obtusum													0.004
Bembidion occultator													0.004
Bembidion pratincola													0.032
Bradycellus lugubris													0.107
Calathus ingratus													5.794
Calosoma frigidum													0.041
Carabus maeander													0.329
Chlaenius emarginatus													0.065
Cicindela limbalis													0.006
Clivina fossor													0.019
Clivina impressifrons													0.011
Cymindis cribricollis													0.321
Harpalus amputatus													0.004
Harpalus egregius													0.378
Harpalus erythropus													0.004
Harpalus fuliginosus													0.140
Harpalus fulvilabris													1.616
Harpalus herbivagus													0.367
Harpalus laevipes													0.014
Harpalus laticeps													0.062
Harpalus nigritarsis													0.058
Harpalus plenalis													0.018
Lebia fuscata													0.004
Loricera pilicornis													0.154
Notiophilus aeneus													1.117
Olisthopus micans													0.004
Olisthopus parmatus													0.049
Patrobus foveocollis													0.374
Patrobus lecontei													0.005
Patrobus longicornis													0.014
Platynus decentis													3.996
Platynus mannerheimi													0.049
Poecilus lucublandus													0.255
Pseudamara arenaria													0.222
Pterostichus adstrictus													5.751
Pterostichus coracinus													17.138
Pterostichus luctuosus													0.011
Pterostichus melanarius													0.219
Pterostichus patruelis													0.008
Pterostichus pensylvanicus													16.163
Pterostichus punctatissimus													1.831
Scaphinotus bilobus													0.476
Sphaeroderus canadensis													0.070
Sphaeroderus nitidicollis													3.083
Sphaeroderus stenostomus													4.343
Syntomus americanus													0.196
Synuchus impunctatus													16.919
Tachyta angulata													0.004
Trechus apicalis													1.417
Trechus crassiscapus													0.205
Total variance explained	27.091	2.236	7.735	1.579	4.287	6.193	1.261	2.794	1.671	1.249	2.002	1.632	100.000

Figure 1.4. Variance explained by individual ground beetle species at each split in the sum of squares multivariate regression tree (ssMRT) model examining the effects of harvest and time-since-harvest on ground beetle community composition. For test statistics, see Appendix A: Table 1A.

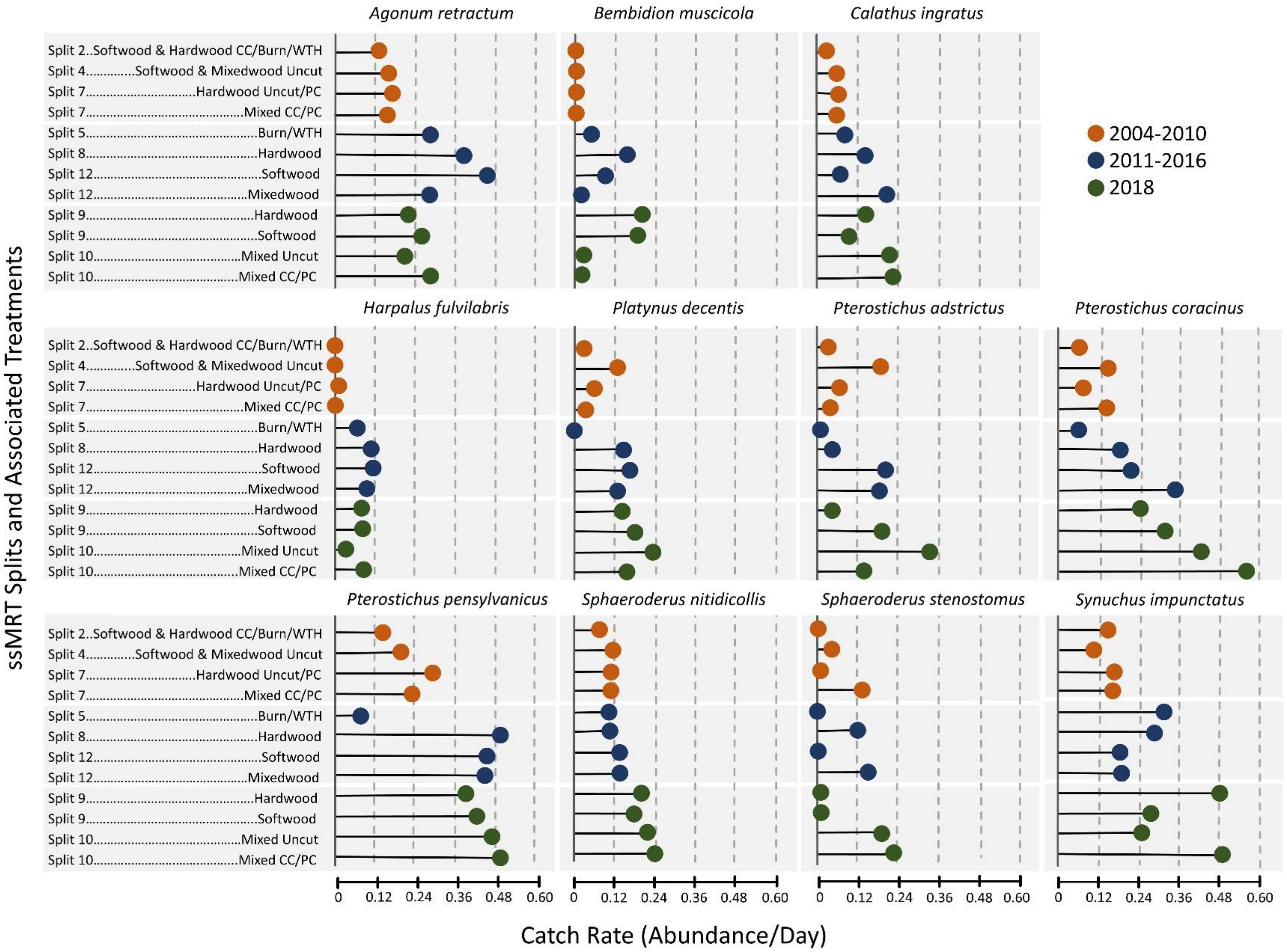


Figure 1.5. Catch rate of the eleven most abundant ground beetle species at each terminal node of the final ssMRT model.

1.10 Appendix A.

1.10.1 Results

Changes in ground beetle assemblages (70,877 individuals from 69 species) were best characterized by a sum of squares multivariate regression tree (ssMRT) with 13 terminal nodes. This model explained 59.7% of the total variance within the ground beetle assemblages (Table 1A).

Table 1A. Variance explained by individual ground beetle species at each split in the ssMRT model examining the effects of harvest and time-since-harvest on ground beetle community composition.

Species and total variance	Split 1	Split 2	Split 3	Split 4	Split 5	Split 6	Split 7	Split 8	Split 9	Split 10	Split 11	Split 12	Tree total	Species total
Agonum affine	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.020
Agonum cupripenne	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.014
Agonum gratiosum	0.000	0.023	0.008	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.004	0.000	0.038	0.449
Agonum melanarium	0.013	0.000	0.022	0.000	0.000	0.006	0.000	0.000	0.000	0.001	0.001	0.001	0.045	0.156
Agonum obsoletum	0.001	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.170
Agonum retractum	3.232	0.066	0.579	0.003	0.039	0.053	0.010	0.220	0.017	0.054	0.169	0.500	4.941	10.027
Agonum superioris	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011
Agonum tenue	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004
Amara cupreolata	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008
Amara laevipennis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.006
Amara littoralis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008
Amara lunicollis	0.001	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.022
Amara patruelis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009
Amerizus wingatei	0.067	0.004	0.006	0.001	0.000	0.004	0.000	0.059	0.007	0.003	0.012	0.008	0.172	0.415
Badister obtusus	0.004	0.001	0.000	0.003	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.027	0.089
Bembidion canadianum	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004
Bembidion concretum	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.001	0.016
Bembidion grapei	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011
Bembidion muscicola	1.333	0.000	0.616	0.000	0.002	0.997	0.000	0.608	0.007	0.000	0.067	0.094	3.724	5.094
Bembidion obtusum	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004
Bembidion occultator	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004
Bembidion pratincola	0.002	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.032
Bradycellus lugubris	0.003	0.005	0.000	0.001	0.000	0.001	0.004	0.000	0.002	0.000	0.001	0.000	0.017	0.107
Calathus ingratus	1.967	0.075	0.010	0.000	0.147	0.266	0.000	0.026	0.056	0.003	0.012	0.269	2.832	5.794
Calosoma frigidum	0.000	0.001	0.000	0.001	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.006	0.041
Carabus maeander	0.004	0.010	0.009	0.000	0.000	0.017	0.000	0.001	0.005	0.000	0.000	0.003	0.049	0.329
Chlaenius emarginatus	0.004	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.065
Cicindela limbalis	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.006
Clivina fossor	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.001	0.019
Clivina impressifrons	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.011
Cymindis cribricollis	0.008	0.000	0.013	0.000	0.002	0.012	0.000	0.006	0.010	0.001	0.000	0.003	0.055	0.321
Harpalus amputatus	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004

Table 1A continued

Species and total variance	Split 1	Split 2	Split 3	Split 4	Split 5	Split 6	Split 7	Split 8	Split 9	Split 10	Split 11	Split 12	Tree total	Species total
Harpalus egregius	0.015	0.065	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.083	0.378
Harpalus erythropus	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004
Harpalus fuliginosus	0.012	0.006	0.000	0.002	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.025	0.140
Harpalus fulvilabris	1.086	0.000	0.009	0.000	0.016	0.003	0.001	0.025	0.001	0.024	0.040	0.008	1.212	1.616
Harpalus herbivagus	0.143	0.003	0.000	0.003	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.158	0.367
Harpalus laevipes	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.014
Harpalus laticeps	0.002	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.062
Harpalus nigritarsis	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.058
Harpalus plenalis	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.018
Lebia fuscata	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004
Loricera pilicornis	0.008	0.000	0.001	0.000	0.002	0.002	0.000	0.006	0.000	0.000	0.023	0.012	0.053	0.154
Notiophilus aeneus	0.045	0.003	0.148	0.027	0.000	0.139	0.027	0.099	0.144	0.000	0.000	0.000	0.633	1.117
Olisthopus micans	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004
Olisthopus parmatus	0.000	0.000	0.001	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.001	0.004	0.049
Patrobus foveocollis	0.011	0.001	0.003	0.011	0.005	0.009	0.000	0.015	0.002	0.009	0.001	0.012	0.078	0.374
Patrobus lecontei	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
Patrobus longicornis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.014
Platynus decentis	0.954	0.149	0.275	0.284	0.305	0.025	0.036	0.042	0.022	0.048	0.107	0.031	2.275	3.996
Platynus mannerheimii	0.002	0.000	0.003	0.000	0.000	0.001	0.000	0.000	0.000	0.001	0.000	0.001	0.008	0.049
Poecilus lucublandus	0.011	0.051	0.001	0.000	0.000	0.001	0.000	0.000	0.001	0.000	0.000	0.000	0.064	0.255
Pseudamara arenaria	0.005	0.004	0.001	0.000	0.002	0.002	0.000	0.007	0.008	0.000	0.001	0.019	0.049	0.222
Pterostichus adstrictus	0.346	0.258	0.003	0.793	0.285	0.380	0.030	0.411	0.380	0.340	0.266	0.006	3.497	5.751
Pterostichus coracinus	5.824	0.198	1.320	0.113	0.777	2.212	0.206	0.284	0.082	0.165	0.156	0.288	11.624	17.138
Pterostichus luctuosus	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.011
Pterostichus melanarius	0.008	0.002	0.050	0.003	0.000	0.002	0.001	0.000	0.011	0.002	0.000	0.000	0.078	0.219
Pterostichus patruelis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.002	0.008
Pterostichus pensylvanicus	5.457	0.978	0.341	0.138	2.177	0.254	0.174	0.569	0.024	0.006	0.879	0.002	10.999	16.163
Pterostichus punctatissimus	0.281	0.005	0.001	0.042	0.065	0.214	0.003	0.172	0.093	0.019	0.044	0.003	0.941	1.831
Scaphinotus bilobus	0.004	0.002	0.032	0.001	0.001	0.043	0.049	0.002	0.012	0.000	0.008	0.000	0.154	0.476
Sphaeroderus canadensis	0.003	0.000	0.004	0.000	0.001	0.000	0.000	0.022	0.000	0.000	0.000	0.001	0.030	0.070
Sphaeroderus nitidicollis	0.301	0.063	0.849	0.011	0.000	0.059	0.004	0.001	0.006	0.003	0.128	0.000	1.425	3.083
Sphaeroderus stenostomus	0.540	0.207	0.043	0.002	0.265	1.480	0.651	0.001	0.000	0.012	0.012	0.370	3.583	4.343
Syntomus americanus	0.001	0.015	0.002	0.000	0.000	0.000	0.003	0.001	0.002	0.001	0.003	0.000	0.029	0.196
Synuchus impunctatus	4.589	0.001	3.383	0.120	0.180	0.000	0.002	0.211	0.772	0.558	0.043	0.000	9.859	16.919
Tachyta angulata	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004
Trechus apicalis	0.754	0.007	0.000	0.005	0.015	0.009	0.015	0.005	0.004	0.000	0.025	0.001	0.841	1.417
Trechus crassiscapus	0.048	0.007	0.000	0.013	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.076	0.205
Total variance explained	27.092	2.236	7.735	1.578	4.287	6.193	1.260	2.794	1.671	1.249	2.003	1.632	59.729	100.000

1.11 Appendix B.

1.11.1 Landscape scale forest matrix

The forested landscape surrounding the SAFE (Silviculture et aménagement forestier écosystémique) project located in the boreal forests of northern Quebec, Canada (48°29'07"N, 79°24'27"W) is, for the most part, intact (Figure 1B (a)). In comparison, the forest matrix which surrounds the EMEND (Ecosystem Management Emulating Natural Disturbance) project, located in the boreal forests of northwestern Alberta, Canada (56°46’13”N, 118°22’28”W; Wu et al. 2020), is fragmented due to more extensive harvesting in the area (Figure 1B (b)).

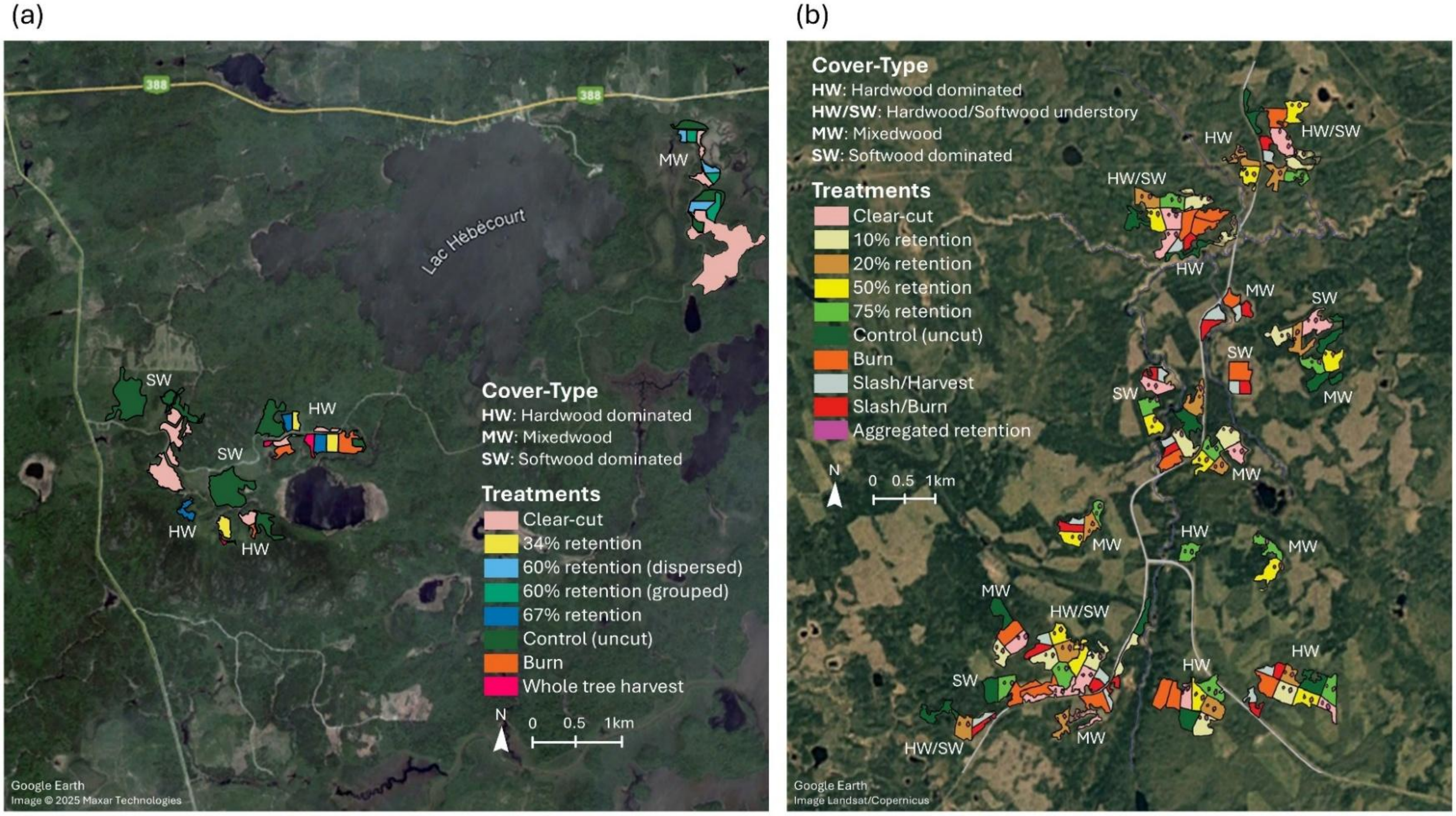


Figure 1B. Comparison of forest matrix surrounding silvicultural treatments of (a) the SAFE (Silviculture et aménagement forestier écosystémique) project, located in the boreal forest of eastern Canada and (b) the EMEND (Ecosystem Management Emulating Natural Disturbance) project, located in the boreal forest of western Canada (map modified from Wu et al. 2020).

CHAPITRE 2

Increased retention after harvest better maintains carabid abundance in boreal mixedwood forests under two climate change scenarios

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2.1 Abstract

Climate models predict shifting temperature and precipitation regimes across the boreal forest which may lead to losses of biodiversity in managed landscapes. Mitigating climate change stress on forest biodiversity will depend on developing sustainable approaches to forest management that preserve forest organisms over long timeframes. Silvicultural strategies which retain significant standing trees may better maintain forest organisms under climate change as compared to conventional practices such as clear-cutting and may provide an effective and achievable strategy for conservation of biodiversity. We predicted the long-term, combined impacts of partial-retention harvesting and climate change on the abundance of carabid beetles, an important group of generalist predators, in boreal mixedwood forests. We combined repeated sampling of carabid communities in replicated harvesting treatments over 20 years from a large-scale experiment in northeastern North America with site-specific models of forest stand dynamics and meteorological data to predict changes in carabid species over the next two decades under emission scenarios SSP1-2.6 and SSP5-8.5. Abundance of most carabid species was greatest in stands with more standing retention. Additionally, most species increased in abundance with increased precipitation throughout the breeding season but declined with warming winters. Under SSP1-2.6, most species were expected to increase through the coming decades, particularly in stands with significant post-harvest retention. High-retention treatments conferred a numerical advantage for carabid populations, which in turn were more resilient to short-term periods of stress such as pest outbreaks or senescence of overstory trees. Under SSP5-8.5, many species increased initially but then declined. While carabid abundance was highest in the high-retention treatments, populations within all treatments reached low density by ca. 2038. Our findings suggest that under lower emission scenarios, high-retention harvesting is an effective strategy to conserve carabids over the next two decades and can increase species' resilience throughout short-term periods of stress. Under more extreme emissions scenarios, high-retention harvesting can be used to conserve carabid populations for approximately the next decade and may permit species with poor dispersal abilities increased time to develop adaptations to rising temperatures..

Key words: Carabidae; ecological forestry; ground beetles; natural disturbance-based management; partial-cut harvesting; retention forestry; variable retention.

2.2 Introduction

Climate models predict that increases in temperatures are likely to exceed 2 °C across the circumboreal forest before the end of the century (IPCC 2022). Changing temperatures – combined with greater variability in precipitation, increasing frequency of insect outbreaks and altered fire regimes – are resulting in substantial shifts in local conditions which fall outside of the range of variability observed over the last century (D'Orangeville et al. 2018; IPCC 2022). Stress on forest organisms from climate change is expected to be exacerbated in forested ecosystems that are managed through conventional harvesting practices such as clearcutting (Guignabert et al. 2024). For instance, increasing temperatures due to climate change are expected to add to post-harvest increases in soil temperatures, resulting in exponentially higher metabolic demands in ectothermic taxa such as insects as well as increased mortality due to desiccation or heat stress (González-Tokman et al. 2020). To mitigate the impacts of climate change stressors on forest organisms, alternative and adaptive climate-smart silvicultural practices may be needed (Achim et al. 2022).

Climate-smart silvicultural practices are often separated into two distinct approaches. The first approach focuses on augmenting or replacing existing tree species with native or non-native species with functional traits which are better adapted to warmer and drier habitats to create stands better suited to changing climatic conditions (Messier et al. 2022). The second approach focuses on increasing resilience of managed forests by maintaining uneven-aged, multi-species stands with continuous canopy cover (Achim et al. 2022). Silvicultural approaches which encourage heterogeneous stand structures may improve resilience under climate change, as stands with greater genetic variation and wider size and age distributions are generally less vulnerable to biotic and abiotic hazards (O'Hara and Ramage 2013). Resilience focused approaches to climate-smart forestry often build on management strategies that emulate natural disturbance regimes (Bergeron and Harvey 1997) and integrate partial-retention harvesting, either via grouped selection (*i.e.* gap-cutting) or single-tree selection with retention of unharvested mature trees to maintain canopy cover even after harvest. These silvicultural treatments allow managers to select resilient tree species for retention and reduce within-stand vulnerability to drought stress and crown fires (Nolet et al. 2014). Furthermore, continuous canopy coverage associated with high-retention partial-harvests buffers microhabitats from local shifts in temperature and humidity as compared to clearcutting and has the potential to mitigate climate change stress in forest organisms (De Frenne et al. 2021).

In this study, we evaluated the combined impact of climate change and partial-retention harvesting on dominant carabid beetle species (Coleoptera, Carabidae) in hardwood and mixedwood stands in northeastern Canada's boreal forest. We selected carabids, as they are an abundant and species rich component of forest biodiversity which has been used globally to evaluate impacts of anthropogenic disturbances including forest harvesting (Work et al. 2008) and climate change (Weiss et al. 2024). We selected nine species which represent a significant proportion of the total catch and have been found to drive post-harvest recovery of carabid species assemblages. Additionally, these species encompass a range of habitat preferences (open habitat adapted, forest generalists, closed-canopy specialists) and typically demonstrate either autumn- or spring-breeding strategies (Lindroth 1969; Larochelle & Lariviere 2003). Autumn-breeding species overwinter in the soft-bodied, larval stage prior to reaching maturity and are, therefore, more vulnerable to desiccation due to temperature/moisture extremes. Alternatively, spring-breeding species mature throughout the summer and overwinter in the more robust, adult life-stage (Lindroth 1969; Thiele 1977).

For these species, we quantified the drivers of post-harvest changes in abundance by combining repeated sampling over 20 years from a large-scale experiment (the SAFE project), with site specific models of forest stand dynamics and meteorological data, and then projected changes in species' abundance over the next two decades under two climate change emissions scenarios. We predicted that high-retention harvesting would mitigate climate change stress on carabids as compared to more intensive harvests, as maintaining significant standing retention is expected to buffer local shifts in temperature and humidity (De Frenne et al. 2021). Additionally, we expected species associated with closed canopies to have reduced abundance in lower retention harvests and to decline more steeply over time under the high emissions climate change scenario, as these species are expected to have lower tolerance to increasing temperatures/reduced soil moisture as compared to forest generalist and open canopy adapted species (Thiele 1977).

2.3 Materials and methods

2.3.1 Study area and design

We conducted our study in hardwood and mixedwood stands within the SAFE project (Silviculture et aménagement forestier écosystémique), a large-scale experiment located in Quebec, Canada. The SAFE experiment consists of a range of silvicultural treatments meant to emulate natural disturbances and forest succession applied across replicated stands (Fig. 2.1; Brais et al. 2004; Bergeron and Harvey 1997). Hardwood stands within SAFE originated from a fire in 1923 and were primarily trembling aspen (*Populus tremuloides* Michx.) with a sparse conifer understory (Dansereau and Bergeron 1993). Harvests in hardwood stands occurred in 1998-1999 through single-tree selection where 34% or 67% of the total basal area was retained. In the 34% partial-retention, large diameter marketable trees were harvested. In the 67% partial-retention, non-vigorous small stems were selected for harvest. Additionally, unharvested hardwood stands were maintained as long-term experimental controls. Mixedwood stands originated from fire in 1910 and were dominated by mature trembling aspen, balsam fir (*Abies balsamea* (L.) Mill), black spruce (*Picea mariana* Mill.) and white spruce (*Picea glauca* (Moench) Voss) (Dansereau and Bergeron 1993). Harvests in the mixedwoods occurred in 2000-2001 through two partial-retention harvests, both of which retained 60% of the total basal area. For these silvicultural treatments, residuals were either dispersed through the stand (*i.e.* "60% dispersed retention") or located around a gap cut of approximately 400 m² (*i.e.* "60% grouped retention"). Unharvested mixedwood stands were also maintained as long-term experimental controls. For both stand types, each treatment was replicated three times in a randomized complete block design, resulting in a total of 18 experimental stands which ranged from 1-3 hectares in size (Fig. 2.1).

2.3.2 Carabid sampling and focal species selection

We sampled carabids within five 400 m^2 permanent sampling plots located within each experimental stand using paired pitfall traps (90 sampling plots and 180 traps total; Fig. 2.1; Spence and Niemelä 1994). Pitfall traps were spaced approximately 4 m apart and oriented north and south of each plot centroid. We collected carabids at approximately 4-week intervals throughout the frost-free field season (late-May through August) in 2004-2006, 2010-2011, 2016 and 2018 (approximately 5-, 10-, 15- and 20-years post-harvest) and identified these specimens to species using Larochelle (1976), Lindroth (1969) and Bousquet (2010).

For this study, we selected nine species that represented 71% of the total carabid catch (50142/70877 individuals). These species included *Agonum retractum* LeConte 1846*, Calathus ingratus* Dejean 1828 and *Synuchus impunctatus* (Say 1823), which are frequently associated with open habitat, *Pterostichus* *pensylvanicus* LeConte 1873*, Sphaeroderus nitidicollis* Guérin-Méneville 1829 and *Sphaeroderus stenostomus* (Weber 1801), which are typically considered forest generalist species, and *Platynus decentis* (Say 1823)*, Pterostichus adstrictus* Eschscholtz 1823 and *Pterostichus coracinus* (Newman 1838), which are typically associated with closed-canopies or unharvested stands (Lindroth 1969; Larochelle and Lariviere 2003). Of these species, *C. ingratus*, *P. coracinus* and *S. impunctatus* are thought to be autumn-breeding species while the remaining species are considered spring-breeders (Larochelle & Lariviere 2003; Lindroth 1969).

2.3.3 Site Specific Models of Forest Stand Dynamics and Meteorological Data

We compiled measurements of stand growth and recovery over time, quantified as change in live tree basal area (diameter at breast height (DBH) > 9cm), within each treatment at SAFE using Bose et al.'s (2015) spatially explicit, localized SORTIE-ND simulations of forest stand dynamics. These simulations were parameterized using empirical data collected within each experimental stand at SAFE and can be used to predict stand structure and composition for each silvicultural treatment for 100 years following harvest (see Appendix A for additional details). Thus, the initial 20 years of simulations by Bose et al. (2015) reflect the actual period of carabid sampling in our study. Within these simulations, periodic disturbance by spruce budworm (*Choristoneura fumiferana* (Clemens, 1865)) were projected to occur in 2024 and 2040. Model performance was evaluated by Bose et al. (2015) using short- and long-term empirical data collected at SAFE and was found to be in strong agreement with the simulations.

We compiled monthly mean temperature and total monthly precipitation using the software tool BioSIM (Saint-Amant 2017) and took the averages for May-September to account for the breeding season and December-February to account for the overwintering period. For projections of future temperature and precipitation, we selected one low emission and one high emission climate model from the World Climate Research Program's (WCRP) Climate Model Intercomparison Project (CMIP6) which span the most likely range of predicted climate change for the region: Shared Socioeconomic Pathway (SSP) scenarios SSP1-2.6 and SSP5-8.5 (O'Neill et al. 2016; see Appendix A for details). We then used BioSIM to compile the mean temperature and average precipitation accumulation for the breeding season (May-September) and overwintering period (December-February) under SSP1-2.6 and SSP5-8.5 for our sampling locations.

2.3.4 Statistical analysis

We modelled the effect of change in basal area over time, derived from growth models (Bose et al. 2015), as well as temperature and precipitation during breeding season and overwintering period within two forest cover-types (hardwood and mixedwood) on carabid abundance using generalized linear mixed models (GLMMs). We started with full models including all the biologically relevant combinations of fixed effects (see Appendix A for details) and then discarded interactions and/or explanatory variables which did not improve model fit as measured as AIC, or model validity as assessed by pseudo-R^2 and AUC (Burnham and Anderson 2004). We included the number of operational trapping days in our models as an offset to account for any minor differences in trapping season length and included a plot level identifier (*i.e.* "subject") as a random effect to account for repeated measurements taken over time at each permanent sampling plot. All continuous variables were centered and scaled prior to analysis. For the final models we selected negative binomial GLMMs, as Poisson models were overdispersed. Regressions were completed using packages lme4 (Bates et al. 2015) and MASS (Venables and Ripley 2002) in RStudio (R version 4.2.3; R Core Team 2023), while model selection and validation were completed using R packages AICcmodavg (Mazerolle 2023), pROC (Robin et al. 2011) and sjstats (Lüdecke 2024; see Appendix A for fitted models in R syntax).

We then projected changes in species abundance for 2019 through 2038 under SSP1-2.6 and SSP5-8.5 by replacing the values of the climate variables used in the original models with the projected values. Additionally, we replaced basal area values used in the original models with those simulated by Bose et al. (2015) for 2019-2038 to account for projected stand growth/recovery over time. We retained the plot level identifier (*i.e.* "subject") as a random effect and included the average number of operational trapping days as a model offset to ensure comparability of the predicted carabid catch rate with the empirical data from 2004-2018. We assessed the direction and significance of these projected trends using Kendall's Tau (Chen 2012) and the magnitude of the projected trends using Sen's slope (Zade et al. 2023). Projected changes in species abundance and assessments of trend significance/magnitude were completed using R packages stats (R Core Team 2023) and trend (Pohlert 2023).

2.4 Results

2.4.1 Species-level response to changes in habitat and climate variables

While we found no visible patterns among species response to the habitat or climatic variables when species were grouped by either habitat preference or breeding strategy (Fig. 2.2), both forest composition and structure affected abundance of over half the species considered. Habitat preferences for mixedwood stand composition were apparent for *P. adstrictus, P. coracinus* and *S. stenostomus* (Table 2.1), while increases in basal area favored greater abundance of *C. ingratus, P. decentis* and *P. adstrictus* (Table 2.1; Fig. 2.2).

Throughout the breeding season, warmer temperatures favored greater abundance of *A. retractum, C. ingratus, P. coracinus* and *S. nitidicollis* but reduced abundance of *P. decentis* and *S. impunctatus* (Table 2.1; Fig. 2.2). Increased precipitation favored greater abundance of *P. decentis, P. adstrictus, P. coracinus* and *S. nitidicollis* but reduced abundance of *C. ingratus* (Table 2.1: Fig. 2.2). AIC-based model section frequently identified interactions between temperature and precipitation as meaningful covariates. At low temperatures in the breeding season, responses of carabid abundance to precipitation were negative for all species other than *S. nitidicollis* (Fig. 2.3). At average temperatures, responses of carabid abundance to precipitation were varied (*e.g.* negative for *A. retractum* and positive for *P. decentis* and *S. nitidicollis*). However, as temperatures increase, the response to precipitation became positive overall for all species considered (Fig. 2.3).

During the overwintering period, warmer temperatures favored greater abundance of *A. retractum* and *C. ingratus* but reduced abundance of *P. decentis, S. nitidicollis* and *S. impunctatus* (Table 2.1; Fig. 2.2). Increased precipitation favored greater abundance of these same three species as well as *S. stenostomus,* but reduced abundance of all other species (Table 2.1; Fig. 2.2). For *A. retractum, C. ingratus, P. coracinus* and *P. pensylvanicus,* we also identified interactions between overwintering temperature and precipitation as meaningful covariates. Interactions were weaker as compared to the breeding season, such that effects of precipitation on these four species remained negative over a broad range of winter temperatures (Fig. 2.4).

2.4.2 Projections of post-harvest recovery of carabids under SSP1-2.6

Beyond the initial 20-year sampling period, six of the species studied were predicted to increase over the following two decades in at least one cover-type x treatment combination under low emissions scenario SSP1-2.6 (Tables 2.2 and 2.3). Species were generally more abundant in uncut stands within a given cover-type (Fig. 2.5). For species such as *A. retractum, P. coracinus* and *S. stenostomus,* abundance was predicted to increase in each cover-type x treatment combination (Tables 2.2 and 2.3). For species such as *C. ingratus,* future increases were predicted in all treatments within the hardwoods (Table 2.2) and in the 60% dispersed retention in the mixedwood stands (Table 2.3). The 60% dispersed retention in the mixedwood stands also promoted abundance of *P. adstrictus* and *P. pensylvanicus* (Table 2.3). Predicted declines in carabids were relatively limited under this scenario. *Pterostichus adstrictus* was predicted to decline in uncut mixedwood stands, whereas *P. decentis* was predicted to decline in all cover-type x treatment combinations save the 60% dispersed retention in the mixedwoods (Tables 2.2 and 2.3). Declines in *P. adstrictus* and *P. decentis* in the mixedwood stands between 2020-2025 correspond with predicted declines in basal area related to anticipated outbreaks of spruce budworm (Fig. 2.5). Subsequent attacks by spruce budworm projected to occur in 2040 correspond with predicted declines of *P. decentis* (Fig. 2.5).

2.4.3 Projections of post-harvest recovery of carabids under SSP5-8.5

In stark contrast to species responses in the low emission scenario, species declines were much more prevalent in high emission scenario SSP5-8.5. Under SSP5-8.5, two-thirds of the species studied, including *P. decentis, P. pensylvanicus, S. nitidicollis* and *S. impunctatus,* were predicted to decline over the following two decades in each cover-type x treatment combination (Tables 2.4 and 2.5). In the mixedwood stands, these species are predicted to obtain maximal abundance during the spruce budworm outbreak in 2024 and decline thereafter (Fig. 2.6). However, *P. pensylvanicus, S. nitidicollis* and *S. impunctatus* also reached maximal abundance near 2024 then declined in hardwood stands as well (Fig. 2.6).

Declines were less prevalent for *P. adstrictus* and *P. coracinus*. For *P. adstrictus,* declines were predicted to occur in all cover-type x treatment combinations except for the 34% retention in hardwood stands (Table 2.4) and the 60% dispersed retention in mixedwood stands (Table 2.5). For *P. decentis,* declines were predicted only in uncut hardwood stands. Only one species, *A. retractum,* was predicted to increase under SSP5-8.5 (Tables 2.4 and 2.5).

2.5 Discussion

2.5.1 Impact of breeding season temperature/precipitation interactions

For many carabid species in our study, rapid increases in abundance were triggered by interactions between breeding season temperature and precipitation. For most of these species, abundance had the greatest potential to increase when low precipitation converged with low temperatures throughout the breeding season, or alternatively, when higher breeding season precipitation converged with higher temperatures (Fig. 2.3). For species like *P. pensylvanicus* and *S. impunctatus*, rapid changes in abundance related to interactions between temperature and precipitation defined an important confluence of specific climatic conditions that must be met if species are to persist under climate change. Whether or not these conditions are expected to be met in the future, however, depends on the emission scenario.

Under the low emissions scenario, environmental conditions were expected to shift from low temperature/high precipitation, to high temperature/high precipitation by ca. 2023. Interactions between breeding season temperature and precipitation associated with this change contributed to predicted increases for several carabid species from ca. 2023-2038. This confluence of high precipitation and moderate warming is a key component of the boreal refuge hypothesis, a theory which posits that northeastern North America's boreal forests will be the only area across the circumboreal region with sufficient precipitation to compensate for increasing evaporative stress induced by rising temperatures of up to 2 °C (D'Orangeville et al. 2016). Unlike central and western portions of North America and Europe's boreal forests, which are expected to experience a water deficit and corresponding declines in insect abundance (Wagner 2020; Harris et al. 2019), ample precipitation in the northeastern North America should allow local tree species to better withstand, or even thrive, in a warming climate (D'Orangeville et al. 2018). Likewise, for carabid species such as *P. pensylvanicus* and *S. impunctatus* which require increased temperatures and precipitation to persist, boreal forests in northeastern North America may emerge as an important climatic refuge under SSP1-2.6.

Under the high emissions scenario, increased temperatures are expected to be combined with declining precipitation by 2030. This transition corresponds with a fall in abundance for most carabid species after 2030, particularly in *P. pensylvanicus* and *S. impunctatus* where the climatic conditions no longer meet their requirements for persistence. This shift supports the theory that warming-induced benefits for carabids in northeastern North America's boreal forest will be transitory under higher emissions scenarios, as reductions in available water increases vulnerability of forests to excess warming and drying (D'Orangeville et al. 2018), and is consistent with significant linear declines in abundance of carabids detected in Europe following high temperature/low precipitation conditions (Weiss et al. 2024).

2.5.2 Advantages of high-retention harvesting under climate change

In line with our initial hypothesis, our findings suggest that maintaining forest structure may be an important lever of influence to increase resilience of carabids. For example, under the low emissions scenario, high-retention harvesting conferred a numerical advantage throughout transient periods of stress (*e.g.* spruce budworm outbreak conditions combined with a short-term drought from ca. 2024-2026) as compared to stands with less standing retention, maintaining higher abundance of species such as *P. decentis* and *P. adstrictus* in the mixedwoods and *A. retractum, C. ingratus* and *P. adstrictus* in the hardwoods. This may be a reflection of the insulating effects of a closed canopy, as high-retention harvesting has been found to increase resilience of carabids following harvests in western Canada and Europe (Wu et al. 2020; Koivula et al. 2019) and is likely to benefit species like *A. retractum* and *C. ingratus* which are negatively affected by interactions between precipitation and temperature during the breeding season. High-retention harvesting leading to increased resilience of carabids under insect outbreak conditions may be of particular value under climate change, as pest outbreaks are expected to occur more frequently (Régnière et al. 2012).

Under the high emissions scenario, the majority of the species considered are expected to reach peak abundance ca. 2025, due to a confluence of moderate warming and ample precipitation, and decline thereafter as warming continues but precipitation declines. For most species considered, the highest peaks in abundance are predicted to occur within the unharvested stands, likely due to the closed canopy providing greater insulation from short-term fluctuations in moisture and temperature (De Frenne et al. 2021). Throughout the following period of decline, the numerical advantage conferred by the unharvested and high-retention stands resulted in these populations remaining at higher density as compared to the lower retention treatments. On a landscape scale, a benefit for high-retention harvesting preserving higher density of carabid populations may be the reduction of species turnover, as more intensive harvesting combined with increasing severity of climate change is expected to increase dissimilarity of ground-dwelling beetle assemblages (Bouderbala et al. 2023).

2.5.3 Variation in species level response to climate/habitat variables

Although we expected species associated with closed canopies to have reduced abundance in lower retention harvests and to decline more steeply with warming temperatures and reduced precipitation as compared to forest generalists and open canopy adapted species, species' responses to changes in habitat or climate variables were generally inconsistent with habitat-use categories. The large variety in species' response to even this limited number of habitat/climate variables highlights the difficulty in generalizing the impacts of climate change on species within these broad categories. Species' responses to climate change will likely depend on physiological constraints and differences in life-history traits. For example, of the three species within this study which are categorized as closed-canopy associated, only *P. coracinus* is obligated to overwinter in the larval life stage (Larochelle and Larivière 2003; Thiele 1977). Because of this physiological constraint, *P. coracinus* cannot adapt to warming weather by shortening the quantity of time spent as a larva, a life stage which is particularly vulnerable to mortality due to heat stress or desiccation (Egli and Work 2024; Fox and Czesak 2000). Alternatively, *P. decentis* and *P. adstrictus*, which are also categorized as closed-canopy associated, mature over the summer months and therefore have the capacity to adapt to warming climates by producing offspring which reach maturity more rapidly (Egli and Work 2024). These differences in adaptive capacity may adjust the trajectory of these species under climate change, a subtlety which is not captured by broad categorization such as habitat-use.

2.5.4 Conclusions and management implications

Our predictions suggest that high-retention harvesting strategies may be effective to conserve carabid populations over the coming decades across the predicted range of temperature and precipitation under SSP1-2.6. A major advantage of mitigating the effects of climate change using forest management is that the benefits of high-retention strategies for species (*e.g.* conferring a numerical advantage post-harvest) are rapidly realized following the intervention. This allows a certain amount of local control over mitigation that can be implemented at the planning phase by land managers. Furthermore, given that high-retention strategies are expected to mitigate climate change stress for the next two decades under SSP1-2.6, it may be sufficient for forest managers to prioritize promoting stand resilience rather than investing in alternative strategies, such as planting non-native tree species, which have the potential to negatively impact forest biodiversity (Wohlgemuth et al. 2022).

Based on the finding of this study, increasing carabid abundance in northeastern North America is likely to be transitory over the long-term as warming beyond 2 °C is expected to result in substantial declines in forest productivity as evaporative stress surpasses compensatory effects of initial increases in precipitation (D'Orangeville et al. 2018). Under the low emission scenario, this turning point is projected to occur around 2050. Under SSP5-8.5, however, a 2 °C increase in average annual temperature is expected to occur by 2037, suggesting major declines in carabid abundance could occur in the next decade if global emissions proceed to increase unchecked. This underscores the importance of prioritizing climate change mitigation as our results suggest that high-retention harvesting can conserve carabids for approximately the next decade but becomes a less effective strategy as temperatures rise. However, throughout this period of decline, high-retention harvesting may have the potential to offset, at least to some degree, declines in abundance. Given that stands with a greater basal area sustain a higher population density throughout periods of stress, high-retention harvesting may permit forest organisms additional time to develop rapid adaptations to increasing temperatures (Egli and Work 2024). This may be particularly important in forest organisms like carabids which have limited dispersal capabilities and are therefore expected to be less capable of shifting their ranges with climate change (Bouderbala et al. 2023).

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2.7 Contribution statement

The carabid abundance data utilized in this chapter is a subset of the data described in Chapter 1. For this chapter, I led the conception of the study design, methodology, data analysis and writing of the manuscript. Timothy Work provided project support and guidance throughout as well as reviewing the manuscript for important intellectual content.

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2.9 Tables

Table 2.1. Parameter estimates and standard errors for the final models for each of the nine carabid species.

	Agonum retractum	*Calathus ingratus*	*Platynus decentis*	*Pterostichus adstrictus*	*Pterostichus coracinus*
(Intercept)	-3.664(0.282)***	-5.291(0.257)***	-4.397(0.152)***	-6.877(0.289)***	-4.473(0.304)***
Habitat					
Basal area (m^2/ha)	0.141(0.120)	0.340(0.169)*	0.649(0.143)***	1.151(0.186)***	0.085(0.125)
Cover-type†	0.250(0.271)			1.995(0.370)***	1.535(0.287)***
Breeding Season					
Temperature (°C)	0.356(0.093)***	0.296(0.095)**	-0.290(0.130)*		0.342(0.108)**
Precipitation (mm)	-0.156(0.105)	-0.272(0.094)**	0.539(0.144)***	1.268(0.163)***	0.314(0.123)*
Temperature x Precipitation	0.505(0.078)***	1.120(0.077)***	0.878(0.110)***		1.102(0.089)***
Winter					
Temperature (°C)	0.760(0.188)***	0.509(0.172)**	-1.782(0.176)***		-0.387(0.214)•
Precipitation (mm)	-1.444(0.355)***	-2.516(0.331)***	1.345(0.159)***	-1.438(0.296)***	-1.227(0.394)**
Temperature x Precipitation	0.944(0.213)***	1.862(0.197)***			1.119(0.233)***
Breeding Season/Winter Interaction					
Precipitation x Precipitation				1.796(0.355)***	

	Pterostichus pensylvanicus	*Sphaeroderus nitidicollis*	*Sphaeroderus stenostomus*	*Synuchus impunctatus*
(Intercept)	-2.610(0.146)***	-3.990(0.136)***	-6.220(0.264)***	-1.780(0.159)***
Habitat				
Basal area (m^2/ha)	0.106(0.077)	0.119(0.119)	0.014(0.111)	-0.083(0.095)
Cover-type†			2.748(0.314)***	-0.798(0.205)***
Breeding Season				
Temperature (°C)	0.062(0.068)	0.302(0.075)***	0.416(0.341)	-0.162(0.090)•
Precipitation (mm)	0.127(0.084)	0.839(0.093)***	-0.057(0.215)	0.007(0.104)
Temperature x Precipitation	0.505(0.058)***	0.299(0.067)***	1.056(0.226)***	1.184(0.085)***
Winter				
Temperature (°C)	-0.101(0.140)	-1.149(0.097)***	-0.403(0.309)	-1.041(0.121)***
Precipitation (mm)	-0.830(0.260)**	0.463(0.087)***	0.879(0.284)**	0.398(0.102)***
Temperature x Precipitation	0.884(0.156)***			
Breeding Season/Winter Interaction				
Precipitation x Precipitation				

• $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; †Hardwoods used as reference

Table 2.2. Kendall’s rank correlation (τ), Sen’s slopes and their lower confidence limits (LCL) and upper confidence limits (UCL) for the predicted changes in carabid abundance in the hardwood harvesting treatments under low emissions scenario SSP1-2.6.

	Uncut (hardwood)				67% retention				34% retention			
	τ	Sen’s slope	LCL	UCL	τ	Sen’s slope	LCL	UCL	τ	Sen’s slope	LCL	UCL
Agonum retractum	↑***	1.591	0.888	2.446	↑***	0.788	0.496	1.159	↑***	1.011	0.678	1.389
Calathus ingratus	↑***	0.286	0.171	0.441	↑***	0.086	0.038	0.132	↑***	0.154	0.077	0.230
Platynus decentis	↓***	-0.069	-0.106	-0.035	↓***	-0.052	-0.084	-0.025	↓**	-0.038	-0.072	-0.012
Pterostichus adstrictus	↓•	-0.020	-0.046	0.006	↓	-0.008	-0.032	0.019	↑•	0.015	0.000	0.029
Pterostichus coracinus	↑**	0.209	0.070	0.390	↑**	0.134	0.037	0.258	↑**	0.129	0.046	0.218
Pterostichus pensylvanicus	↑	0.196	-0.446	0.801	↑	0.129	-0.251	0.531	↑	0.258	-0.240	0.732
Sphaeroderus nitidicollis	↓	-0.081	-0.214	0.006	↓•	-0.060	-0.155	0.015	↓	-0.035	-0.140	0.045
Sphaeroderus stenostomus	↑**	0.010	0.004	0.017	↑**	0.011	0.005	0.018	↑**	0.011	0.005	0.018
Synuchus impunctatus	↑	0.321	-0.120	0.741	↑	0.277	-0.129	0.657	↑	0.189	-0.211	0.528

↑ Increasing trend; ↓ Decreasing trend; • $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 2.3. Kendall's rank correlation (τ), Sen’s slopes and their lower confidence limits (LCL) and upper confidence limits (UCL) for the predicted changes in carabid abundance in the mixedwood harvesting treatments under low emissions scenario SSP1-2.6.

	Uncut (mixedwood)				60% retention (dispersed)				60% retention (grouped)			
	τ	Sen’s slope	LCL	UCL	τ	Sen’s slope	LCL	UCL	τ	Sen’s slope	LCL	UCL
Agonum retractum	↑***	0.453	0.138	0.765	↑***	0.886	0.553	1.231	↑***	0.613	0.345	0.903
Calathus ingratus	↑	0.076	-0.044	0.234	↑**	0.260	0.064	0.455	↑•	0.065	-0.044	0.231
Platynus decentis	↓**	-0.182	-0.327	-0.070	↓	-0.033	-0.098	0.014	↓*	-0.040	-0.079	-0.009
Pterostichus adstrictus	↓*	-0.349	-0.548	-0.096	↑***	0.309	0.163	0.471	↑	0.007	-0.028	0.036
Pterostichus coracinus	↑*	0.507	0.061	0.953	↑***	0.719	0.350	1.083	↑**	0.584	0.219	0.953
Pterostichus pensylvanicus	↑	0.141	-0.118	0.440	↑*	0.237	-0.029	0.601	↑	0.136	-0.155	0.430
Sphaeroderus nitidicollis	↑	-0.003	-0.084	0.081	↑	0.026	-0.085	0.152	↑	0.014	-0.093	0.118
Sphaeroderus stenostomus	↑**	0.147	0.023	0.288	↑**	0.210	0.063	0.311	↑**	0.184	0.038	0.322
Synuchus impunctatus	↑	-0.042	-0.294	0.165	↓	-0.068	-0.468	0.310	↓	-0.118	-0.531	0.276

↑ Increasing trend; ↓ Decreasing trend; • $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 2.4. Kendall's rank correlation (τ), Sen’s slope and their lower confidence limits (LCL) and upper confidence limits (UCL) for the predicted changes in carabid abundance in the hardwood harvesting treatments under high emissions scenario SSP5-8.5.

	Uncut (hardwood)				67% retention				34% retention			
	τ	Sen’s slope	LCL	UCL	τ	Sen’s slope	LCL	UCL	τ	Sen’s slope	LCL	UCL
Agonum retractum	↑***	1.509	0.785	2.371	↑***	0.735	0.434	1.120	↑***	0.959	0.610	1.375
Calathus ingratus	↓	-0.102	-0.344	0.068	↓	-0.007	-0.064	0.035	↓	-0.004	-0.107	0.059
Platynus decentis	↓***	-0.067	-0.101	-0.046	↓***	-0.059	-0.081	-0.041	↓***	-0.056	-0.079	-0.039
Pterostichus adstrictus	↓**	-0.040	-0.067	-0.008	↓*	-0.030	-0.055	-0.002	↓	-0.002	-0.019	0.014
Pterostichus coracinus	↓*	-0.103	-0.224	0.006	↓•	-0.054	-0.138	0.010	↓•	-0.065	-0.137	0.001
Pterostichus pensylvanicus	↓***	-0.896	-1.513	-0.338	↓***	-0.735	-1.139	-0.376	↓**	-0.648	-1.120	-0.186
Sphaeroderus nitidicollis	↓***	-0.223	-0.299	-0.123	↓***	-0.181	-0.236	-0.111	↓***	-0.131	-0.217	-0.057
Sphaeroderus stenostomus	↓	-0.005	-0.011	0.002	↓	-0.004	-0.011	0.003	↓	-0.004	-0.010	0.004
Synuchus impunctatus	↓***	-0.687	-1.050	-0.333	↓***	-0.632	-0.950	-0.309	↓***	-0.675	-1.057	-0.386

↑ Increasing trend; ↓ Decreasing trend; • P < 0.1; * P < 0.05; ** P < 0.01; *** P < 0.001

Table 2.5. Kendall's rank correlation (τ), Sen’s slope and their lower confidence limits (LCL) and upper confidence limits (UCL) for the predicted changes in carabid abundance in the mixedwood harvesting treatments under high emissions scenario SSP5-8.5.

	Uncut (mixedwood)				60% retention (dispersed)				60% retention (grouped)			
	τ	Sen’s slope	LCL	UCL	τ	Sen’s slope	LCL	UCL	τ	Sen’s slope	LCL	UCL
Agonum retractum	↑***	0.752	0.394	1.131	↑***	1.349	0.967	1.792	↑***	1.001	0.679	1.384
Calathus ingratus	↑	0.041	-0.105	0.164	↑•	0.177	-0.041	0.380	↑	0.037	-0.079	0.163
Platynus decentis	↓***	-0.280	-0.392	-0.199	↓***	-0.104	-0.156	-0.065	↓***	-0.075	-0.096	-0.047
Pterostichus adstrictus	↓***	-0.617	-0.817	-0.411	↓	-0.036	-0.178	0.075	↓*	-0.034	-0.066	-0.008
Pterostichus coracinus	↓	-0.185	-0.609	0.188	↓	-0.189	-0.529	0.178	↓	-0.178	-0.509	0.132
Pterostichus pensylvanicus	↓**	-0.433	-0.662	-0.137	↓**	-0.439	-0.666	-0.153	↓*	-0.449	-0.677	-0.165
Sphaeroderus nitidicollis	↓***	-0.149	-0.199	-0.103	↓***	-0.146	-0.234	-0.067	↓***	-0.146	-0.230	-0.080
Sphaeroderus stenostomus	↓	-0.048	-0.146	0.053	↓	-0.009	-0.110	0.095	↓	-0.045	-0.140	0.070
Synuchus impunctatus	↓***	-0.497	-0.646	-0.363	↓***	-0.746	-1.036	-0.511	↓***	-0.889	-1.202	-0.537

↑ Increasing trend; ↓ Decreasing trend; • $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

2.10 Figures

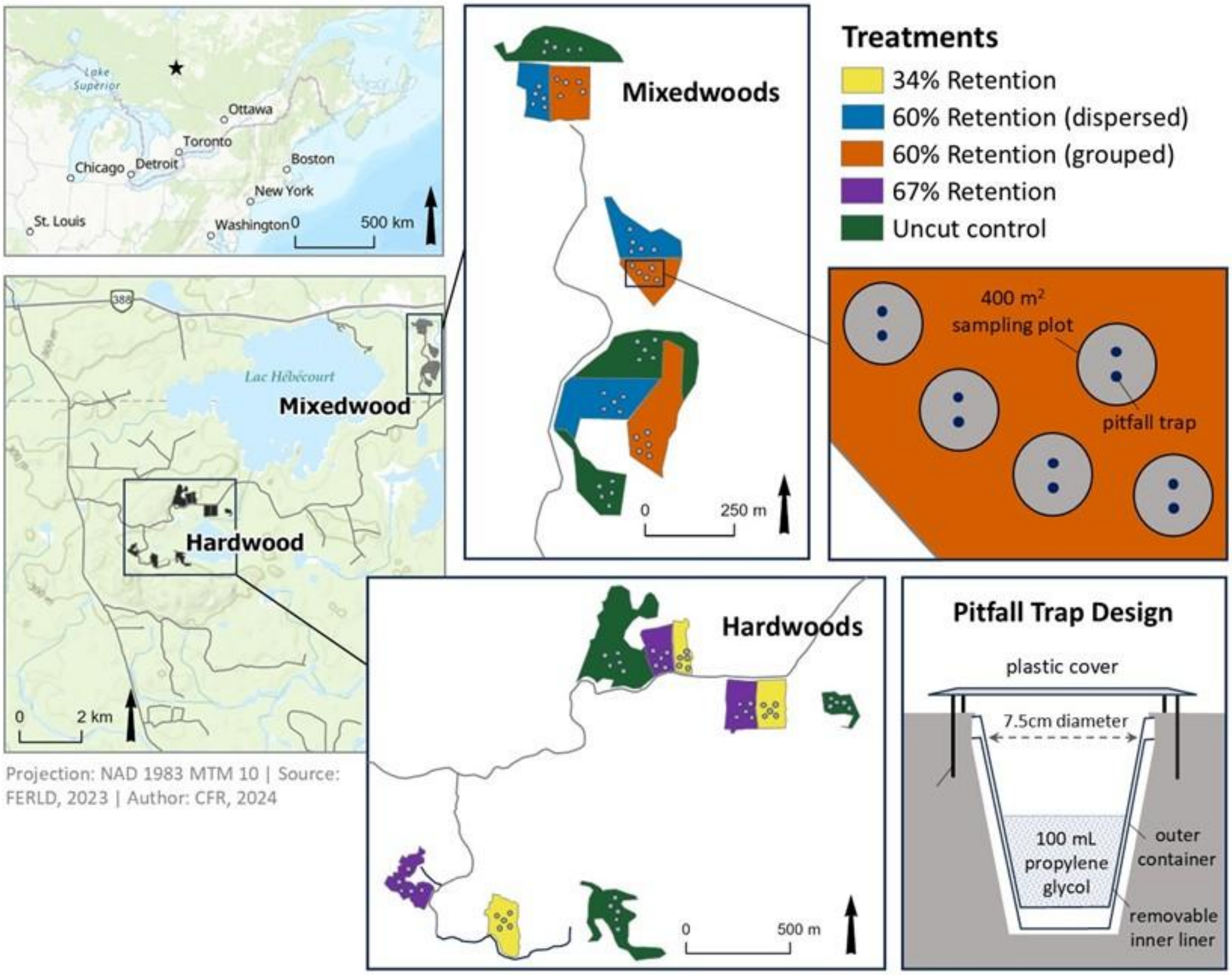

Figure 2.1. Map of the study area showing the location in northwestern Quebec (top left), the location of each forest cover-type within the Lake Duparquet research and teaching forest (bottom left), the experimental design within each cover-type (center), an example of within plot pitfall trap distribution (top right) and pitfall trap design (bottom right).

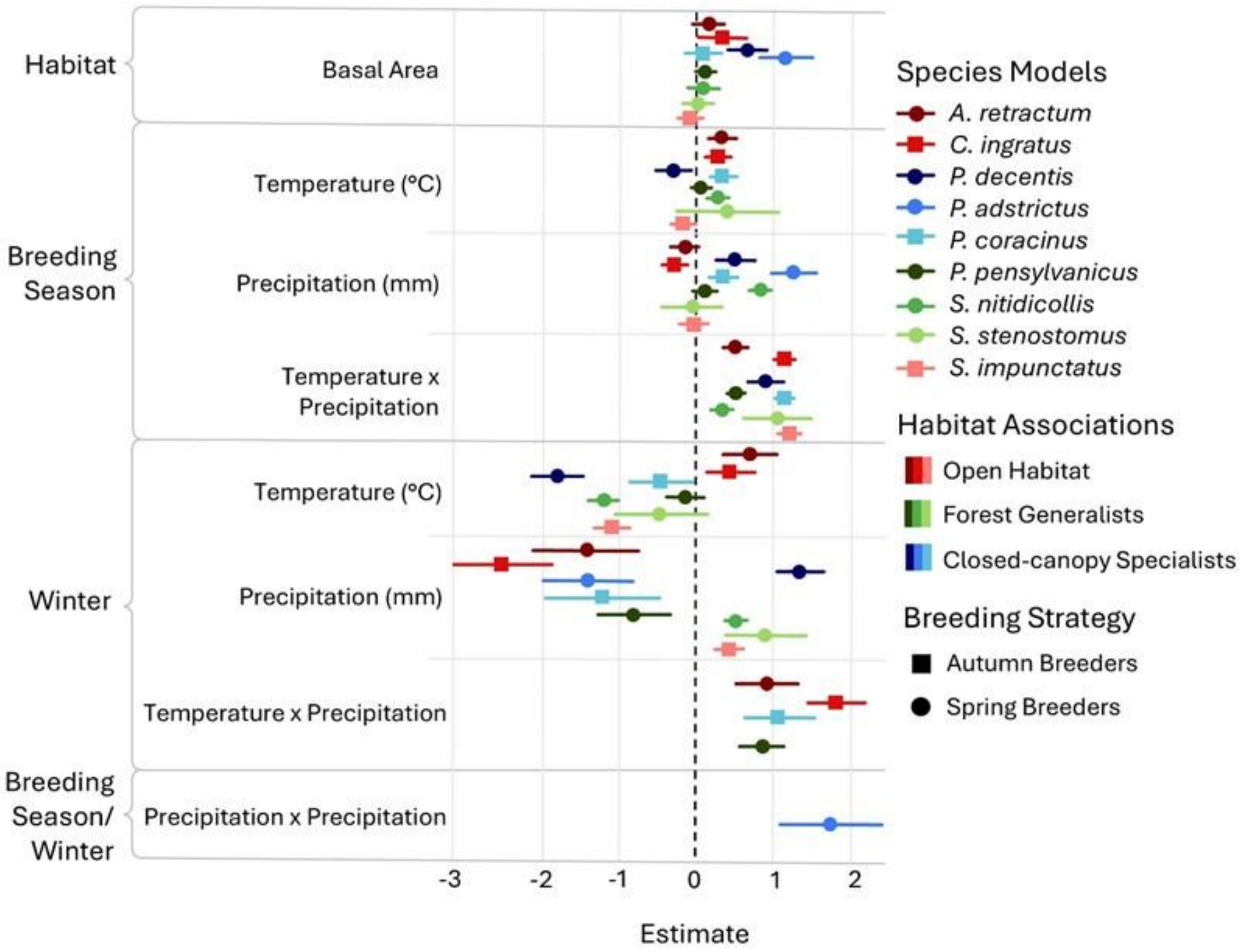

Figure 2.2. The impact of environmental and climate variables on carabid abundance based on generalized linear mixed models. For test statistics, see Table 2.1.

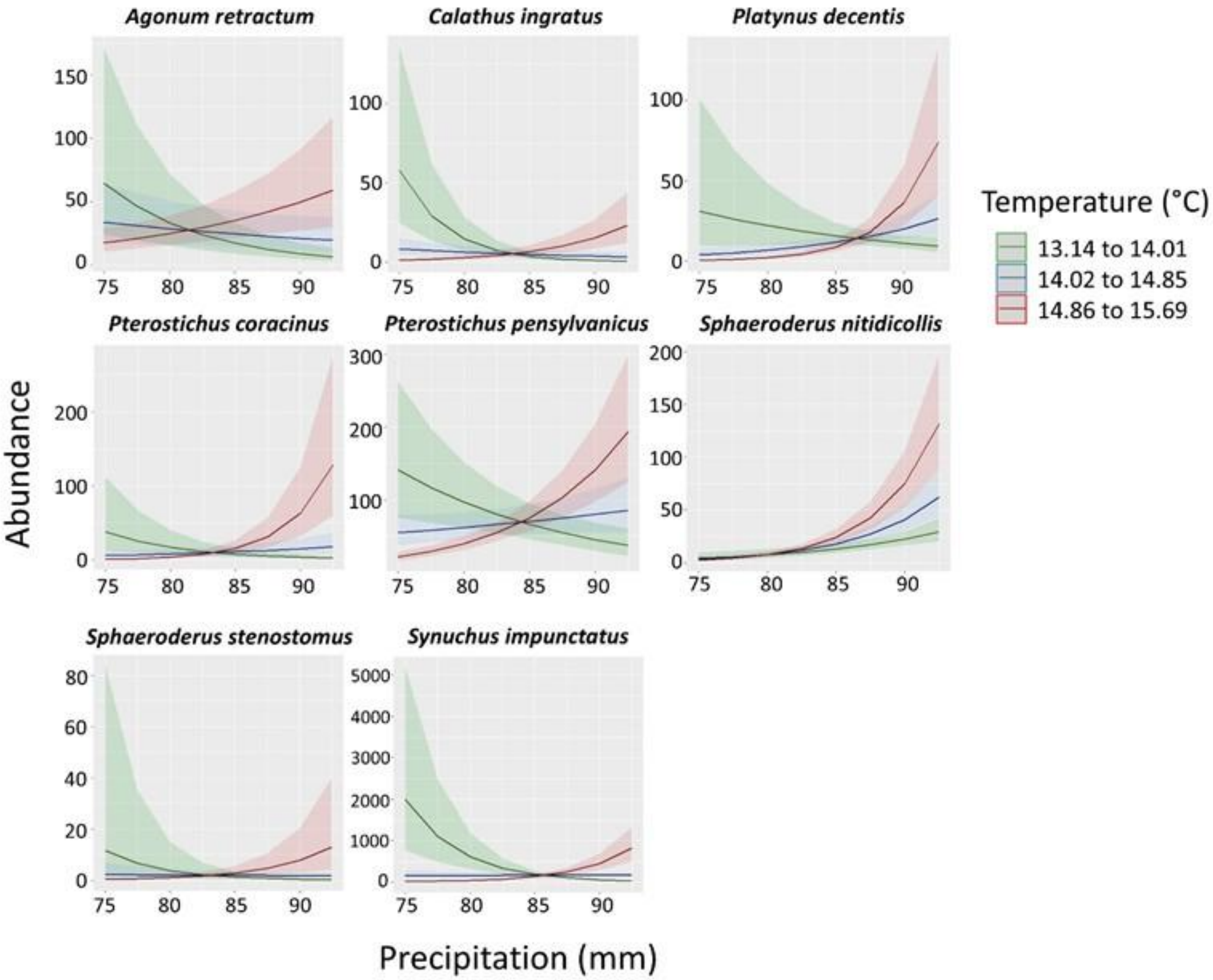

Figure 2.3. Relationship between precipitation and carabid abundance, as it varies in interaction with temperature over the breeding season. For test statistics, see Table 2.1.

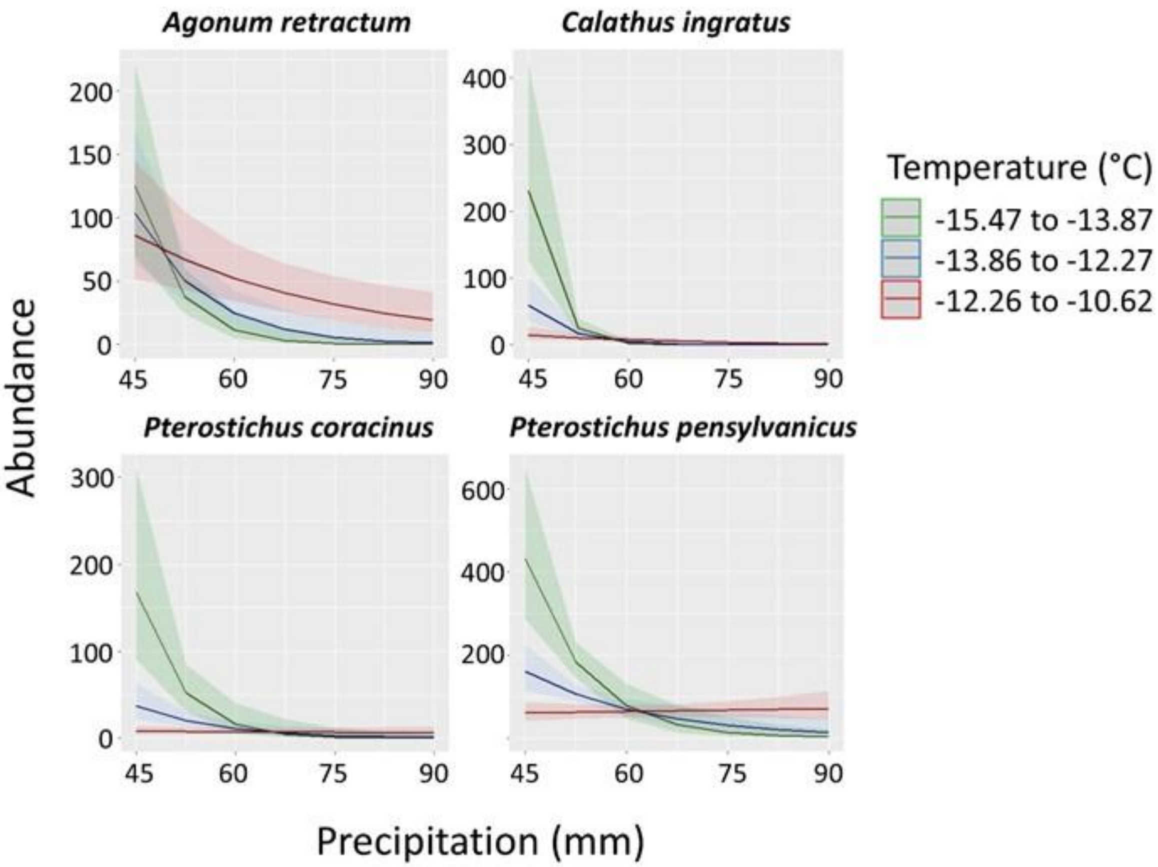

Figure 2.4. Relationship between precipitation and carabid abundance, as it varies in interaction with temperature throughout the overwintering period. For test statistics, see Table 2.1.

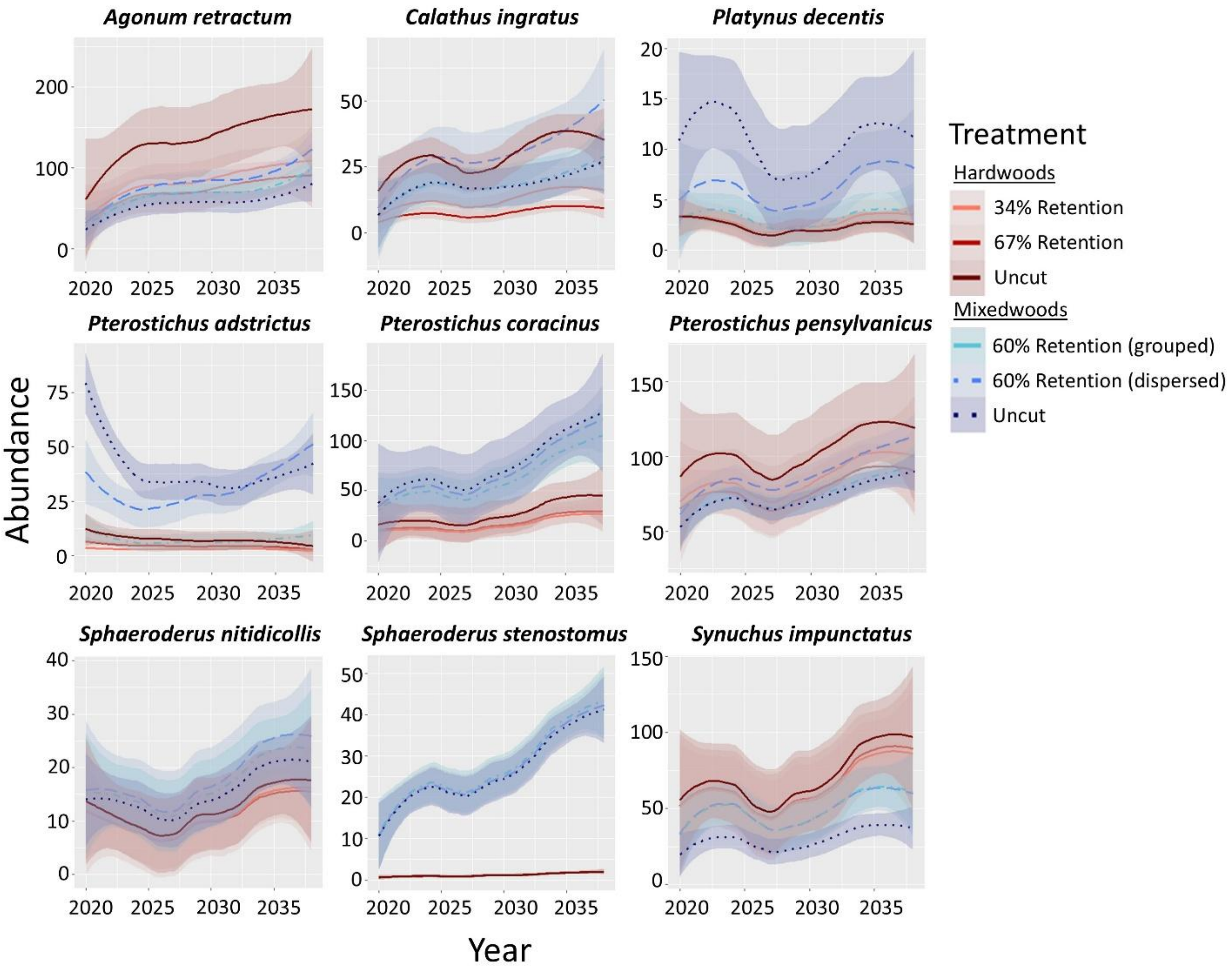

Figure 2.5. Projected change in carabid abundance in relation to changing basal area and temperature/precipitation over time within each harvesting treatment under low emissions scenario SSP1-2.6. For test statistics, see Tables 2.2 and 2.3.

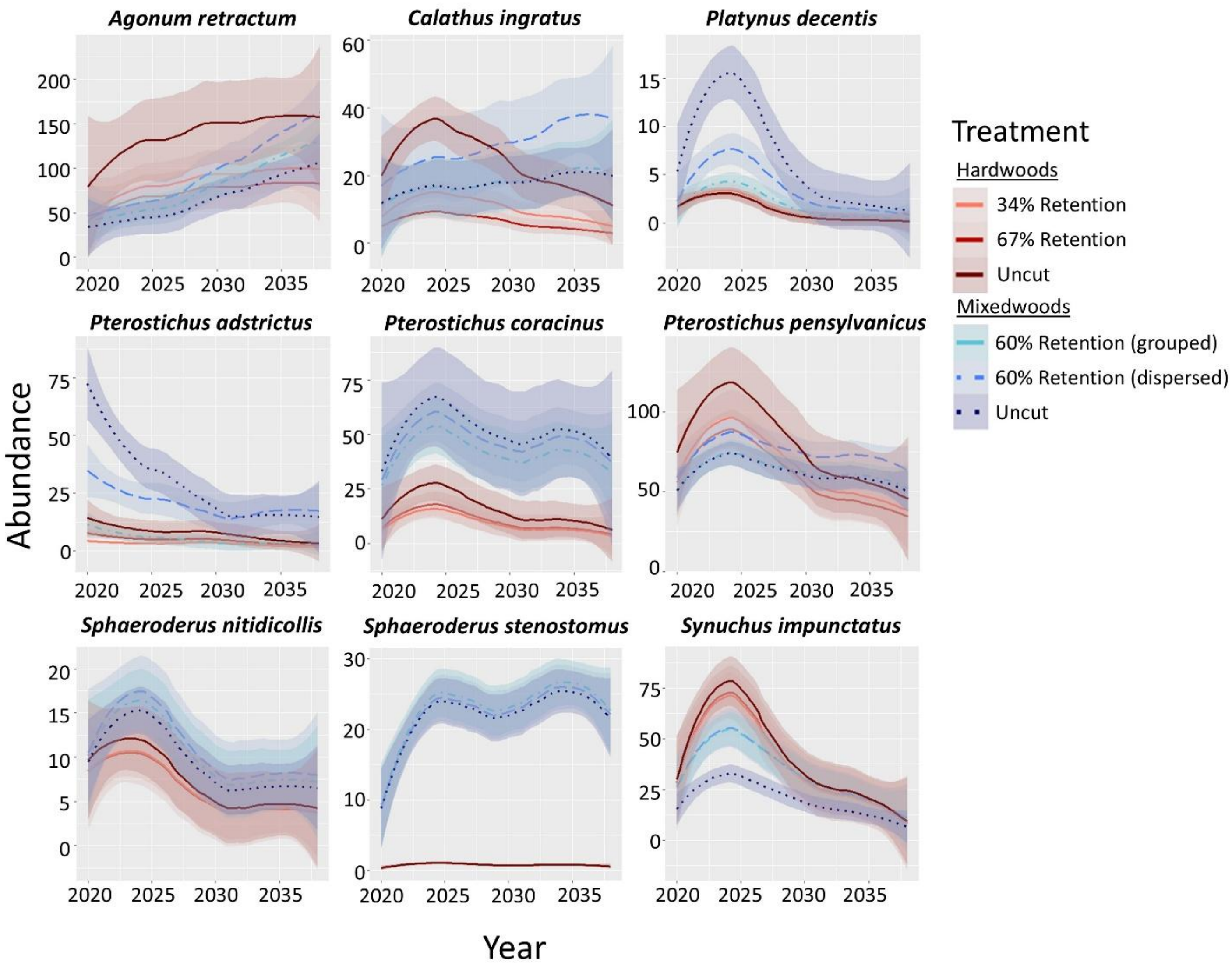

Figure 2.6. Projected change in carabid abundance in relation to changing basal area and temperature/precipitation over time within each harvesting treatment under high emissions scenario SSP5-8.5. For test statistics, see Tables 2.4 and 2.5.

2.11 Appendix A.

2.11.1 Additional detailed methodology

2.11.1.1 Study area and design

Spatially explicit, localized models of forest stand dynamics created by Bose et al. (2015) were specific to the hardwood and mixedwood partial-retention harvests in the SAFE project (Silviculture et aménagement forestier écosystémique) and simulate tree growth over time as a function of substrate behaviors, understory light availability and species-specific competitive effects (Bose et al. 2015). In these simulations, Bose et al. (2015) also included periodic disturbance by spruce budworm (*Choristoneura fumiferana* (Clemens, 1865)), a defoliating insect that causes extensive defoliation and mortality of conifer trees across the region, which they projected to occur in 2024 and again in 2040. Bose et al. (2015) validated the model predictions with short- (12-year) and long-term (168-year) empirical data collected from the experimental stands at SAFE and found simulations of tree growth over time to be in strong agreement with the empirical data.

2.11.1.2 Statistical analysis

Projections from Shared Socioeconomic Pathway (SSP) scenarios SSP1-2.6 and SSP5-8.5 selected from the World Climate Research Program's (WCRP) Climate Model Intercomparison Project (CMIP6; Eyring et al. 2015) are expected to span the most likely range of predicted climate change for our study region (O'Neill et al. 2016; Meinshausen et al. 2020) and indicate that mean annual temperature within SAFE will increase by approximately 2.5 °C (SSP1-2.6) to 6.5 °C (SSP5-8.5) by 2100 (compared with 2000), while average precipitation is projected to increase by approximately 18% under SSP1-2.6 and by 8% under SSP5-8.5.

2.11.1.3 Fitted models

Formulas of all fitted models in R syntax are as follows:

```
Mod_Agonum.retractum = glmer.nb(Agonum.retractum ~ Basal_AreaCS + Cover_Type +
Temp_BreedingSeasonCS * Prcp_BreedingSeasonCS + Temp_WinterCS * Prcp_WinterCS +
offset(log(TrapDays)) + (1|Subject),  data=Carabids)
```

```
Mod_Calathus.ingratus = glmer.nb(Calathus.ingratus ~ Basal_AreaCS + Temp_BreedingSeasonCS *
Prcp_BreedingSeasonCS + Temp_WinterCS * Prcp_WinterCS + offset(log(TrapDays)) + (1|Subject),
data=Carabids)

Mod_Platynus.decentis = glmer.nb(Platynus.decentis ~ Basal_AreaCS + Temp_BreedingSeasonCS *
Prcp_BreedingSeasonCS + Temp_WinterCS + Prcp_WinterCS + offset(log(TrapDays)) + (1|Subject),
data=Carabids)

Mod_Pterostichus.adstrictus = glmer.nb(Pterostichus.adstrictus ~ Basal_AreaCS + Cover_Type +
Prcp_BreedingSeasonCS * Prcp_WinterCS + offset(log(TrapDays)) + (1|Subject),  data=Carabids)

Mod_Pterostichus.coracinus = glmer.nb(Pterostichus.coracinus ~ Basal_AreaCS + Cover_Type +
Temp_BreedingSeasonCS * Prcp_BreedingSeasonCS + Temp_WinterCS * Prcp_WinterCS +
offset(log(TrapDays)) + (1|Subject),  data=Carabids)

Mod_Pterostichus.pensylvanicus = glmer.nb(Pterostichus.pensylvanicus ~ Basal_AreaCS +
Temp_BreedingSeasonCS * Prcp_BreedingSeasonCS + Temp_WinterCS * Prcp_WinterCS +
offset(log(TrapDays)) + (1|Subject),  data=Carabids)

Mod_Sphaeroderus.nitidicollis = glmer.nb(Sphaeroderus.nitidicollis ~ Basal_AreaCS +
Temp_BreedingSeasonCS * Prcp_BreedingSeasonCS + Temp_WinterCS + Prcp_WinterCS +
offset(log(TrapDays)) + (1|Subject),  data=Carabids)

Mod_Sphaeroderus.stenostomus = glmer.nb(Sphaeroderus.stenostomus ~ Basal_AreaCS + Cover_Type
+ Temp_BreedingSeasonCS * Prcp_BreedingSeasonCS + Temp_WinterCS + Prcp_WinterCS +
offset(log(TrapDays)) + (1|Subject),  data=Carabids)

Mod_Synuchus.impunctatus = glmer.nb(Synuchus.impunctatus ~ Basal_AreaCS + Cover_Type +
Temp_BreedingSeasonCS * Prcp_BreedingSeasonCS + Temp_WinterCS + Prcp_WinterCS +
offset(log(TrapDays)) + (1|Subject),  data=Carabids)
```

Interactions between seasonal temperature and precipitation were included in model selection, as juvenile carabids are particularly affected by the combined impacts of these variables. Carabid eggs, larvae and pupa are highly permeable to the environment (Lovei and Sunderland 1996; Thiele 1977), thus, the combination of warm and dry conditions throughout the breeding season can result in mortality due to desiccation (Buxton 1932; Goulet 1974). Alternatively, moist conditions combined with high temperatures can also increase mortality for larvae and pupa, as increased soil moisture reduces evaporative cooling capacity (Punzo and Mutchmor 1980). Throughout the overwintering period, the combined impacts of low temperatures and ample precipitation can form an insulating layer of snow which can improve survival (Aitchison 2001). Alternatively, high precipitation combined with warmer temperatures may increase mortality if the soil become inundated, particularly throughout freeze/thaw cycles (Thiele 1977).

2.11.1.4 Potential model limitations

Models of stand dynamics created by Bose et al. (2015) were based on the current climate for the region (mean annual temperature of 0.7 °C and precipitation of 889.8 mm) and do not incorporate climate change impacts on tree growth or spruce budworm outbreaks. This is a potential limitation in our experimental design. However, climate change impacts are not expected to increase the frequency of spruce budworm outbreaks within our sampling region throughout the timeframe considered in our study (*i.e.* 2020-2038; Candau and Fleming 2011). Additionally, performance of the majority of tree species in eastern North America's boreal forest is expected to remain within the status quo under both emission scenarios selected for this time period (Boulanger et al. 2021). Therefore, we do not expect the lack of climate change impacts on Bose et al's (2015) models to have a significant impact on our results.

CHAPITRE 3

Forest harvest causes rapid changes of maternal investment strategies in ground beetles

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3.1 Abstract

Species recovery following anthropogenic disturbances will depend on adaptations in survivorship and fecundity. Life history theory predicts increased environmental stress will result in (1) shifts in resource allocation from fecundity to body growth/maintenance and (2) increased provisioning among offspring at the cost of reproductive output. For remnant populations that persist after forest harvesting, selection mediated through anthropogenic disturbances may affect resilience to additional stressors such as climate change. We tested how rapid changes in environmental conditions affected maternal investment strategies in two ground beetle species, *Pterostichus pensylvanicus* and *Pterostichus coracinus*, by comparing fecundity and survivorship in populations from recently clear-cut and uncut habitats. Using parents drawn from clear-cut or uncut stands, we reared progeny in both common garden and reciprocal transplant experiments. In *P. pensylvanicus*, we found that neither lineage nor rearing habitat affected the number of eggs laid per female or survivorship of offspring. However, eggs laid by females from clear-cuts were more likely to hatch and offspring reached maturity more quickly, suggesting increased provisioning per offspring. In *P. coracinus,* females from clear-cuts laid more eggs, their eggs hatched more rapidly and had greater hatching success suggesting increased investment in overall reproductive output and increased offspring provisioning. In the reciprocal transplant, we observed significant habitat by lineage interactions on survival in *P. coracinus*, with survivorship increasing when progeny was reared in novel habitats. In both species, increased maternal investment among offspring was not associated with a reduction in overall reproductive output, as anticipated. However, maternal investment among offspring declined with increasing female size, implying trade-offs between increased metabolic demand and fecundity. Taken together, our work suggests that females from more stressful, clear-cut habitats increased investment in fecundity, as compared to females from uncut habitats, and may compensate for larval mortality. These changes were driven by smaller individuals, suggesting that increased environmental stress can influence the relationship between female size and maternal investment strategy. Additionally, reciprocal increases in offspring survivorship in habitats other than the parents suggest that adjacent areas between unharvested and clear-cut habitat may be useful in maintaining biodiversity under future climate stressors.

Key words: boreal mixedwoods; Carabidae; fecundity; life-history evolution; offspring quality; parental investment; rapid evolution; recovery after clear-cut

3.2 Introduction

Timber harvesting is a major anthropogenic disturbance in forested ecosystems, resulting in abrupt changes to forest structure and composition which can have persistent, multi-generational impacts on remnant populations (Chaudhary et al. 2016). Over the long-term, impacts from forest harvesting such as increased light and soil temperatures, reduced soil water-retention capacity and homogenization of microhabitats may compound with the pressures of climate change to fundamentally affect remnant population dynamics and distributions (Travis 2003). The magnitude of these impacts will depend not only on species' ecological requirements, but also on evolutionary forces such as maternal effects which can facilitate persistence of remnant populations in changing environments (Räsänen and Kruuk 2007).

Maternal effects occur when an offspring's phenotype is influenced not only by the genes contributed by the mother, but also by the mother's phenotype or environmental conditions (Rossiter 1991b, 1996; Mousseau and Fox 1998b). Maternal effects can impact evolutionary dynamics either by affecting the rate or direction of genetic change in response to natural selection (*e.g.* McAdam and Boutin 2004) or by generating immediate phenotypic change through high levels of transgenerational phenotypic plasticity (*e.g.* Fox and Savalli 2000; Shama et al. 2014; see also Räsänen and Kruuk 2007 for review).

One route through which maternal effects can shape the overall selection regime is via the female's maternal investment strategy (Beckerman et al. 2006). At the time of producing offspring, a female may allocate resources between her physical growth and maintenance, overall reproductive output (*i.e.* offspring quantity) and investment among individual offspring (*i.e.* offspring "quality"; Mousseau and Fox 1998a; 1998b). Increased investment per offspring can result in larger progeny with faster growth rates and increased survival to maturity (Kyneb and Toft 2006). A larger per offspring investment is often favored in stressful environments, as the adaptive benefit of increased offspring provisioning is generally greatest in adverse conditions (Räsänen et al. 2008; Sinervo 1999; Einum and Fleming 1999). However, trade-offs are expected between investment in offspring quantity and quality (Roff 1992; Stearns 1992). Therefore, when environments are physiologically benign, females are expected to favor investment in offspring quantity, as benefits conveyed by increased provisioning per offspring declines with increasing habitat quality (Rollinson and Hutchings 2013).

Maternal effects also occur in relation to the absolute body size of the mother. If environmental conditions are benign, large females may be able to increase investment in reproduction either because they are in better physical condition or because increased abdominal size relaxes trade-offs between offspring size and number (Hendry et al. 2001; Einum and Fleming 2000). This can result in offspring which are physically larger and more fecund, irrespective of the environmental conditions they experience as adults (*i.e.* the silver spoon effect; Grafen 1988). However, when conditions are stressful, large females can face additional costs related to more difficult to meet metabolic demands (Shina 1988). In exothermic taxa such as insects, increased metabolic demands associated with a large body size increase exponentially as temperatures rise (González-Tokman et al. 2020). Given the increase in soil temperatures resulting from forest harvesting, large females may shift investment towards physical growth/maintenance at the cost of reproduction (Zera and Harshman 2001).

Post-harvest maternal effects are likely to be further impacted by the ecological requirements of each species, as the magnitude of stress experienced can change the intensity with which maternal effects are expressed (Rossiter 1991a; 1998). Ground beetles (Coleoptera, Carabidae) are often broadly classified as habitat generalist or specialist species and are frequently used to evaluate the impacts of anthropogenic disturbances including forest harvesting (Wu et al. 2020; Kotze et al. 2011; Baker et al. 2004). In ground beetles, generalists often have wide thermal and moisture niche requirements, allowing these species to occupy a diverse range of habitats (Lindroth 1966; Thiele 1977). Forest specialists are expected to have narrower thermal and moisture requirements as they are characteristically found in high abundance only under closed canopies (Palviainen et al. 2004; Thiele 1977). Because forest specialists experience the post-harvest environmental quality to be ‘poorer’ than generalists, maternal effect expression may intensify for these species (Rossiter 1991a; 1998).

Here we tested whether forest harvesting can cause rapid changes in maternal investment in remnant populations of one habitat generalist (*Pterostichus pensylvanicus* LeConte 1873) and one forest specialist species (*Pterostichus coracinus* [Newman 1838]) of ground beetle. We mated beetles collected from recently clear-cut or unharvested forests and reared progeny in a series of common garden and reciprocal transplant experiments to test three main predictions. First, assuming that stressful environments favor investment in offspring quality over quantity, we predicted that females from the clear-cuts would lay fewer eggs but would increase investment per egg. We expected increased investment to manifest through higher hatching rates (Warner and Lovern 2014) and more rapid larval development (Kyneb and Toft 2006). Second, assuming that increasing temperatures cause large females to shift allocation of resources towards higher metabolic demands at the cost of fecundity, we predicted that large females from the clear-cuts would lay fewer eggs than equally sized females from the uncut stands. Finally, we predicted that increased post-harvest stress in the forest specialist would intensify maternal investment into offspring quality as compared to the habitat generalist (traditionally manifesting as increased hatching and growth rates; Kyneb and Toft 2006). However, larval growth rate in the specialist is expected to be constrained by this species obligation to overwinter as larvae prior to pupation (Thiele 1977). Therefore, we expect investment per offspring in the forest specialist to manifest as higher hatching rates only.

3.3 Methods/Materials

3.3.1 Study species

Pterostichus pensylvanicus and *P. coracinus* are broadly distributed across North American forests (Barlow 1970) but differ in their habitat affinities and breeding strategies. *Pterostichus pensylvanicus* is a spring-breeding species and considered a habitat generalist (Goulet 1974; Koivula 2001). Spring-breeding species, like *P. pensylvanicus*, reproduce from spring to early summer, pupate prior to fall and overwinter as mature adults (Thiele 1977). *Pterostichus coracinus* is an autumn-breeding species and considered a forest specialist (Lindroth 1966). Autumn-breeding species, like *P. coracinus,* reproduce from mid-summer through fall, overwinter as larvae and do not pupate until the following spring (Thiele 1977). While abundance in *P. coracinus* declines more sharply following clear-cutting as compared to *P. pensylvanicus*, both species are negatively impacted by habitat changes associated with clear-cutting (*i.e.* increased light and soil temperatures, decreased moisture and homogenization of microhabitats) and are expected to find post-harvest conditions stressful (Wu et al. 2020; O’Connor 2009). Additionally, both species have limited dispersal capabilities and populations are expected to be highly localized (Lindroth 1966; Den Boer 1970).

3.3.2 Study Site

Collection of adult beetles and reciprocal transplant experiments using larvae were conducted May through August of 2021 within clear-cut and uncut stands located in the Lake Duparquet research and teaching forest in the Abitibi region of western Quebec, Canada (48°30'14.8"N 79°16'15.6"W). We selected three stands, separated by approximately 200-500 m of unharvested forests and logging roads, to use as replicates for the clear-cut treatment. Each stand was harvested between 2015 and 2016 and was between 8 and 20 acres in size. Prior to harvest, clear-cuts were dominated by mature trembling aspen (*Populus tremuloides* Michx). We also selected three uncut stands, separated by 1-2 km of mixed- and softwood forest, which were dominated by mature trembling aspen to use as replicates for the uncut treatment. These stands originated after a fire in 1923 (Dansereau and Bergeron 1993) and were each approximately 24 acres in size. The clear-cut stands and the uncut stands were separated by 3-5 km.

3.3.3 Maternal investment in fecundity and hatching success

We collected beetles using 25 dry pitfall traps (7.5 cm in diameter) within each stand, set at approximately 10 m intervals (Spence and Niemelä 1994). Traps were set a minimum of 50 m interior from edge habitat. Adult beetles were collected from traps three times/week to minimize cannibalism or negative effects on fecundity due to starvation (Van Dijk 1979). Beetles were paired in the lab with opposite sexed conspecifics from the same stand. For *P. pensylvanicus*, we collected 23 pairs from the clear-cuts and 26 pairs from the uncut stands. For *P. coracinus*, we collected 11 pairs from the clear-cuts and 23 pairs from the uncut stands. Mated pairs were fed ad libitum and remained together throughout the reproductive period to allow for repeated copulations (see Appendix A for additional details).

Eggs laid from mated females were removed weekly and incubated at 20°C (see Appendix A). We recorded the total number of eggs laid/female/week, the length of the incubation period for each egg prior to hatching and the proportion of eggs which hatched/female/week. For *P. pensylvanicus,* we collected a total of 509 eggs from the clear-cut mated pairs and 514 eggs from the uncut mated pairs. For *P. coracinus,* we collected a total of 843 eggs from the clear-cut mated pairs and 1811 eggs from the uncut pairs. When a female did not produce eggs for three consecutive weeks, we determined she was finished laying eggs for the season and the pair was then preserved in 70% ethanol. Following preservation, we measured each specimen’s elytra length which is a reliable proxy for body size in beetles and highly correlated with measurements of energy reserves (Zanchi et al. 2022).

3.3.4 Offspring fitness

3.3.4.1 Common garden experiment

To evaluate whether differences in maternal investment affected fitness traits in offspring, we reared progeny from clear-cut and uncut parental lineages in a common garden experiment in the lab. We reared up to three larval replicates from each mated pair which produced eggs. For *P. pensylvanicus*, we reared 34 larvae contributed by 14 clear-cut mated pairs and 44 larvae contributed by 16 uncut mated pairs. For *P. coracinus*, we reared 27 larvae contributed by 10 clear-cut mated pairs and 59 larvae contributed by 20 uncut pairs. Larvae were reared in individual containers and fed with equal amounts of a mealworm diet (see Appendix B for additional details). At 35 days, larvae which had not pupated were weighed to the nearest 0.0001 g (Lundgren et al. 2005). We recorded the number of days larvae took to emerge as an adult. For larvae that did not reach maturity, we recorded total lifespan from emergence to death. All offspring which reached maturity were preserved in 70% ethanol and elytra lengths measured to be used as a proxy for mature body size (Zanchi et al. 2022).

3.3.4.2 Reciprocal transplant experiment

To evaluate how differing maternal investment strategies interacted with environmental conditions and affected offspring survivorship, we reared offspring in field enclosures placed in clear-cut and uncut habitats. Field enclosures were segments of PVC (7.6 cm in diameter) sealed with micromesh on either end to allow free passage of rainwater. We placed two enclosures within a 2 m radius of each pitfall trap resulting in 50 enclosures/stand. For *P. pensylvanicus*, we selected up to 12 larvae from each mated pair to be used as replicates (two replicates per pair reared per stand, contributed by 17 clear-cut mated pairs and 10 uncut pairs; Appendix C: Table 3C). For *P. coracinus*, we selected up to 6 larvae from each mated pair to be used as replicates (one replicate per pair reared per stand, contributed by 8 clear-cut mated pairs and 10 uncut pairs; Appendix C: Table 3C). We randomly assigned one first instar larva with an uncut parental lineage and one larva from clear-cut parental lineage to each of the paired enclosures. This resulted in larvae being reared in identical habitat to that of the parental collection (*e.g.* larvae with clear-cut lineage reared in clear-cut habitat) and in habitat which was reciprocal to that of their parental collection (*e.g.* larvae with clear-cut lineage reared in uncut habitat). All larvae were provided equal amounts of a mealworm diet to standardize resource availability (See Appendix C; Van Dijk & Boer 1992).

We evaluated survivorship in *P. pensylvanicus* offspring after 49 to 52 days. This period reflected the average development time to reach maturity when reared in the common garden. Field enclosures were transported to the lab where larval survivorship was assessed by careful hand sorting of enclosure contents. Any *P. pensylvanicus* individuals still in larval or pupal stage at time of collection were placed in individual rearing containers until they reached maturity. Following sclerotization, mature *P. pensylvanicus* were preserved in 70% ethanol and elytra length were measured. In *P. coracinus,* survivorship was evaluated on our last day with access to the field site (August 20th, 2021) to provide maximum developmental time. As *P. coracinus* is an autumn-breeding species which overwinters as larvae, all survivors remained as larvae. Larvae were weighed to the nearest 0.0001g immediately following collection (Lundgren et al. 2005).

3.3.5 Statistical analysis

3.3.5.1 Maternal investment in fecundity and hatching success

We evaluated whether adult elytra length, a proxy for mature body size/potential energy reserves, differed between populations from clear-cuts or uncut stands using simple linear models. We compared the number of eggs laid/female between clear-cut and uncut populations using negative binomial generalized linear models (GLMs) with the number of days each female laid eggs as a model offset. To test if habitat or body size affected maternal investment/offspring, we used binomial GLMs to compare differences in the overall proportion of eggs which hatched/female, weighted by the number of eggs laid/female. We also tested to see if the length of time the eggs incubated prior to hatching varied by the parent's habitat using nonparametric time-to-event models (Onofri et al. 2022). We used time-to-event models because we recorded emergence from eggs on a weekly basis. Time-to-event models are specifically designed to account for this type of interval-censoring in data and result in more reliable estimates of parameters and related variances (Michelon et al. 2021; Romano and Stevanato 2020). We used an expectation-maximization algorithm to find the nonparametric maximum likelihood estimator

(NPMLE) of the time-to-event curves. The resulting time-to-event curves have a staircase shape defined by a set of non-overlapping time intervals (Turnbull's intervals; Fay and Shaw 2010) and related masses, which can be conceptually regarded as model parameters (Onofri et al. 2022). To test for significance, we used a permutation-based likelihood ratio test (Wilcoxon rank sum score; Gomez et al. 2009).

3.3.5.2 Lineage effects on growth and survivorship in common garden experiment

For larvae reared in the common garden experiment, we compared both larval weight and body size at maturity between parental habitats using linear mixed models. We also evaluated the days required to reach maturity in *P. pensylvanicus,* and overall lifespan in *P. coracinus,* using generalized linear mixed models (GLMMs). In these models, we included replicate larvae taken from the same parents as a random effect and used parental lineage and maternal body size as the explanatory variables. For models examining days to maturity in *P. pensylvanicus*, we used a Poisson distribution. For models examining variations in overall lifespan in *P. coracinus*, we found Poisson distribution to be overdispersed and instead used a negative binomial distribution.

3.3.5.3 Habitat and lineage effects on growth and survivorship in reciprocal transplant experiment

For larvae reared in the reciprocal transplant experiment, we evaluated the effects of the rearing habitat and the parental lineage on survival probability using binomial GLMMs. For *P. pensylvanicus*, we also compared differences in offspring's body size at maturity between habitats using linear mixed models. For *P. coracinus,* which were collected from field enclosures as larvae, we analyzed weight gain per day using GLMMs. For these models we used a gamma distribution and included the number of days each larva was in the field as an offset. For all reciprocal transplant models, we included replicate larvae from the same male/female pair as a random effect and used parental lineage, rearing habitat and parental body size as the explanatory variables.

For all regression analyses, we started with full models including all possible interactions and then removed interactions and/or explanatory variables which did not improve model fit measured as Akaike information criterion (AIC) (Burnham and Anderson 2004). Only results from final models are presented. We completed all regression analyses using packages lme4 (Bates et al. 2015), MASS (Venables and Ripley 2002) and AICcmodavg (Mazerolle 2020) in RStudio (R version 4.2.2; R Core Team 2022). We completed time-to-event analyses using package drcte (Onofri et al. 2022) in RStudio (R version 4.2.2; R Core Team 2022).

3.4 Results

3.4.1 Maternal investment in fecundity and hatching success

For captured adults, body size did not differ by habitat for either species (*P. pensylvanicus*: P=0.178; *P. coracinus*: P=0.481; Table 3.1). For *P. pensylvanicus*, the total number of eggs laid per female did not vary by habitat (P=0.475) or maternal body size (explanatory variable excluded from final model; Table 3.1). Time required for *P. pensylvanicus* eggs to hatch did not differ by habitat (P=0.165; Fig. 3.1C). However, a larger proportion of eggs hatched that were laid by females from clear-cuts (P<0.001) and this proportion increased in smaller females (P<0.001; Table 3.1; Fig. 3.2A). In *P. coracinus*, we found a significant interaction between habitat and maternal body size on the total number of eggs laid per female, with more eggs being laid by smaller females in clear-cuts (P=0.008; Table 3.1; Fig. 3.3). Incubation times for *P. coracinus* eggs was less for eggs laid by females from clear-cuts than from uncut stands (P<0.005; Fig. 3.1D). Similar to *P. pensylvanicus*, we found a significant interaction between habitat and maternal body size on the overall proportion of *P. coracinus* eggs that hatched, with more eggs hatching from smaller females with clear-cut origins (P<0.001; Table 3.1; Fig. 3.2B).

3.4.2 Growth rate and survivorship of offspring in common garden experiment

For offspring reared in the common garden experiment, we found that larval weight was not affected by parental lineage in either species (*P. pensylvanicus*: P=0.34; *P. coracinus*: P=0.388) or maternal body size (*P. pensylvanicus*: P=0.193; *P. coracinus*: P=0.747; Table 3.2). However, *P. pensylvanicus* offspring from clear-cut parental lineages took less time to reach maturity (P=0.01) and time to maturity was quicker among larvae from smaller mothers (P=0.0269; Table 3.2; Fig. 3.4). We also found that *P. pensylvanicus* larvae which matured more quickly had larger body size as adults (P<0.001; Table 3.2). In *P. coracinus*, while 24% of the larvae reared in the common garden reached pupation (30% of uncut lineage, 11% of clear-cut lineage), none survived to maturity. Thus, for this species, we could only evaluate differences in the overall lifespan of the larvae. We found that maternal body size did not affect lifespan (P=0.671) and while lifespan tended to be shorter in *P. coracinus* larvae with clear-cut parental lineages, this relationship was not significant (P=0.063; Table 3.2).

3.4.3 Growth rate and survivorship of offspring in reciprocal transplant experiment

For *P. pensylvanicus* reared in the reciprocal transplant experiment, we found survival probability was not affected by the offspring's parental lineage (P=0.377) or maternal body size (explanatory variable excluded from final model; Table 3.3). When *P. pensylvanicus* were reared in the same habitat as their parents, larval survival was 54% in uncut stands and 47% in clear-cuts. When *P. pensylvanicus* were reared in the reciprocal habitat from their parents, larval survival was 39% in uncut stands and 33% in clear-cuts (Table 3.4). While we found survival of *P. pensylvanicus* larvae reared in clear-cut stands to be lower than those reared in uncut stands regardless of parental lineage, this effect was not significant (P=0.063; Table 3.3). Of the *P. pensylvanicus* which survived to maturity, mature body size was not affected by parental lineage (P=0.951), rearing habitat (P=0.298) or maternal body size (P=0.441; Table 3.3).

For *P. coracinus,* we observed a significant interaction between parental lineage and rearing habitat on larval survivorship (P=0.008; Table 3.3). Survival of *P. coracinus* reared in uncut stands was 17% when larvae's parental lineage originated from uncut stands but increased to 36% when parental lineage originated from clear-cuts. Moreover, survival for offspring reared in clear-cuts was 4% when larvae's parental lineage originated from clear-cut stands but increased to 33% for larvae with parental lineages originating from uncut stands (Table 3.4). Survival probability of *P. coracinus* larvae was not affected by maternal body size (explanatory variable excluded from final model; Table 3.3). Weight gain of *P. coracinus* larvae was not affected by rearing habitat (P=0.750), parental lineage (P=0.856) or maternal body size (P=0.694; Table 3.3).

3.5 Discussion

3.5.1 Adaptation via maternal investment

Stressful environments are expected to favor increased maternal investment in offspring quality to maximize annual offspring survival (Mousseau and Fox 1998a; 1998b). We found that in both species, female ground beetles from clear-cuts had increased hatching success as compared to females from uncut habitats, likely indicating increased provisioning of eggs (Warner and Lovern 2014). Further evidence for increased maternal investment in offspring quality included faster development of eggs (in *P. coracinus*) and larvae (in *P. pensylvanicus*) from clear-cut females. These changes are likely indicative of an adaptive response, rather than non-adaptive plasticity. Given constraints in maternal nutrient status and/or increased difficulty meeting metabolic demands, non-adaptive plasticity is expected to result in stressed females laying poorer quality eggs with reduced hatching success (Fox and Czesak 2000). However, the clear-cut females diverged from the expected, non-adaptive, stress response by laying eggs with increased hatching success. Therefore, this response is unlikely to be attributed to non-adaptive plasticity and could indicate an adaptive response which improved probability of offspring survival (Kingsolver et al. 2011).

Increased maternal investment in offspring quality in the clear-cut populations did not come at the expected cost to total reproductive output (Roff 1992; Stearns 1992). In this case, females may have compensated for increased reproductive output by using other metabolic resources such as reserves stored in the fat body or in the case of *P. pensylvanicus*, by reducing investment in flight muscles. *Pterostichus pensylvanicus* is a wing dimorphic species (Lindroth 1966) and may manifest the oogenesis-flight syndrome like other wing dimorphic ground beetles (Desender 2000). In the oogenesis-flight syndrome, the metabolic cost associated with development and maintenance of wing muscles results in trade-offs with reproduction. When environmental conditions are benign, it is thought that females can re-absorb muscle tissue to increase fecundity. Conversely when conditions are stressful, females may absorb unchorionated eggs to build flight muscle to disperse (Aukema 1991; Kotze et al. 2011). In our study, we found only a single female with developed flight muscles (L. Egli, personal observation). This female originated from the uncut habitat and did not produce any eggs. Females without flight muscles may have allocated metabolic reserves towards increased investment in reproduction. We suggest that after clear-cutting remnant populations of wing dimorphic species may mobilize metabolic reserves to increase fecundity and survival consistent with the flight-oogenesis syndrome. While beneficial in response to the immediate effects of harvest, additional stressors from climate change may impart further metabolic demands on females and reduce resilience of remnant populations in managed forests (Klepsatel et al. 2016; Price et al. 2013).

Pterostichus coracinus not only produced eggs with increased hatching success following clear-cutting, but also produced much larger quantities of eggs than *P. pensylvanicus*. As a forest specialist, *P. coracinus* likely suffers higher egg and larval mortality throughout the summer as compared to generalist species. Additionally, *P. coracinus* cannot adapt to stressful environments by reducing time spent as larvae, as found in *P. pensylvanicus,* because autumn-breeding species require a cold period to trigger pupation (Thiele 1977). This constraint may have shifted investment towards increased offspring quantity and may explain, in part, the differences in overall fecundity between *P. coracinus* and *P. pensylvanicus.* However, simply producing more offspring may not be a viable strategy to offset increased mortality in clear-cuts for *P. coracinus* under climate change, as an increased time lag between larval emergence and diapause can result in mortality in insects which require a cold period to complete development (Marshall and Roe 2021). Considering boreal forests are already experiencing earlier springs and delayed winters (Price et al. 2013), the inability of *P. coracinus* to adapt to these environmental changes by reaching maturity more quickly significantly restricts their abilities to overcome the combined effects of clear-cutting and climate change and will likely lead to increased post-harvest mortality in future generations.

3.5.2 Maternal-size effects

Initially, we predicted that large females from uncut stands would be able to invest in a greater number of offspring given their greater resource reserves, while large females from clear-cuts would be faced with intensified trade-offs between allocation of resources towards physical growth/maintenance and fecundity due to amplified metabolic demands associated with larger body size coupled with higher temperatures (González-Tokman et al. 2020). A possible explanation for why this relationship occurred in *P. coracinus*, but not in *P. pensylvanicus*, might be attributed to differences in baseline body size and fecundity between the two species. In *P. coracinus*, reduced maternal investment in offspring by large females from clear-cuts may reflect increased metabolic demands related to the relatively large body size of this species (12.5-18 mm; Lindroth 1966; Sheridan and Bickford 2011). Furthermore, autumn-breeding species generally have relatively greater overall fecundity than spring breeders (Thiele 1977) which may represent an obligate cost for both larger and smaller females. In contrast, *P. pensylvanicus* may have lower baseline metabolic demands given its smaller body size (9.5-12 mm; Lindroth 1966) and possibly fewer obligate metabolic demands related to reproduction.

3.5.3 Rapid adaptation following forest harvest

Larvae with parental lineages from clear-cuts hatched and developed faster in the common garden experiment suggesting a population level difference in maternal investment strategies in the clear-cut and uncut populations. However, because we reared only one generation of offspring we cannot separate the influence of genetic maternal effects from environmentally based maternal effects. Regardless of the mechanism, adaptations in the clear-cut populations presumably developed within the 5-6 generations since stands were harvested. This short timespan provides an empirical example of maternal effects facilitating population persistence under changing environmental conditions over an ecological timescale.

3.5.4 Interaction between maternal and offspring environment

In *P. coracinus* we found a significant interaction between maternal and offspring environment on probability of survival in larvae. In other words, when there was a discrepancy between maternal and offspring environmental conditions (larvae from clear-cut parents reared in the uncut stands or vice versa) probability of survival increased. The intensity of maternal effect expression is a function of not only the mother's environment, but also the environmental quality experienced by the offspring (Mousseau and Fox 1998b). In many cases, discrepancies between parental and offspring environment have been found to increase intensity of maternal effect expression (reviewed in Rossiter 1998). For example, Lin and Dunson (1995) found that offspring which encountered "good" environmental conditions utilized resources more efficiently when their parents were from poor environmental conditions compared to those with parents from benign conditions. In forest specialists such as *P. coracinus,* this strategy may have developed as a means to improve survivorship of offspring in the heterogeneous mosaic of stand types typical of the boreal forest.

3.5.5 Management Implications

Overall, clear-cutting had greater impacts on fecundity and survival in the forest specialist species, *P. coracinus,* as compared to generalist species, *P. pensylvanicus.* For species like *P. coracinus*, recovery of remnant populations may benefit from not only a numerical influx of individuals from neighboring stands, but also from increased fecundity and survival that is attributable to interactions between maternal and offspring environment realized along the interface between clear-cuts and uncut stands. Given that increased maternal effect expression may occur along these interfaces, management practices which maintain patches of unharvested trees among larger clear-cuts could create important reservoirs of individuals with increased survivorship, speeding recovery of remnant populations after harvest. Creation of these reservoirs may not only promote preservation of forest specialists under current conditions but could also play an important role for maintaining biodiversity in the context climate smart forestry as climate change affects boreal forests (D'Amato et al. 2011).

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3.7 Contribution statement

For this chapter, I conceived the ideas and designed the methodology, collected and analyzed the data and led the writing of the manuscript. Timothy Work revised the manuscript critically for important intellectual content and provided guidance throughout.

3.8 References

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3.9 Tables

Table 3.1. Comparisons of body size, total reproductive output and egg hatching success in the parent's generation of ground beetles collected from clear-cut and uncut habitats.

	Intercept	Habitat†	Maternal body size	Habitat*Maternal body size
P. pensylvanicus - generalist				
Body size	0.640(0.005)***	0.009(0.007)		
Total eggs laid	0.484(0.126)***	0.132(0.185)		
Proportion eggs hatched	6.455(133.2)***	0.481(0.142)***	-8.791(2.078)***	
P. coracinus – forest specialist				
Body size	0.855(0.007)***	0.008(0.011)		
Total eggs laid	-6.561(2.452)**	15.323(5.747)**	7.941(2.785)**	-17.266(6.464)**
Proportion eggs hatched	5.999(1.852)**	27.928(4.148)***	-5.874(2.077)**	-31.059(4.643)***

+ P < 0.1; * P < 0.05; ** P < 0.01; *** P < 0.001; † Uncut habitat used as reference

Table 3.2. Comparisons of growth and survivorship of offspring with parents from clear-cut or uncut habitats, reared in a common garden experiment.

	(Intercept)	Parent's habitat†	Maternal size	Paternal size	Size at maturity	Replicate larvae‡
P. pensylvanicus - generalist						
Larval weight	0.023(0.019)	0.002(0.002)	0.039(0.030)			
Maturation time	5.975(0.691)***	-0.117(0.046)*	1.469(0.664)*	-0.832(0.836)	-3.429(0.765)***	0.071
P. coracinus – forest specialist						
Larval weight	0.042(0.039)	-0.002(0.002)	0.014(0.044)			
Lifespan	5.769(1.577)***	-0.202(0.109)+	-0.757(1.785)			

+ $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; † Uncut habitat used as reference; ‡ Random effect

†

Table 3.3. Comparisons of survivorship and development of offspring with parents from clear-cut or uncut habitats, reared in a reciprocal transplant experiment.

	(Intercept)	Rearing habitat†	Parent's habitat†	Rearing habitat*Parent's habitat	Maternal size	Replicate larvae‡
P. pensylvanicus - generalist						
Survivorship	0.157(0.306)	-0.592(0.318)+	-0.289(0.326)			
Mature size	0.608(0.067)***	-0.007(0.007)	-0.0005(0.007)		0.083(0.107)	
P. coracinus – forest specialist						
Survivorship	-1.609(0.490)**	0.916(0.624)	1.050(0.661)	-3.401(1.278)**		
Larval weight	-8.414(2.835)**	0.030(0.094)	0.034(0.190)		1.247(3.172)	0.199

+ $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; † Uncut habitat used as reference; ‡ Random effect

Table 3.4. Probability of survival of offspring with parents from clear-cut or uncut habitat, reared in a reciprocal transplant experiment.

	Rearing habitat	Parent's habitat	Fit	SE fit	Upper limit	Lower limit	Predicted probability of survival
P. pensylvanicus - generalist							
	Clear-cut	Clear-cut	-0.723	0.260	0.447	0.226	33%
	Clear-cut	Uncut	-0.435	0.296	0.536	0.266	39%
	Uncut	Clear-cut	-0.131	0.255	0.591	0.347	47%
	Uncut	Uncut	0.157	0.306	0.681	0.391	54%
P. coracinus – forest specialist							
	Clear-cut	Clear-cut	-3.045	1.023	0.261	0.006	4%
	Clear-cut	Uncut	-0.693	0.387	0.516	0.190	33%
	Uncut	Clear-cut	-0.560	0.443	0.577	0.193	36%
	Uncut	Uncut	-1.609	0.490	0.343	0.071	17%

3.10 Figures

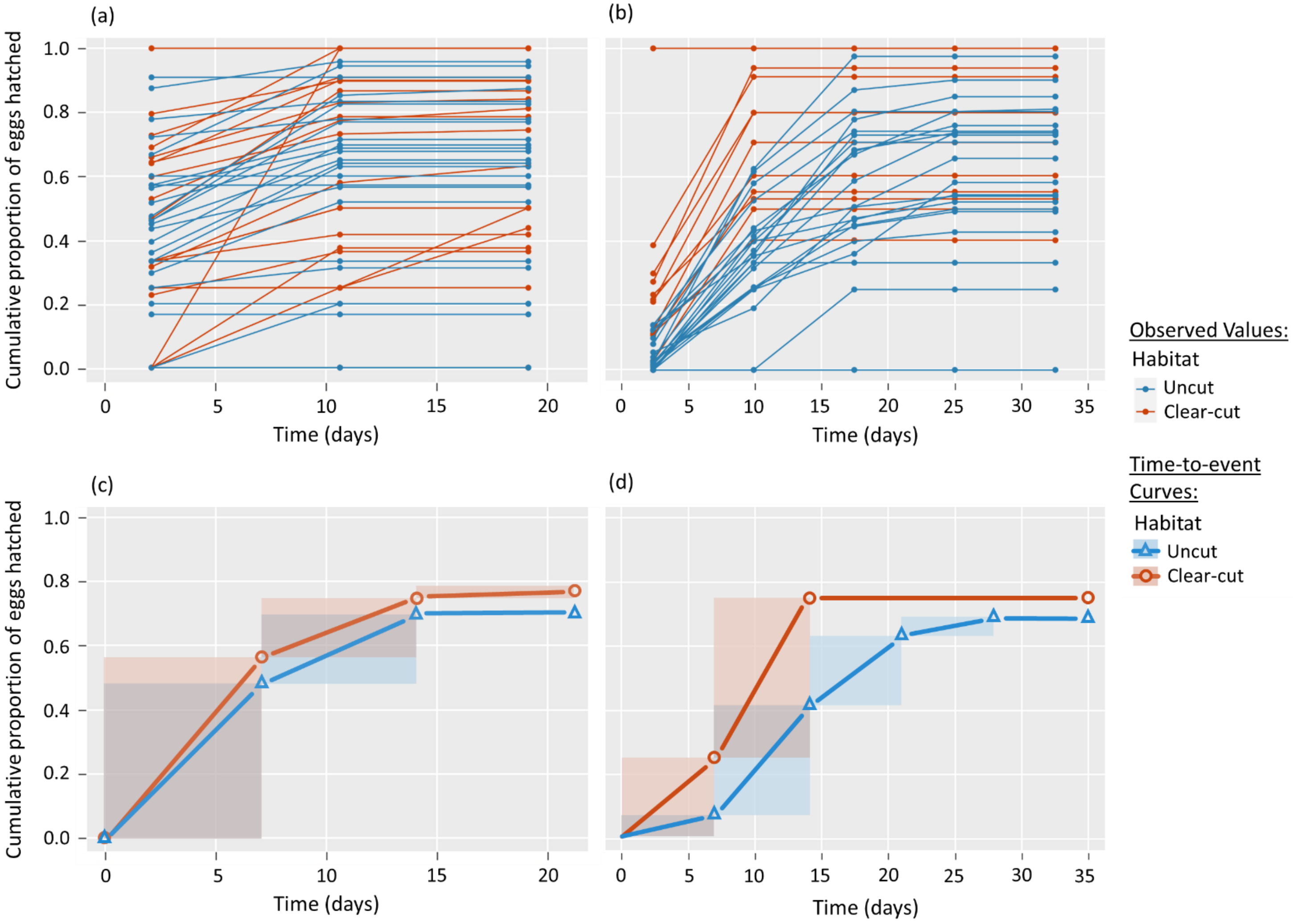

Figure 3.1. Observed incubation periods for eggs laid by *P. pensylvanicus* (a) and *P. coracinus* (b) females from uncut and clear-cut habitat and nonparametric time-to-event curves for egg incubation periods for *P. pensylvanicus* (c) and *P. coracinus* (d) females. In time-to-event curves, symbols show the nonparametric maximum likelihood estimators (NPMLE) for the time to event at the end of Turnbull's intervals, while the shaded areas represent uncertainty due to censoring.

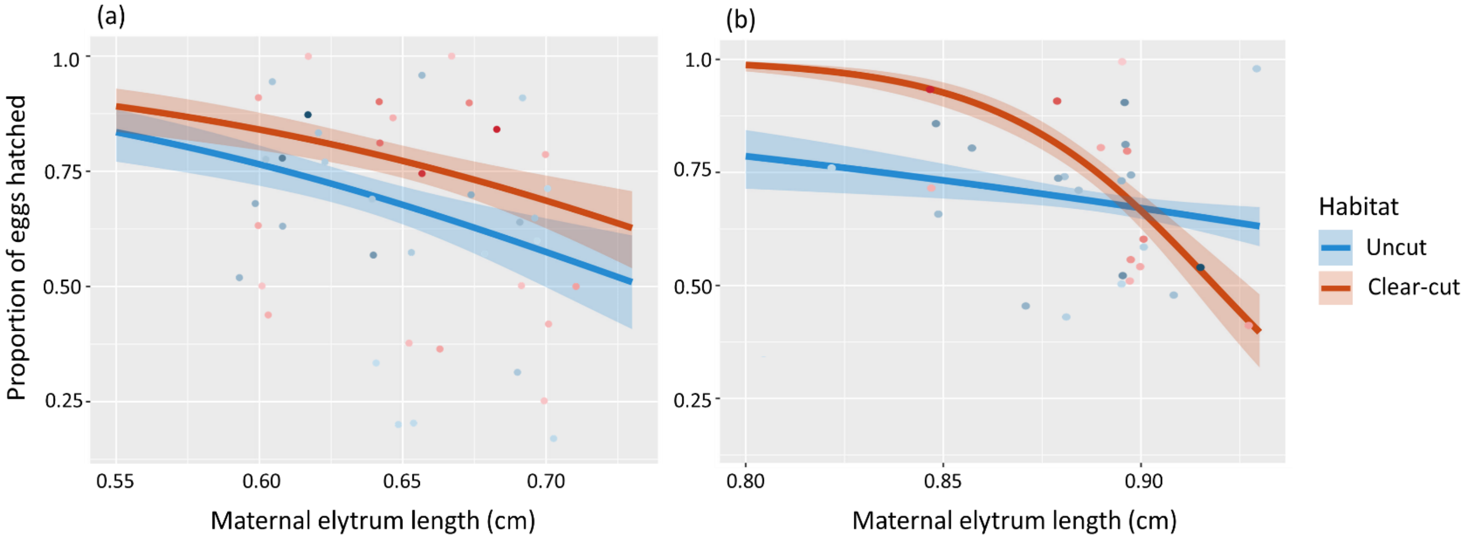

Figure 3.2. Relationship between maternal size and egg hatching success in *P. pensylvanicus* females (a) and *P. coracinus* females (b) collected from clear-cut and uncut habitats. Color gradient in the observed values signifies weight (total eggs laid per female), with darker colors representing values with a greater impact on the weighted regression models. For test statistics, see Table 3.1.

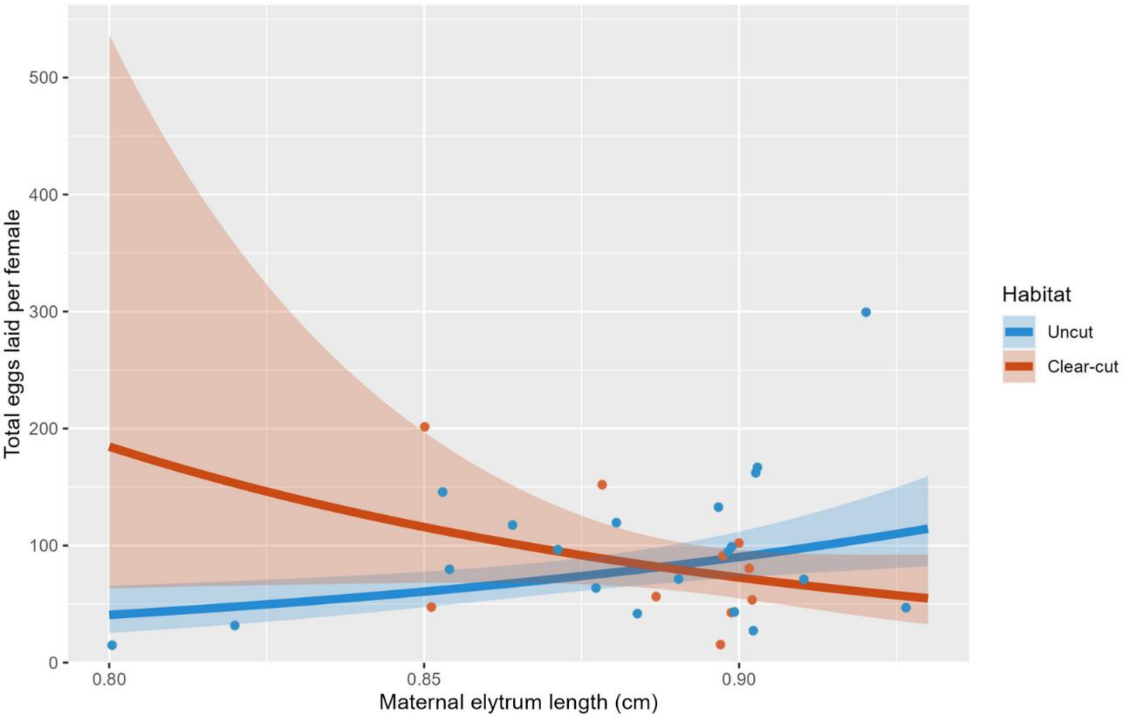

Figure 3.3. Relationship between maternal size and total reproductive output in *P. coracinus* females collected from clear-cut and uncut habitats. For test statistics, see Table 3.1.

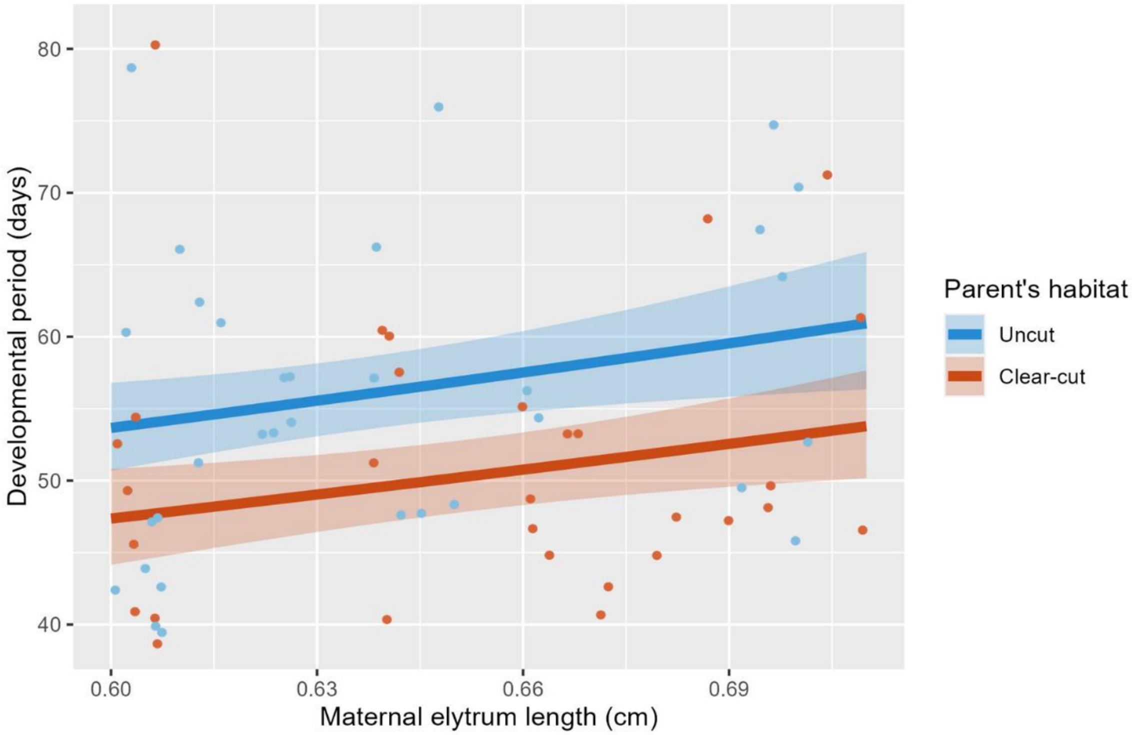

Figure 3.4. Relationships between maternal size, parent's habitat and speed of development from first instar larvae to maturity in *P. pensylvanicus* offspring reared in a common garden experiment. For test statistics, see Table 3.2.

3.11 Appendix A

3.11.1 Additional detailed methodology

3.11.1.1 Maternal investment in fecundity and hatching success

Following collection from pitfall traps, *Pterostichus pensylvanicus* LeConte 1973 and *Pterostichus coracinus* (Newman, 1838) were transported in dark, cool containers to the lab where they were paired with opposite sexed conspecifics originating from the same stand. Each pair was housed on a 1 cm bed of moist, loose peat dust in an individual cup with a tight-fitting lid (Goulet 1976). Cups were 4 oz in size for *P. pensylvanicus,* and 8 oz in size for *P. coracinus* as they are a larger species. Pairs were kept at the daily changing temperature of the field and exposed to natural day/light cycles (Goulet 1976; Mols 1988). Each pair was provided with 1/5th of a mealworm (*Tenebrio molitor* Linnaeus, 1758) daily, with uneaten food scraps from the previous day removed at this time. We provided pairs with food to excess as starvation rarely occurs in the field and rapidly affects fecundity (Van Dijk 1979b). We removed each pair to a new container with fresh substrate every seven days. At this time, we separated eggs from the old substrate using the floatation method (Van Dijk 1979a; Mols et al. 1981). We transferred eggs using a moist paintbrush into incubation chambers designed as per Goulet (1976) where they were incubated at a constant 20°C until larvae had hatched, or eggs proved unviable.

3.12 Appendix B

3.12.1 Additional detailed methodology

3.12.1.1 Common garden experiment

Larvae were removed from incubation chambers within 24 hours of hatching and placed individually in 1 oz plastic cups with tight fitting lids and a 1 cm deep bed of loose, moist peat moss (Goulet 1976). Individuals were kept at ambient temperatures (~23°C; Goulet 1976; Mols 1988). Each larva was provided with 1/6th of a mealworm daily and any food remnants or traces of mold removed at this time (Van Dijk 1979). Individuals were inspected daily for changes to their developmental stage and substrate was exchanged on every seventh day.

As *Pterostichus coracinus* is an autumn-breeding species which requires a cold period to trigger pupation (Larsson 1939; Thiele 1977), *P. coracinus* larvae were housed at approximately 4°C for three months (Oct 2021-Dec 2021; Goulet 1976). Throughout the artificial cold period larvae entered diapause and did not require access to food. We opened larval cups once every seven days to allow a fresh exchange of oxygen. At this time, we moistened the substrate if necessary or replaced the substrate if there was any evidence of mold. At the end of the artificial cold period larvae were returned to ambient temperatures (~23°C) and fed with 1/6th of a mealworm daily until pupation was reached or they expired (Goulet 1976).

3.13 Appendix C

3.13.1 Additional detailed methodology

3.13.1.1 Reciprocal transplant experiment

Field enclosures comprised a modified design as per Van Dijk and Boer (1992) and were constructed as follows: we collected 400 cm^3 soil cores in the field and then housed them, with as little disturbance as possible, inside 3x5 inch segments of PVC pipe. The bottom of each segment of PVC was sealed with micromesh, which prevented even first instar larvae from burrowing out, but allowed free passage of rainwater. We then replaced each segment of PVC into the original coring location, with 3.5 of the 5-inch total length sunk back into the original hole so that the surface of the core was level with the surrounding ground. This allowed 1.5 inches of empty cylinder to stand above the ground to prevent the larvae escaping. We then placed a single first instar larva into each enclosure (Table 3C) and topped it with a micromesh screen to prevent predation. We provided each larva with 1/6th of a mealworm three times per week to standardize resource availability between enclosures (Van Dijk and Boer 1992).

Table 3C. Sample sizes of contributing mated pairs and larval replicates reared in the reciprocal transplant experiment.

Rearing habitat	Parent's habitat	Number parental pairs contributing larvae	Number of larvae contributed by each parental pair	Total number of larval replicates
P. pensylvanicus - generalist				
Clear-cut	Clear-cut	17	2-6	54
Clear-cut	Uncut	10	2-6	34
Uncut	Clear-cut	17	2-6	50
Uncut	Uncut	10	2-6	29
P. coracinus – forest specialist				
Clear-cut	Clear-cut	8	1-3	22
Clear-cut	Uncut	10	3	30
Uncut	Clear-cut	8	1-3	22
Uncut	Uncut	10	3	30

CONCLUSION GÉNÉRALE

Research evaluating the efficacy of partial-retention harvesting is becoming increasingly important in my view, as partial-retention harvesting provides a balance between timber production and conservation of biodiversity and has the benefit of promoting heterogeneity in stand structure and composition which may increase resilience of stands under climate change (D'Amato et al. 2023; O'Hara and Ramage 2013; Itter et al. 2017). While most published studies have focused on early response of ground beetle species assemblages following partial-retention harvesting (Lemieux and Lindgren 2004; Klimaszewski et al. 2003, 2005), future research is likely to reveal significant and interesting medium to long-term findings. The results published as a part of this thesis reflect ground beetle sampling conducted across 5-20 years post-harvest, as well as two decades of projections in changes in ground beetle abundance under climate change (20-40 years post-harvest) and illustrates how our perceptions may change as we are informed by data that reflects longer-term timeframes.

On the whole, our findings suggest that maintaining significant standing retention speeds recovery of ground beetle assemblages as compared to clear-cutting and is likely to maintain relatively greater ground beetle abundance over time. In the hardwood stands, 34% and 67% partial-retentions were sufficient to maintain ground beetle species assemblages as effectively as unharvested control stands over early- to mid-term timeframes (5-20 years post-harvest; Chapter 1). However, abundance of ground beetles in these silvicultural treatments is expected to decrease, as compared to populations within the unharvested controls, over longer-term timeframes (20-40 years post-harvest; Chapter 2). In the mixedwood stands, ground beetle assemblages in the harvested treatments did not recover to that of the controls as of 20 years post-harvest (Chapter 1), however, stands with greater standing retention did maintain higher ground beetle abundance over longer-term timeframes (20-40 years post-harvest) and may result in populations which are more resilient to additional stressors such as insect outbreaks or short-term droughts (Chapter 2). In addition, maintaining significant standing retention post-harvest was more effective at conserving closed-canopy and forest specialist species of ground beetles and minimized the intrusion of open canopy associated species as compared to clear-cutting or lower retention harvesting (Chapters 1 &2; see also Wu et al. 2020; Koivula et al. 2019; Klimaszewski et al. 2005). These results suggest that partial-retention harvesting can be used as a more effective method to conserve biodiversity as compared to conventional clear-cutting practices, however, the results of my thesis also highlight several shortcomings in the current iteration of natural disturbance-based management (NDBM).

Although the harvesting regime at SAFE was designed to emulate natural disturbances and forest succession, harvests were not successful at delaying or advancing beetle species assemblages between different successional stages as would be expected following natural disturbances (Chapters 1 & 2; Bergeron et al. 1999). This is notable, as harvesting operations across Canada's boreal mixedwood forests have converted large quantities of mixed and softwood stands into early successional hardwoods, reducing habitat for species which require stands with older-growth attributes (Schneider 2023). Under current management practices, greater proportions of mixed and softwood stands are unlikely to be restored across the landscape, as harvesting occurs on intervals which are too short to allow for the replacement of early successional hardwoods with later successional species by means of succession alone (Bergeron and Fenton 2012; Kuuluvainen 2009). As the current iteration of NDBM was found to promote recovery of beetle assemblages to pre-harvest conditions, the range of forest cover types within a managed landscape should be carefully considered before harvesting is applied. If regional conservation of species which require stands with older-growth attributes is considered important, management approaches which extend beyond the current iteration of NDBM (*e.g.* integration of seeding or planting to increase softwood regeneration following harvest; Lieffers et al. 2003) may be necessary to meet management aims of transitioning stands from hardwood dominated towards mixedwood or softwood dominated compositions.

Over the past several decades, forest managers have operated under the assumption that harvests which mimic natural disturbances create habitat which falls within the range of environmental conditions forest organisms have been exposed to historically and are therefore well adapted to (Attiwill 1994; Chen and Popadiouk 2002). However, shifting disturbance regimes due to climate change brings into question whether harvests which emulate natural disturbances will effectively conserve biodiversity in the future. Across North America's boreal forests, warmer-than-average temperatures paired with low soil moisture and drought conditions have resulted in increased frequency, intensity and range of forest fires. In Canada's managed forests alone, the area affected by forest fires increased from an average of 2.1 million hectares per year, to 15 million hectares in 2023 (Natural Resources Canada, 2024). Milder winters, combined with warmer and drier summers, have also intensified damage caused by spruce budworm (*Choristoneura fumiferana* Clem.) and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) across North America (Tai and Carroll 2022; Sambaraju and Goodsman 2021), while persistent drought conditions in western North America's boreal forests have led to increased tree mortality and reduced growth rates (Liu et al. 2023). Given the significant increase in the magnitude of natural disturbance impacts on the boreal forest over time, it may no longer be prudent to attempt to truly mimic the full range and intensity of natural disturbances under future iterations of NDBM, as the combined impacts of natural disturbances and forest harvest risks further limiting the availability of habitat with later successional attributes. As such, it may be pragmatic to increase focus on the use of high-retention harvesting, as opposed to clear-cutting or lower retention harvesting, in order to preserve species assemblages associated with later successional habitats.

In addition to significant climate-mediated changes to the natural disturbance regime, uncertainties about the rate and degree of climate change are likely to necessitate a more nuanced approach to the development of conservation-oriented forest management plans. While the results in this thesis suggest that partial-retention harvesting will effectively maintain ground beetle populations for the next two decades under low emissions scenario SSP1-2.6, high emissions scenario SSP5-8.5 resulted in declines in abundance for most species within all silvicultural treatments considered (Chapter 2). Although projections for the coming decades under SSP5-8.5 appear bleak, high-retention harvesting may have the potential to offset, at least to some degree, declines in ground beetle abundance. Stands with greater basal area conferred a numerical advantage to resident populations, resulting in ground beetles in high retention stands remaining at greater density throughout this period of decline as compared to populations within other harvesting treatments. These additional years prior to reaching critically low densities may permit remnant populations the necessary time to develop adaptations. For example, selection for females with increased fecundity and offspring survivorship demonstrated by *Pterostichus pensylvanicus* LeConte, 1873 and *Pterostichus coracinus* (Newman, 1838) within recently harvested stands, or increased survival of *P. coracinus* offspring attributed to the interactions between maternal and offspring environment realized along the interface between harvested and unharvested stands (Chapter 3). If climate change trends towards the higher emissions scenario projections, management strategies which facilitate increased survival via rapid adaptations may be useful in addition to partial-retention harvesting in order to promote population persistence (*e.g.* maintaining uncut stands among larger harvests to form reservoirs of individuals with increased survivorship).

The results from my thesis support partial-retention harvesting, couched within the current iteration of NDBM, as a more effective method to preserve biodiversity as compared to conventional clear-cutting. However, additional research will be necessary to establish best practices for sustainable forest management under rapidly shifting climatic conditions. Simply stated, we cannot count on emulation of the past alone to preserve sensitive species into the future. Therefore, I suggest future research should focus on the following:

1. Continued monitoring of large-scale, established silvicultural experiments (SAFE, EMEND, TRIAD, etc.) over time, as data accumulated over long-term timeframes is likely to be pivotal in understanding complex responses of forest ecosystems following harvest, particularly as climate change drives environmental conditions outside of historical norms

2. Integration of additional silvicultural treatments into future iterations of NDBM which increase the probability of softwood regeneration post-harvest (*e.g.* seeding/planting, control of nonwoody shrubs, etc.) with the objective of transitioning early successional hardwood stands towards later successional mixed or softwood compositions

3. Integration of landscape scale spatial structure into the experimental design of silvicultural experiments, with the objective of quantifying how the level of fragmentation of the surrounding matrix impacts recovery of forest organisms

4. Integration of operational forest harvesting practices (*e.g.* use of heavy machinery) into future large-scale silvicultural experiments, as these practices are expected to affect the likelihood of organisms like ground beetles surviving harvest *in situ* and therefore their speed of recovery

5. Identification of organisms which have physiological limitations to their capacity to adapt to the combined stress of harvesting and climate change and evaluations of how these limitations may influence population persistence over time

It is my hope that the results published within this thesis, combined with future research within the aforementioned areas, may move forest managers closer to the goal of developing sustainable management practices which satisfy both our economic need for timber production, as well as our ecological and ethical desire to conserve biodiversity which may otherwise be lost.

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