University of Alberta

Impacts of aggregated retention harvesting on the diversity patterns of nocturnal moth species assemblages in the mixedwood boreal forest of northwestern Alberta

by

Brett Bain Bodeux

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Renewable Resources

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ABSTRACT

The loss of mature forest habitat from forest harvesting represents a substantial threat to the diversity of nocturnal boreal forest moth assemblages. In this study, I used spatial patterns of species diversity to quantify the effects of aggregated green tree retention harvesting on the diversity and composition of nocturnal forest moths. Ultra-violet light traps were used to sample moths in a 400 ha of intact boreal forest and a similar sized area of harvested boreal forest in northwestern Alberta, Canada. The results showed that the harvested forest supported a significantly lower number of moth species and limited the distribution of the moth species possessing relatively narrow diet breadths. Although relatively large patches of aggregated green tree retention supported diverse moth assemblages similar in composition to those present in undisturbed boreal forest, the substantial loss of mature forest habitat caused by forest harvesting substantially reduced the overall moth species richness.

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<u>Chapter 1</u>: Introduction to thesis

1.1 RESEARCH RATIONALE

Never before have humans altered the global environment so extensively, substantially and rapidly. Exploding human populations have degraded the environment and fragmented large expanses of landscapes into small and disconnected patches (Ferraz *et al.* 2003). One of the grave consequences is that species are going extinct at unprecedented rates, estimated to be hundreds times higher than normal, background rates (Millennium Ecosystem Assessment 2005). Much scientific evidence has shown that loss of species diversity is decreasing ecosystem productivity and other ecosystem functioning (Loreau *et al.* 2001; Tilman *et al.* 2001). Documenting and understanding the response of species diversity to habitat loss and fragmentation across landscapes are critical for the development of successful conservation strategies (Terborgh 1974; Noss 1983).

The impacts of habitat loss and fragmentation on biodiversity have been notoriously inconsistent (Debinksi and Holt 2000; Ewers and Didham 2006). In particular, spatial scale is one of the confounding factors that influences the magnitude and direction of the response of species diversity to habitat loss and fragmentation (Hamer and Hill 2000; Hill and Hamer 2004). Many ecological studies have traditionally focused on documenting the response of alpha-diversity, or local species diversity, in relation to patch size and isolation within anthropogenically fragmented landscapes (Fahrig 2003; Watling and Donnelly 2006; Collinge 2009), which fails to account for the inherent spatial distribution

of species diversity. A large proportion of the regional species diversity in a landscape is derived from the spatial turnover in species composition, or betadiversity. Therefore, the effect of habitat loss and fragmentation on species diversity may not be reflected by the change in alpha diversity but by that of betadiversity. For example, Dumbrell *et al.* (2008) showed that moderate forest harvesting did not impact the diversity of a tropical forest butterfly assemblage at a small spatial scale but decreased the species diversity at larger spatial scales, due to a reduction in beta-diversity. Overall, the change in beta-diversity is less well documented than alpha-diversity but reductions of beta-diversity are a primary concern for the conservation of biodiversity in disturbed landscapes.

Beta diversity quantifies how the similarity in species composition between two locations decreases with the spatial distance between them (Nekola and White 1999). The distance-decay in species similarity is a fundamental property of beta-diversity and is important for understanding the factors that influence the spatial distribution of species across scale (Condit *et al.* 2002; Green *et al.* 2004). The distance-decay relationship has been documented across a wide variety of ecological communities (Soininen *et al.* 2007) and the factors being claimed to be primarily responsible for the distance-decay pattern can include spatial distance, dispersal limitation, and the heterogeneity of environmental conditions (Qian *et al.* 2005; Steinitz *et al.* 2006; Soininen *et al.* 2007). Generally, the slope of the distance-decay relationship becomes steeper in highly fragmented habitats due to the effect of dispersal limitation (Nekola and White 1999). In other words, species with low dispersal abilities are expected to exhibit a high dissimilarity in species composition with distance (Soininen *et al.* 2007; Qian 2009). Although the isolation of habitat remnants and their connectivity can substantially affect the distribution of species diversity (Watling and Donnelly 2006), the effect of habitat loss and fragmentation on the distance-decay relationship in disturbed landscapes has not been well understood.

Another widely used approach to quantifying the effect of landscape fragmentation on species diversity is the species-area relationship (Rosenzweig 1995). Species-area relationships are closely linked to beta-diversity as the spatial turnover in species composition can be represented by the *z*-value of the power law species-area relationship (Rosenzweig 1995) and the similarity of species composition between two points is also related to the *z*-value (Tjørve *et al.* 2008). Several ecological studies have demonstrated that the response of species assemblages to anthropogenic disturbances can be quantified through changes in the *z*-value of the power law species-area model (Lawrey 1991; Passy and Blanchet 2007; Tittensor *et al.* 2007; Dumbrell *et al.* 2008). Explicitly documenting patterns of species diversity through space provides a more informed interpretation of the overall structure and distribution of species diversity in a region (He *et al.* 2002) and it allows for making more valid comparisons between study regions.

From the global perspective, it has been suggested that species assemblages are becoming more compositionally homogeneous owing to the loss of specialist species and the subsequent replacement by invasive and more generalist species following widespread anthropogenic disturbances (McKinney and Lockwood

1999). Recently, a number of studies have shown that the impacts of habitat loss and fragmentation at regional scales frequently result in the biological homogenization of various species assemblages (Swihart *et al.* 2003; Ekroos *et al.* 2010; Lôbo *et al.* 2011).

Species with different life-history traits can respond differently to landscape disturbance (Davies *et al.* 2000; Henle *et al.* 2004; Kolb and Diekmann 2005; Ewers and Didham 2006). In particular, species with narrow niche breadth and relatively poor dispersal ability are frequently documented to be more sensitive to the impacts of habitat loss and fragmentation than species with a wide niche breadth and greater dispersal capacity (Swihart *et al.* 2003; Öckinger *et al.* 2010). Within fragmented landscapes, small habitat patches are more often overrepresented by generalist species while specialist species tend to be underrepresented in such habitats (Edenius and Sjoberg 1997; Summerville 2004). Therefore, species exhibiting poor dispersal abilities or highly specialized habitat requirements are at greater risk of extinction in response to pervasive habitat loss and fragmentation.

Industrial forest harvesting is prevalent throughout the boreal forest biome and has led to considerable loss and fragmentation of mature boreal forests. Past evidence has demonstrated that forest harvesting practices often lead to a reduction in the diversity of boreal forest species assemblages (Hanski and Hammond 1995; Esseen *et al.* 1997) and forest harvesting represents a major threat to boreal forest biodiversity. In addition, studies have demonstrated that forest harvesting shifts the composition of species assemblages towards species

that are adapted to open habitats while old growth species are typically lost (Niemela *et al.* 1993; Koivula *et al.* 2002; Roberts and Zhu 2002). There are concerns that the continued loss and fragmentation of mature boreal forest stands will decrease the beta-diversity of diverse species assemblages, such as arthropods (Spence *et al.* 2008), especially as the boreal forest landscape is increasingly becoming dominated by young age class forest stands (Cyr *et al.* 2009).

Implementing ecologically sound silvicultural techniques is a vital component of maintaining boreal forest biodiversity (Niemelä 1997; Spence 2001). A variety of silvicultural techniques have been developed to reduce the impacts of harvesting on ecological assemblages and to sustain non-timber values such as biodiversity (Lindenmayer *et al.* 2006). One strategy that has proven to be effective at maintaining biodiversity within harvested forest areas is the use of residual green tree retention (Tittler *et al.* 2001; Vanha-Majamaa and Jalonen 2001; Rosenvald and Lõhmus 2008), where living trees are left uncut within the harvested landscape. However, the majority of past studies examining the impacts of green tree retention harvesting on boreal forest species assemblages have been conducted at relatively small areas rarely exceeding 10 ha (Pawson *et al.* 2006). This is particularly concerning because harvested areas frequently reach as large as 400 ha in size in the boreal forest of Alberta.

Aggregated residual green tree retention, where variously sized patches of living trees are left unharvested, is a technique increasingly being applied with forest harvesting in Alberta (Figure 1-1). At a regional scale it has been shown

that retaining relatively large forest patches (i.e. > 10 ha) within disturbed boreal forest landscapes promotes regional avian species diversity (Edenius and Sjoberg 1997). Similarly, in other forest ecosystems across the globe it has been shown that patches of forest remnants are quite valuable for maintaining regional species diversity and conserving overall biodiversity (Benedick *et al.* 2006; Arroyo-Rodrìguez *et al.* 2009). Within the boreal forest the use of aggregated green tree retention in harvested areas may be especially valuable for maintaining arthropod diversity since these species are highly dependent on small-scale habitat heterogeneity (Spence *et al.* 2008).

Forest moth assemblages are regarded as strong indicators of forest disturbance (Kitching *et al.* 2000). In fragmented forest environments both the size of forest patches and the plant communities within them have been shown to play key roles in determining the local composition and diversity of moth species assemblages (Usher and Keiller 1998; Summerville and Crist 2003; Summerville *et al.* 2004; Summerville *et al.* 2005). Moth assemblages from restored forests in northeastern North America have been shown to exhibit a convergence in terms of the diversity and dominance of moth species, which threatens to reduce the beta-diversity of moths across this forest landscape (Summerville and Crist 2008). Previous studies conducted in the boreal forest have consistently shown that the local diversity of nocturnal moths declines in response to high levels of forest loss (Thomas 2002; Morneau 2002; Schmidt and Roland 2006) and the effects are especially detrimental to boreal forest moth species with larvae that feed on woody plants (Schmidt and Roland 2006). Therefore, a widespread loss of woody

plant feeding moths is expected within harvested boreal forests and that may in turn reduce the overall beta-diversity of moth assemblage through a process of biotic homogenization. In addition, many species of nocturnal boreal forest moths are known to exhibit strong preferences to occupy forested habitats and avoid clear-cut or open habitats (Mönkkönen and Mutanen 2003; Várkonyi *et al.* 2003), indicating that large clear-cut areas may limit the dispersal of individual moths among fragmented forest patches and cause increased intraspecific species aggregation.

Aggregated green tree retention harvesting is expected to negatively impact the species diversity of nocturnal boreal forest moth assemblages. Documenting the diversity patterns of moth species in terms of species-area relationships and beta-diversity was an important first step in this study. This would lay a foundation for understanding how harvesting and landscape fragmentation affected spatial distribution of moth species diversity at large spatial scales and provided quantitative tools for comparing the difference in diversity between disturbed forests and control areas. Ultimately, the goals of this study were: (1) to document and explain the impacts of aggregated green tree retention harvesting on the spatial distribution and maintenance of moth species diversity and (2) to determine whether diet breadth or dispersal ability influenced the response of moth species to the effects of aggregated green tree retention harvesting.

The rest of the thesis is organized as follows. The second chapter investigates whether forest harvesting alters the spatial distribution of nocturnal boreal forest moth species diversity and reduces their overall beta-diversity. The third chapter

seeks to determine whether aggregated green tree retention harvesting reduces the diversity and distribution of small bodied and diet specialist moth species in comparison to large bodied and generalist species. The thesis is concluded by a discussion of the spatial patterns of nocturnal moth species diversity and the implications of aggregated green tree retention on the maintenance of nocturnal moth species diversity in boreal forests.

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<u>Figure 1-1</u>: Example of aggregated green tree retention within a harvested boreal forest.

<u>Chapter 2</u>: Impacts of aggregated green tree retention on the spatial distribution and beta-diversity of nocturnal boreal forest moths

2.1 INTRODUCTION

Spatial heterogeneity of species diversity in landscapes is commonly measured by two complementary components: alpha-diversity representing the diversity at a single location and beta-diversity describing the differentiation or spatial turnover in species composition across landscapes (Whittaker 1960; Lande 1996; Jost 2007). Alpha-diversity as measured by species-area relationship has been widely used to quantify the impact of landscape fragmentation and habitat loss on diversity. However, the concept of beta-diversity has recently attracted much attention, in part due to its ability to connect local with regional diversity (Lande 1996; Jost 2007; Soininen *et al.* 2007a; Tuomisto 2010). Beta diversity can be measured in many different ways (Koleff *et al.* 2003; Jurasinski *et al.* 2009; Legendre *et al.* 2005; Toumisto 2010; Anderson *et al.* 2011), but the decay relationship in species composition over distance is a major form that has played an important role in developing an understanding of the spatial patterns of diversity (Nekola and White 1999, Condit *et al.* 2002; Soininen *et al.* 2007b).

Alpha and beta diversity are the two most important community metrics for assessing the impacts of natural and anthropogenic disturbances on diversity as disturbances are deemed to leave footprints in the spatial distribution of species (Passy and Blanchet 2007; Tittensor *et al.* 2007; Dumbrell *et al.* 2008; Hamer and

Hill 2000; Hamer *et al.* 2003; Hill and Hamer 2004; Benedick *et al.* 2006). In this study, I used them to assess the impacts of forest management on moth diversity in a boreal forest in Alberta, Canada.

The natural patterns and processes of boreal forests worldwide have been considerably altered by forest management practices (Hansson 1992) and in boreal forests of northern Europe it has been recognized that intensive forest harvesting represents a major threat to the integrity of boreal forest biodiversity (Hanksi and Hammond 1995). To protect boreal forests and sustain the diversity therein, much effort has been directed to shifting the timber-only forest management to sustainable forest management targeting for various non-timber values including the conservation of species diversity (Spence 2001). For example, the use of aggregated green tree retention by which patches of living trees are left within harvested forests is one of such shift. In this case, those retention patches are putatively considered to act as "lifeboats" and provide important habitats to forest associated species in the midst of the harvested forest matrix, thus allowing individuals to move more freely through the fragmented landscape (Franklin et al. 1997; Vanha-Majamaa and Jalonen 2001). However, previous studies on the effect of forest harvesting on diversity of boreal forests have been mostly conducted at relatively small spatial scales (Pawson et al. 2006) and thus are of limited use for understanding the efficacy of retention harvesting on maintaining species diversity at the scale of landscape.

Boreal forest insects are known to be vulnerable to the disturbance of forest harvesting (Niemelä 1997; Hanski 2008) and they have also been regarded

as valuable ecological indicators due to their functional roles (e.g., nutrient cycling, trophic interactions and pollination) and high levels of diversity within boreal forest ecosystems (Langor and Spence 2006). In particular, forest moths have been suggested to be an especially useful model taxon for evaluating the impacts of anthropogenic disturbances on forest biodiversity (Kitching et al. 2000; Pohl et. al. 2004). Previous studies of nocturnal boreal forest moths have mostly addressed the response of moth assemblages to gradients of forest loss and have shown that moth diversity exhibits a non-linear response to forest loss and diversity significantly declines at a threshold where the loss of forest cover approaches 60-80% within a given region (Thomas 2002; Schmidt and Roland 2006). Little is known regarding the effects of large-scale forest disturbances on moth diversity in the boreal forest, although there is evidence from temperate forest moth assemblages that large-scale harvesting activities can reduce overall heterogeneity in moth species diversity throughout disturbed forest landscapes (Summerville and Crist 2008). In this study I documented and compared the spatial structure and distribution of nocturnal moth diversity between a large intact and a harvested forest containing aggregated green tree retention. The objectives of this study were: (1) to determine the impact of forest harvesting with aggregated green tree retention on the beta-diversity and overall spatial distribution of nocturnal moth species diversity and (2) to determine the influence of aggregated green tree retention on maintaining nocturnal moth species diversity within a harvested boreal forest.

2.2 METHODS

2.2.1 STUDY SITE

Two boreal forest sites were located near the EMEND (Ecosystem Management by Emulating Natural Disturbance) research facility in northwestern Alberta, Canada (56°46' N, -118°22' W). The first site was a 400 ha largely intact boreal forest dominated by a mixture of broadleaf and coniferous tree species. In comparison, the second site (26 km away from the first site) of similar size was harvested by the technique of aggregated green-tree retention in 2000. By this technique, the harvested landscape was left with retention patches of various sizes that were randomly distributed on the harvested landscape (i.e., a clear-cut matrix) (Figure 2-1). Following the forest harvesting the disturbed matrix was planted with seedlings of two coniferous tree species, Lodgepole pine (*Pinus contorta* Douglas ex Loudon) and White spruce (*Picea glauca* (Moench) Voss).

The intact forest of the first site and the pre-harvested forest of the second site were both mature boreal mixedwood forests, sharing similar canopy tree species composition. Previous studies in this region have demonstrated that the diversity and composition of understory plant species are rather similar across different types of stands (e.g., mixedwood versus conifer dominated stands) (Macdonald and Fenniak 2007) and the assemblages of ground dwelling arthropods are also similar (Work *et al.* 2004). Therefore, the two mixedwood boreal forest sites studied here were expected to be similar in terms of their species assemblages despite their spatial separation.

2.2.2 SAMPLING METHODS

Moths were sampled using ultra-violet (UV) light traps with 12-V, 12-W bulbs that were powered by rechargeable 20 amp-hour batteries. A total of 22 light traps used in each study site and they were suspended approximately 1.5 m above the ground using homemade tripods. To avoid the possibility that any pair of light traps would have an overlapping sample area, I established a predefined minimum distance of 100 m between light trap locations. This distance was considered to be a conservative because moths generally responded to a UVemitting light source within a distance of approximately 3 m (Baker and Sadovy 1978). Under this constraint, for the intact forest site, the light traps were randomly positioned throughout the study area and the actual distances between any given pair of light traps ranged from 124 to 2,564 m. In contrast, for the harvested site, the 22 light traps were located as follows: 3 light traps were placed in the intact forest immediately adjacent to the disturbed matrix, 2 light traps placed in the middle of the disturbed matrix, and the remaining 17 light traps were positioned inside pre-selected patches of aggregated green tree retention varying in size from 0.13 to 5.1 ha. The distance between any given pair of light traps within the harvested study site ranged from 104 to 3,073 m.

Due to the large areas and intensity of our sampling, light trapping for the intact study site was conducted between May and August of 2007, and for the fragmented study site it was conducted between May and August 2008. In each year there were a total of 6 collection nights that were spaced out approximately

every 12 days. All individual macro-moths collected were identified to species following the nomenclature of Pohl *et al.* (2010) (Appendix A). Voucher specimens of all moth species identified are deposited at the E. H. Strickland Entomological Museum of the Department of Biological Sciences at the University of Alberta.

I also collected data on habitat conditions characterizing the local vegetation structure at each light trap location. The vegetation variables were separated into two growth forms: woody plants (i.e. shrubs) and non-woody plants (i.e. forbs). Shrub species composition was sampled using 4 m radius circular plots, which were centered under each light trap. Forbs were sampled using four 1 m² plots located 2 m away from the light trap in each of the four cardinal directions. All species of forbs within each plot were identified and their relative percent cover was recorded. The nomenclature of all plant species follows the Integrated Taxonomic Information System, Accessed April 21, 2012) (Appendix B).

2.2.3 DATA ANALYSIS

The power law species-area model was used to describe the relationship between moth species and number of sampling traps, taking the form: $S = cA^z$, where *S* is species richness, *A* is area sampled and *c* and *z* are parameters. Slope *z* is often considered as a measure of the overall beta-diversity in a landscape (Rosenzweig 1995; Tjørve *et al.* 2008). The empirical species-area data were constructed by averaging the species richness observed from traps randomly

drawn (with 100 replications) from a sample size of 1 to 22 traps for each study site. The power law model was fitted to the data by non-linear least squares regression using the nls function from the stats package version 2.9.2 in R (R Development Core Team 2009).

Distance-decay plots, where the pair-wise similarity in species composition is plotted against distance, were created to quantify the spatial pattern of moth beta-diversity. Pair-wise similarity in moth species composition was calculated using Jaccard's similarity index based on presence/absence data. The Jaccard's similarity index is calculated by dividing the number of species that are shared between two sites by the total number of species that were recorded from both sites (see Koleff et al. 2003). Simple linear regression was performed to determine the slope of the distance-decay in moth species similarity. A significant decay in compositional similarity with geographic distance indicates that species are not randomly distributed in space but rather show some level of spatial aggregation at the given scale of the study (Morlon *et al.* 2008). In order to confirm the degree of spatial aggregation of individual moth species populations I used Moran's I to test for the presence of significant spatial autocorrelation in the abundances of moth species that occupied 15 or more traps in their respective study sites. The calculations of Moran's I coefficients and their statistical significance were determined by using the function moran.test from the package spdep version 0.4-36 (Bivand 2009) in R.

The influence of variations in biotic habitat conditions between trap locations on patterns of moth beta-diversity was examined using Mantel tests.

Shrub and forb species data matrices were converted into distance matrices using Jaccard's dissimilarity distance (i.e. 1-Jaccards similarity index) based on presence/absence data. Mantel tests produced correlation coefficients for the correlations between the shrub and forb dissimilarity matrices and the dissimilarity matrices for the moth species assemblages. All Mantel tests were then performed in R using the function mantel, from the vegan package (Oksanen *et al.* 2009).

To determine if the richness of shrub and forb species at each light trap location influenced the local moth species richness, I calculated Pearson's correlation coefficients between the moth species richness at each light trap location and the corresponding species richness of forbs and shrubs. I also used the correlation coefficients to test if there was a significant relationship between the abundance and species richness of moths at each study site. Additionally, within the harvested site I specifically investigated the influence of retention patch size on the local moth species richness by testing for a significant relationship of local moth abundance or species richness with patch size.

2.3 RESULTS

In total, 9,728 macro-moths representing 209 species were collected from the two sites and were included in the data analyses. Of them there were 106 (51%) species shared between the intact and harvested sites, 61 (29%) species unique to the intact site and 42 (20%) species unique to the harvested site. Therefore, nearly twice as many individual moths were sampled in the intact site

compared to the harvested site and subsequently the total moth species richness was considerably larger within the intact forest site (Table 2-1). In the harvested site there were significant and positive correlations between the size of retention patches and both the abundance and species richness of moths (Table 2-2). Moth species richness was also significantly correlated with the richness of both the forb and shrub species in the intact forest, while moth species richness was only significantly correlated with the forb species richness in the harvested site (Table 2-2).

A comparison between the two species-area models revealed that the species-area curve derived from the intact forest was consistently above that of the harvested forest across the sample sizes (Figure 2-2). More specifically, the intercept, *c*, of the species-area model was significantly higher for the intact forest (c = 74.46, SE = 1.46) than the harvested forest (c = 54.11, SE = 1.69), indicating that the alpha diversity was higher within the intact forest. In addition, the slope *z* was significantly smaller for the intact forest (z = 0.23, SE = 0.008) than that of the harvested site (z = 0.33, SE = 0.010), suggesting more homogeneous distribution of moth species in the intact forest than the harvested forest.

In concordance with the above result, I found Jaccard's similarity index was higher among trap locations within the intact forest (mean similarity = 0.52) than among traps specifically located in retention patches within the harvested forest (mean similarity = 0.34). A significant correlation ($R^2 = 0.14$, *p*-value = <0.000) between the pair-wise similarity in moth species composition and spatial distance was observed for the moth assemblage from the intact forest although the slope of the distance-decay was rather shallow (Figure 2-3). Oppositely, moth species similarity among retention patch habitats within the harvested forest did not exhibit significant turnover over space (Figure 2-3).

The Mantel tests also showed that moth species beta-diversity in the harvested site was significantly related to the beta-diversity of shrub species composition but no similar relationship was observed in the intact site (Table 2-3). At both sites no significant relationship between the beta-diversity of moths and the beta-diversity of forbs was detected (Table 2-3).

There was also no significant distance-decay detected in the harvested site when all trap locations were included (Figure 2-4). It is interesting to observe that the pair-wise Jaccard's similarity was strongly influenced by the intensity of harvesting disturbance (Figure 2-4). Higher similarity values were observed among sites of control and retention patches, while lower similarity values were observed between trap locations within the disturbed matrix and trap locations within retention patches. This finding provides clear evidence that control sites and retention patches share fewer species with the disturbed forest matrix.

In addition to the above community level analysis, I also investigated the differences in the spatial distribution of individual species between the two sites. The results showed that many more species (47) in the intact forest are widely distributed (occupying more than 15 traps) than in the harvested site (18 species). Out of the 47 species that occupied 15 or more traps within the intact forest site 11 species showed significant spatial autocorrelation (Table 2-4). In comparison, only 1 out of 11 species occupying 15 or more traps within the harvested site

exhibited significant spatial autocorrelation (Table 2-5). Although the proportion of moth species exhibiting significant spatial autocorrelation was not significantly different between the two forest sites (Fisher exact test with *p*-value =0.27), intraspecific spatial aggregation was more common for moth species inhabiting the intact forest site. For those species the spatial autocorrelation can span up to 100-650 m.

2.4 DISCUSSION

Our study demonstrated that aggregated green tree retention harvesting had two main consequences on the spatial distribution of nocturnal moth species diversity. First, it significantly reduced the number of species within a given area compared to the intact forest (Figure 2-2). Second, it resulted in an increase in the overall beta-diversity (low similarity) of moth assemblages and reduced the slope of the distance-decay of the beta-diversity (Figure 2-3b). Interestingly, Hovestadt and Poethke (2005) demonstrated that it is common to observe high *z*-values that are associated with weak patterns of distance-decay in situations where local species richness is limited by the ability of species to establish abundant local populations. Therefore, the spatial patterns of moth beta-diversity that I documented within the harvested boreal forest site suggested that moth species were less able to establish and maintain abundant local populations compared to the intact forest site.

The strong influence of patch area on the local abundance and richness of moth species within the harvested boreal forest site demonstrated that the

establishment of abundant moth populations was limited by the availability of forested habitat within the harvested matrix. Indeed, previous studies have also consistently shown that harvested forest areas are relatively inhospitable to nocturnal forest moths that support low moth abundance and diversity (Summerville and Crist 2002; Thomas 2002). The majority of nocturnal forest moths require relatively large patches of forest for the establishment and maintenance of abundant local populations, which in turn increases alphadiversity. The spatial distribution of large retention patches therefore plays an important role in determining the relationship between pair-wise moth species similarity and spatial distance because relatively large patches with a high richness of moths have an elevated chance of sharing species.

The high beta-diversity within the harvested site may reflect the fact that the moth species richness was consistently lower in the harvested site than the intact site and harvesting activities fragmented the otherwise continuously distributed moth assemblages into discrete patches. Although nocturnal moth species occurred at low abundance within the disturbed forest matrix and in relatively small retention patches, the high spatial turnover in species composition with area showed that unique and numerically rare moth species were still widely distributed throughout the harvested site (Figure 2-2). This suggests that the majority of nocturnal moth species are capable of dispersing to retention patches within a harvested forest matrix in the site of this study.

It has been previously shown that moth species with larvae feeding specifically on woody plants are often disproportionately impacted by forest loss

(Summerville and Crist 2003; Summerville and Crist 2004; Schmidt and Roland 2006). Consequently, the overall reduction in moth species richness within the harvested site may be primarily associated with the loss of moth species that feed on woody plants. It is likely that the significant relationship between moth species beta-diversity and shrub species beta-diversity documented in the harvested forest stand (Table 2-3) occurred because the loss of forest habitat altered the composition of shrub species and reduced the abundance and diversity of certain species, which subsequently limited the amount of available resources for moth species that feed on shrubs and thereby reduced the abundance and diversity of these moth species. Therefore, the richness of moth species with larvae that feed on shrubs is possibly maintained within patches of aggregated green tree retention in part due to the presence of a specific composition of shrub species. Patches of aggregated green tree retention could therefore help ameliorate the impoverishment of moth species by providing suitable larval food plants for shrub feeding moths.

Overall, this study showed that spatial patterns of species diversity were useful for documenting and understanding the impacts of aggregated green tree retention harvesting on nocturnal moth species diversity in the boreal forest. Low alpha-diversity, high beta-diversity (high dissimilarity) and flat distance-decay of moth species similarity were signs of an impoverished moth assemblage in harvested forests. Aggregated green tree retention played an important role in the maintenance of moth species diversity within the harvested forest site (Figure 2-4) but the severity of forest loss dramatically reduced the overall abundance and
richness of nocturnal boreal forest moths. Identifying the composition of moth species that are lost due to the impacts of pervasive forest harvesting is an important next step to ensure the long-term conservation of nocturnal moths throughout the boreal forest landscape.

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<u>Table 2-1</u>: Summary of total species richness and abundance in the intact and harvested forest sites.

	Intact forest	Harvested forest
Total moth species	167	147
Total moth abundance	6,084	3,644

<u>Table 2-2</u>: Pearson's correlations between moth species richness, moth abundance, plant species richness and retention patch size in the intact and harvested forest sites.

	Intact forest		Harvested forest	
	r	Р	r	Р
Moth richness – Moth abundance	0.5597	0.0068	0.8731	<0.0001
Moth richness – Forbs species richness	0.6086	0.0021	0.5183	0.0135
Moth richness – Shrubs species richness	0.5308	0.0092	0.2689	0.2262
Moth abundance – Retention patch size	Not applicable	Not applicable	0.7679	0.0003
Moth richness – Retention patch size	Not applicable	Not applicable	0.5129	0.0353

<u>Table 2-3</u>: Mantel test calculated using dissimilarity matrices (i.e. 1- Jaccard's index) for both the intact and harvested forest sites. A = Pair-wise dissimilarity in moth species composition, B = Pair-wise dissimilarity in forbs species, and C = Pair-wise dissimilarity in shrub species.

	Intact	Intact forest		Harvested site	
	r _M	Р	r _M	Р	
r _M (AB)	0.0408	0.3250	0.1250	0.1740	
r _M (AC)	0.0967	0.1780	0.3972	0.0080	

Table 2-4: Moran's I autocorrelation coefficient for moth species occupying 15 or

Genus species	Moran's I	Variance	D
	Statistic	v allance	1
Acronicta grisea	-0.0287	0.0249	0.4576
Anaplectoides prasina	-0.184	0.0217	0.8267
Anaplectoides pressus	0.3269	0.0215	0.0055
Apamea cogitata	-0.0995	0.0247	0.6346
Aplectoides condita	0.2419	0.0226	0.028
Cabera erythemaria	0.102	0.0233	0.1672
Cabera variolaria	-0.1783	0.0264	0.793
Callizzia amorata	-0.0406	0.024	0.4874
Campaea perlata	0.2915	0.0256	0.0177
Caripeta divisata	0.4704	0.0241	0.0004
Clostera albosigma	0.2505	0.0257	0.0323
Clostera brucei	0.2471	0.0258	0.0342
Cyclophora pendulinaria	-0.135	0.0259	0.7109
Dasychira plagiata	-0.3645	0.0246	0.9791
Dysstroma citrata	0.2098	0.024	0.0498
Ecliptopera silaceata	-0.0351	0.0258	0.4744
Eurois astricta	-0.0689	0.0011	0.7617
Eurois occulta	-0.1285	0.026	0.6967
Eustroma semiatrata	-0.0304	0.0255	0.4624
Graphiphora augur	0.0903	0.0244	0.1922
Hydriomena furcata	0.1779	0.022	0.0659
Hydriomena ruberata	0.0488	0.0266	0.2819
Idia aemula	-0.0949	0.0257	0.6212
Lithacodia albidula	0.0158	0.0257	0.3513
Macaria signaria	-0.1885	0.0238	0.823
Metanema determinata	0.1349	0.0251	0.1275
Metanema inatomaria	0.0763	0.0233	0.2126
Panthea acronyctoides	-0.1695	0.0143	0.8506
Perizoma basaliata	0.3622	0.0268	0.0064
Pheosia rimosa	-0.027	0.0261	0.4546
Phlogophora periculosa	0.0964	0.026	0.1896
Phyllodesma americana	-0.0479	0.0263	0.5061
Plagodis pulveraria	-0.3255	0.026	0.9588
Polia nimbosa	0.3808	0.0225	0.0022
Protoboarmia porcelaria	0.1106	0.0229	0.1513
Rivula propinqualis	0.1012	0.0252	0.1776
Scopula frigidaria	0.1859	0.0246	0.0701
Smerinthus cerisyi	0.2704	0.0244	0.0216
Spargania luctuata	-0.027	0.0218	0.4503
Speranza loricaria	0.2844	0.0256	0.0197

more traps in the intact forest site.

Syngrapha alias	0.0734	0.0191	0.1946
Xanthorhoe abrasaria	-0.3479	0.0246	0.9732
Xanthorhoe decoloraia	0.1364	0.0258	0.1287
Xestia mixta	-0.0906	0.0011	0.9134
Xestia perquiritata	-0.0456	0.0189	0.5003
Xestia smithii	-0.04	0.0254	0.4862
Zenophleps alpinata	-0.3093	0.0229	0.9595

Genus species	Moran's I	Variance	Р	
	Statistic			
Anaplectoides pressus	-0.097	0.0142	0.6535	
Apamea cogitata	0.0584	0.0157	0.1932	
Autographa mappa	-0.1425	0.0135	0.787	
Campaea perlata	0.0979	0.0099	0.0681	
Dysstroma citrata	-0.0618	0.0125	0.5421	
Eurois astricta	0.0978	0.0133	0.0999	
Eurois occulta	-0.0259	0.0094	0.4017	
Eustroma semiatrata	-0.0097	0.0146	0.3691	
Lacinipolia lorea	-0.095	0.0159	0.6395	
Polychrysia esmerelda	0.0055	0.0152	0.3263	
Speranza loricaria	0.1553	0.014	0.0415	
Syngrapha viridisigma	0.1337	0.0133	0.766	
Xanthorhoe abrasaria	-0.1898	0.0161	0.8647	
Xanthorhoe decoloraria	-0.2406	0.0156	0.9363	
Xanthorhoe ramaria	0.0051	0.0142	0.3221	
Xestia homogena	-0.0785	0.0155	0.5906	
Xestia mixta	-0.0091	0.0159	0.3728	
Xestia smithii	-0.0799	0.0159	0.5937	

<u>Table 2-5</u>: Moran's *I* autocorrelation coefficient for moth species occupying 15 or more traps in the harvested forest site.



<u>Figure 2-1</u>: Aggregated green tree retention patches (irregular gray shapes) within harvested matrix (light gray and grayish white areas) of harvested boreal forest study site. The white areas are unnamed waterbodies. Dashed lines represent seismic and/or cutlines.



Figure 2-2: Species-area relationships for moth assemblages in the intact (black) and harvested (gray) boreal forest sites. The curves are the fits of the power-law species-area model.



Figure 2-3: (a) Distance decay of moth species composition in the intact forest fitted with a simple linear regression. (b) Distance decay of moth species composition from retention patches within harvested forest site fitted with a simple linear regression.



<u>Figure 2-4</u>: The relationship between pair-wise moth species similarity and spatial distance in the harvested forest stand for all trap combinations. Symbols indicate comparisons between traps from three distinct forest conditions: controls, patches and clearcuts.

<u>Chapter 3:</u> Life-history traits affect the response of nocturnal boreal forest moth species to forest harvesting

3.1 INTRODUCTION

The impacts of habitat loss and fragmentation on the composition and diversity of ecological assemblages have been studied from a variety of perspectives. Ecologists have long been interested in understanding the roles of habitat patch size and isolation in determining the diversity and composition of species within habitat (Debinski and Holt 2000; Fahrig 2003; Ewers and Didham 2006). An important observation is that different species respond to habitat disturbance differently, with some species being more susceptible to habitat degradation than others (Debinksi and Holt 2000; Ewers and Didham 2006). This is in large part due to variation in life-history traits among species (Kolb and Diekmann 2005; Ewers and Didham 2006) and the fact that the relative risk of extinction between species is strongly associated with their life-history traits (Koh et al. 2004; Cowlishaw et al. 2009). In particular, life-history traits that are related to the diet breadth and dispersal capacity of species have been shown to be valuable predictors of species' responses to habitat loss and fragmentation (Swihart et al. 2003; Bommarco et al. 2010; Öckinger et al. 2010). Species that possess more general habitat or diet requirements often respond less strongly to the impacts of habitat loss in comparison with more specialist species because generalist species are more capable of utilizing the limited resources that occur within or outside any remaining habitat patches (Öckinger *et al.* 2010). A narrow

niche breadth has been shown to limit the occupancy of species in fragmented landscapes (Swihart *et al.* 2006) and there is also evidence that specialists are poorly represented within small habitat patches (Bommarco *et al.* 2010).

The isolation or fragmentation of local habitats has important consequences for the persistence of populations in a landscape because isolation often reduces chances that individuals will successfully immigrate between local populations. Immigration of individuals between local populations is important for population persistence because immigration can help to stabilize the dynamics of populations through the rescue effect (Brown and Kodric-Brown 1977) and thus enhance the richness of species assemblages. A relatively high dispersal rate allows species to colonize a larger number of potential habitats and it has been documented that increased dispersal or migration rates can increase the abundances of local populations (Nieminen and Hanski 1998; Löbel et al. 2006). Therefore, species with high dispersal abilities are less likely to exhibit population declines in fragmented environments (Davies et al. 2000; Driscoll and Weir 2005). In contrast, species that possess relatively poor dispersal abilities are generally at greater risk of becoming extinct in fragmented environments and are, therefore, more sensitive to habitat loss and fragmentation (Öckinger *et al.* 2010).

The species diversity of many boreal forests across the globe has been severely threatened by forest harvesting (Hanksi and Hammond 1995; Niemelä 1997; Hanski 2008). To minimize the adverse effect of forest harvesting on boreal biodiversity, various forest harvesting and silvicultural techniques have been developed and practiced. Of them, the technique of variable retention harvesting

is widely practiced: for large areas of forest to be harvested with various sized patches of residual green tree retention distributed throughout the harvested forest matrix. Part of the intended role of the residual green tree retention is to provide local habitats for forest dependent species directly within the harvested forest matrix so that the retention patches provide a lifeboat effect and to increase the connectivity of forest habitats throughout the landscape so that a greater number of species can persist within the landscape as the forest regenerates (Franklin et al. 1997). The size and isolation of forest patches are known to affect the distribution and diversity of boreal forest bird species; specialist bird species avoid small (< 5 ha) patches of forest (Edenius and Sjöberg 1997) and resident bird species have been documented to decline in isolated forest fragments (Schmiegelow et al. 1997). It remains unclear whether aggregated green tree retention within harvested areas provides long-term conservation value by maintaining the abundance and diversity of specialist and dispersal limited species.

Nocturnal boreal forest moths are known to be sensitive to the impacts of intensive forest loss (Thomas 2002; Schmidt and Roland 2006) and many species are known to exhibit a strong avoidance to open areas that have been cleared by forest harvesting (Mönkkönen and Mutanen 2003; Várkonyi *et al.* 2003). The size and quality of forest patches have been documented as important determinants of the diversity and composition of nocturnal forest moth assemblages (Summerville and Crist 2003, 2004) and it has been shown that moth species with larvae that feed on woody plants tend to be more impacted by forest loss than species with

larvae that feed on herbaceous plants and grasses (Summerville and Crist 2004; Schmidt and Roland 2006). Various life-history traits have been linked to the extinction risk of forest moths (Mattila *et al.* 2006) and traits such as diet breadth and body size have been shown to be useful for explaining the response of moth abundance and diversity to the impacts of habitat loss and fragmentation (Öckinger *et al.* 2010). However, it remains unknown as to whether intensive forest harvesting will change the relationship between life-history traits and the abundance and occupancy of moths in a harvested forest stand or aggregated green tree retention will allow for maintaining moth species diversity for species that possess contrasting life-history strategies.

In this study I investigated the effect of forest harvesting on the diversity of nocturnal moths by comparing the composition and occupancy patterns of the moth species between a 400 ha intact boreal forest and a similarly sized forest area that was harvested using the technique of aggregated green tree retention. Specifically, our study had three objectives. (1) To determine whether the biological traits of diet breadth and body size influence the diversity of moth species within the intact and harvested forests. (2) I then consider if there are differences in the relationships between the biological traits and the abundance and occupancy between the two forests. (3) Finally, I split the moth species assemblages into groups with contrasting biological traits and compare spatial patterns of diversity for each group between the two forests to determine whether the loss and fragmentation of boreal forest habitat influences species differently.

3.2 METHODS

3.2.1 STUDY SITE

Two boreal forest sites were located near the EMEND (Ecosystem Management by Emulating Natural Disturbance) research facility in northwestern Alberta, Canada (56°46'13" N - 118°22'28" W). The first site was a 400 ha largely intact boreal forest stand dominated by a mixture of broadleaved and coniferous tree species. In contrast, the second site of similar size was highly fragmented and was dominated mainly by coniferous tree species. This second forest site (26 km away from the first site) was harvested by the technique of aggregated green-tree retention in 2000. By this technique, the harvested landscape was left with retention patches of various sizes that were randomly distributed throughout the harvested forest matrix. Following the forest harvesting the disturbed matrix was planted with seedlings of two coniferous tree species, Lodgepole pine (Pinus contorta) and White spruce (*Picea glauca*). The intact forest of the first site and the pre-harvested forest of the second site were both mature boreal mixedwood forests, sharing similar canopy tree species composition. Previous studies in this region have demonstrated that the diversity and composition of understory plant species are rather similar across different types of stands (e.g., mixedwood versus conifer dominated stands) (Macdonald and Fenniak 2007) and the assemblages of ground dwelling arthropods are also similar (Work et al. 2004). Therefore, the mixedwood boreal forest sites studied here were expected to be homogeneous in terms of their species assemblages despite their spatial separation.

3.2.2 DATA COLLECTION

Moths were sampled using ultra-violet (UV) light traps with 12-V, 12-W bulbs that were powered by rechargeable 20 amp-hour batteries. There were a total of 22 light traps used in each study site and they were suspended approximately 1.5 m above the ground using homemade tripods. To avoid the possibility that any pair of light traps may have an overlapping sample area, I established a predefined minimum distance of 100 m between any two light traps. This distance was considered to be conservative since Baker and Sadovy (1978) have previously shown that moths generally responded to a UV-emitting light source within a distance of approximately 3 m.

For the intact forest site, the light traps were randomly positioned throughout the study area and the actual distances between any given pair of light traps ranged from 124 m to 2,564 m. In contrast, for the harvested site, the 22 light traps were located as follows: 3 light traps were placed in the intact forest directly adjacent to the harvested forest matrix, 2 light traps placed in the middle of the harvested forest matrix, and the remaining 17 light traps were positioned inside pre-selected patches of aggregated green tree retention varying in size from 0.13 ha to 5.1 ha. The distance between any given pair of light traps within the fragmented site ranged from 104 m to 3,073 m. Due to the large areas and intensity of our sampling, light trapping for the intact study site was conducted between May and August of 2007, and for the fragmented study site it was conducted between May and August 2008. In each year there were a total of 6

collection nights that were spaced out approximately every 12 days. All individual macro-moths collected were identified to species following the nomenclature of Pohl *et al.* (2010) (Appendix A). Voucher specimens of all moth species identified are deposited at the E. H. Strickland Entomological Museum of the Department of Biological Sciences at the University of Alberta.

3.2.3 LIFE HISTORY TRAITS

I gathered information on two different biological traits including the number of larval host plant families that have been recorded for each moth species and the mean forewing length. The number of larval host plant families served as a measure of the niche breadth for each species and I obtained this information from Robinson et al. (2002) and the HOSTS website (Robinson et al. 2010). In addition, for moth species where there was larval diet information available I classified each species as polyphagous (i.e. moth species that feed on multiple host plant families), oligophagous (i.e. moth species that only feed on one host plant family) or monophagous (i.e. moth species that only feed on only one particular host plant species). The mean forewing length was directly measured to the nearest millimeter from sub samples of individuals of each species that were collected and it was used as a proxy for the dispersal ability of each moth species, where I assumed that moths with larger forewing lengths would be relatively better dispersers than moths with smaller forewing lengths. Nieminen (1996) previously demonstrated that wingspan was positively and

significantly related to the frequency of moth dispersal among a network of small islands in the south-western archipelago of Finland.

3.2.4 DATA ANALYSIS

Each moth species was sorted based on their larval diet specificity as either monophagous, oligophagous or polyphagous species and arranged into a contingency table. A Fisher's exact test was performed to determine whether there was a significant difference between the proportions of moth species that were characterized as monophagous, oligophagous and polyphagous between the two forests.

Generalized linear models were used to test for a relationship between two trait variables (i.e. the number of larval host plant families that each moth species is known to feed on and the mean forewing length) and the total abundance of each moth species at each study site. The function glm from the stats package version 2.9.2 in R (R Development Core Team 2009) was used to conduct the analyses for all generalized linear models.

Occupancy was used to characterize the spatial distribution of individual moth species and it was measured as the fraction of light traps that individuals of a particular species were recorded from in relation to the total number of light traps at a given study site. To test for the influence of traits in predicting the occupancy of moth species a logistic model was used that related the response variable, occupancy, to both of the explanatory variables (i.e. the number of known larval host plant families and mean forewing lengths). Non-linear least

squares regression was used to parameterize the logistic model and this was conducted using the nls function from the stats package version 2.9.2 in R (R Development Core Team 2009).

In addition to the above regression analyses, moth diversity patterns between the intact and harvested forests were also compared. I first evaluated the species-area relationship for moth richness of different traits (e.g., specialist vs generalist) using the power law model ($S=cA^z$, where S is the number of species, A is area, and c and z are parameters) and the parameters c and z were estimated and compared for each site using non-linear least squares regression. I also modeled beta diversity to compare the difference in the spatial distribution of moth species of different traits in the two forests. Pair-wise similarity in moth species composition between two light traps was calculated using Jaccard's similarity index. The distance-decay in Jaccard's similarity was plotted against spatial distance. A simple regression was used to determine the strength of the distancedecay relationships for different trait groups of moth species.

Direct comparisons of the species-area relationships and distance-decay relationships were made between groups of moths with contrasting life-history traits. First, all moths were split into either large (mean forewing length > 15 mm) or small (mean forewing length <15 mm) species. Second, all moths were split according to their larval diet breadth where moths with larvae that are known to feed on three of more host plant families were considered to be generalist species and moths with larvae that are known to feed on less than 3 host plant families were considered to be specialist species.

3.3 RESULTS

156 moth species were observed in the intact forest stand. The majority of species were polyphagous (121 species) with nearly equal numbers of oligophagous (18) and monophagous species (17) (Table 3-1). In comparison, 119 moth species in the harvested forest stand were observed, of which there were 89 polyphagous species, 18 oligophagous and 12 monophagous. There was no significant difference in the proportions of polyphagous, oligophagous and monophagous moth species between the intact and harvested forests (Fisher's exact test, *p*-value = 0.696).

A generalized linear model showed that both the number of larval host plant families and mean forewing length were significantly related to the regional abundance of moths in the intact forest (Table 3-2). Therefore, nocturnal moths with a wider diet breadth and large body size were predicted to be more abundant than moth species with a narrow diet breadth and small body size in the intact boreal forest. In contrast, the number of larval host plant families was the only trait that significantly predicted regional moth abundance in the harvested forest (Table 3-2). This result suggests that intensive forest harvesting may have altered the composition or structure of the moth assemblage in harvested forests.

A non-linear least squares regression showed that neither the number of larval host plant families nor the mean forewing length significantly predicted the occupancy of boreal forest moths within the intact forest stand (Table 3-3). Therefore, at the scale of a 400 ha boreal forest there is no evidence to suggest

that diet breadth or body size limits the spatial occupancy of nocturnal moth species. In contrast, the number of host plant families was significantly and positively related to occupancy within the harvested forest (Table 3-3), indicating that moth species with larvae that feed on a wider range of potential host plants occurred more frequently throughout the harvested forest than moth species that possess a narrow diet breadth. Therefore, in a region where a limited amount of local forest habitat exists, in the form of aggregated green tree retention, specialist moth species are more restricted than generalist species in the habitat patches where they can potentially occupy.

In the intact forest the parameters of the power law species-area model were $c = 31.35\pm0.42$ and $z = 0.23\pm0.01$ for large moth species and $c = 35.79\pm0.95$ and $z = 0.24\pm0.01$ for small moth species suggesting that the turnover in moth species composition with area was quite similar between large and small moth species (Figure 3-1). Spatial distance was significantly and negatively related to the pair-wise similarity of both large ($R^2 = 0.02461$, *p*-value = 0.01) and small (R^2 = 0.03554, *p*-value = <0.00) moth species within the intact boreal forest indicating that there was a certain degree of intraspecific spatial aggregation for both large and small moth species groups (Figure 3-3). Overall, this evidence shows that there was little difference in the structure and spatial distribution of moth species diversity between large and small moth species in the intact boreal forest.

In contrast, the parameters of the power law species-area model were $c = 17.94\pm0.47$ and $z = 0.37\pm0.01$ for large moth species and $c = 19.99\pm0.61$ and $z = 0.34\pm0.01$ for small moth species within the harvested boreal forest (Figure 3-2).

Therefore, both large and small moth species exhibited lower *c* parameter values and higher *z* parameter values in the harvested boreal forest compared to that in the intact forest, showing that both groups were negatively affected by habitat loss and fragmentation. Spatial distance was not significantly correlated with pair-wise similarity in moth species composition for either large ($R^2 = -0.00435$, *p*-value = 0.95) or small ($R^2 = -0.00303$, *p*-value = 0.58) moth species within the harvested forest (Figure 3-3). The lack of spatial structure and relatively high turnover in moth species composition in harvested site in comparison with the intact site suggested that establishment of abundant local populations of both large and small moth species was limited in the harvested forest. However, given these results there was little evidence to suggest that body size played any role in determining the response of moth species to habitat loss and fragmentation.

The parameters of the power law species-area model were $c = 29.53\pm0.26$ and $z = 0.29\pm0.00$ for generalist moth species and $c = 37.69\pm0.97$ and $z = 0.21\pm0.01$ for specialist moth species in the intact boreal forest indicating that specialist species exhibited a lower alpha-diversity and a higher beta-diversity than generalist moth species (Figure 3-1). Spatial distance was not significantly related to the pair-wise similarity of moth species composition for generalist moth species ($R^2 = -0.00218$, *p*-value = 0.48). In contrast, spatial distance was highly significantly related to the pair-wise similarity in moth species composition for specialist moth species ($R^2 = 0.08452$, *p*-value = <0.00) within the intact boreal forest. This suggests that there is a certain degree of intraspecific spatial

aggregation for specialist moth species in the intact boreal forest while generalist moth species do not exhibit intraspecific spatial aggregations (Figure 3-3).

In comparison, for the harvested forest the parameters of the power law species-area model were c = 26.10+0.84 and $z = 0.26\pm0.01$ for generalist species and $c = 19.61 \pm 0.64$ and $z = 0.39 \pm 0.01$ for specialist moth species. Once again, this is similar to the results from the intact forest specialist moth species that exhibited a lower alpha-diversity and a higher beta-diversity than generalist moth species (Figure 3-2). However, the c value for specialist moth species was considerably lower within the harvested forest than in the intact forest and the z value was much higher, suggesting that specialist moth species were more negatively impacted by the effects of habitat loss and fragmentation within the harvested boreal forest. Spatial distance was not significantly related to the pair-wise similarity in moth species composition for either generalist ($R^2 = 0.00237$, p-value = 0.22) or specialist (R^2 = -0.00022, *p*-value = 0.33) moth species within the harvested boreal forest (Figure 3-3). The weak spatial structure and relatively high z values indicate that the establishment in local habitats was limited for both generalist and specialist moth species within the harvested boreal forest. However, the substantial shift in the species-area relationships of specialist moth species between the intact and harvested forests suggests that habitat loss and fragmentation have a more negative effect on the abundance and diversity of specialist moth species.

3.4 DISCUSSION

In this study I first examined the influence of diet breadth and body size on the abundance and occupancy patterns of nocturnal moth species within an intact and harvested boreal forest and then I tested if species with contrasting biological traits responded differently to the loss and fragmentation of forest habitat. Our results suggest that diet breadth plays a key role in determining abundances and diversity of nocturnal moth species. More importantly, our results demonstrate that diet breadth is an important biological trait influencing the responses of moth species to intensive forest harvesting. Specialist moth species were less abundant than generalist species in both forests and they were more negatively affected by the habitat loss and fragmentation caused by forest harvesting. Therefore, forest habitat loss and fragmentation would likely accelerate the loss of specialist species (Polus *et al.* 2007).

The significant and positive relationship between regional moth abundance and diet breadth (Table 2-2) suggests that available host plant resources play an important role in determining the structure and diversity of nocturnal boreal forest moth species assemblages. In addition to the fact that diet breadth was an important determinant of moth abundance in both forests, it was also an important predictor of occupancy within the harvested forest. It has been observed that there is a distinctive shift in plant species composition and a general reduction in the beta-diversity of understory plant communities in harvested forests (Macdonald and Fenniak 2007; Craig and Macdonald 2009), indicating that there are fewer available host plant species within intensively harvested forest

areas for the forest moth larvae. Diet specialist moth species were relatively less abundant and occupied fewer sites than diet generalist species within the harvested site likely because of the limited biomass of their host plant resources (Yamamoto et al. 2007). In addition, there was a distinctive difference in the shape of the species-area relationships between the diet specialist and diet generalist moth species within the intact and harvested forests. Diet specialist moth species exhibited lower intercepts and higher slopes within the harvested forest stand, which are characteristics of species-area relationships for assemblages with a large number of species that are numerically rare. Similar to Thomas (2002) I suggest that the majority of individuals belonging to diet specialist moth species that occurred within the harvested site were likely those individuals dispersing to different habitat locations from adjacent undisturbed areas. Regardless, our results provide support for previous findings that diet breadth is a critical factor influencing the response of moth species to habitat loss and fragmentation (Hilt and Fiedler 2006; Öckinger et al. 2010).

Body size had little influence on the abundance and occupancy patterns of boreal forest moths except for within the intact forest site where it showed a significantly positive relationship with regional moth abundance (Table 3-2). This finding was unexpected since relatively small-bodied species are generally expected to attain larger populations in comparison with large-bodied species due to higher rates of reproduction. I suspect that the positive relationship between moth body size and abundance within the intact forest stand is probably an artefact of the sampling method of automatic light trapping. It has previously been

documented that the method of automatic light trapping tends to underrepresent the abundances of small nocturnal moth species (Axmacher and Fiedler 2004; Brehm and Axmacher 2006) likely because these species tend to be weaker and more agile fliers that are less likely to be captured in the light trap bucket. Despite this probable artefact of sampling, the lack of a relationship between body size and regional moth abundance in the harvested forest suggests that intensive forest harvesting altered the nocturnal moth assemblage from the harvested forest stand. I previously established the strong influence of larval diet breadth on determining the abundance and occupancy patterns of boreal forest moths within the harvested forest, which likely confounded the relationship between body size and abundance within the harvested site.

Small moth species have previously been documented to have lower migration rates among islands than large moth species (Nieminen 1996). However, in this study our results showed that body size was not related to the occupancy of local habitats, including green tree retention patches, within the harvested forest. No evidence showed dispersal limitation of small moth species between local retention patches within the harvested site. In addition, our study showed that body size did not play an important role in determining the response of nocturnal boreal forest moth species to habitat loss and fragmentation caused by forest harvesting.

At the scale of a large boreal forest I determined that aggregated green tree retention mainly provides habitat for diet generalist moth species. Therefore, the habitat loss and fragmentation caused by intensive forest harvesting tended to

homogenize nocturnal moth assemblage. This result is similar to the situation documented by Ekroos *et al.* (2010) for moths in a grassland landscape affected by intensive agricultural practices. In the boreal forest, I predict that the pervasive habitat loss and fragmentation throughout landscapes may lead to reduction in the regional beta-diversity of nocturnal moth assemblages due to the loss of dietary specialist species. However, the surrounding intact forest can provide refugia for the more sensitive species (Hilt and Fiedler 2005) and therefore it will be important to maintain large areas of intact forest throughout the boreal forest landscape. To maintain moth diversity after forest harvesting I would recommend management practices use small cut blocks with large size patches of aggregated green tree retention. Finally, for the purposes of conserving the diversity of nocturnal boreal forest moths, the floristic composition of intact areas should be carefully considered in order to ensure that a wide number of host plant resources are available to species with restricted diet breadths.

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<u>Table 3-1</u>: Contingency table of moth species arranged according to their larval host plant specificity in the intact and harvested forest sites. Fisher's exact test revealed that the proportions of moths in each category were not significantly different between the two forests (*p*-value = 0.696).

	Intact forest	Harvested forest
Polyphagous	121	89
Oligophagous	18	18
Monophagous	17	12

<u>Table 3-2</u>: The generalized linear models relating the number of larval host plant families (NHF) and the mean forewing length (FWL) to the total recorded abundance of each species for the two study sites.

		Intact forest		Harvested forest			
	Estimate	Standard Error	<i>p</i> -value	Estimate	Standard Error	<i>p</i> -value	
NHF	0.0459	0.00263	<0.001	0.0633	0.00805	<0.001	
FWL	0.0579	0.00288	<0.001	0.0000779	0.00660	0.991	

<u>Table 3-3</u>: The non-linear least squares regression relating the number of larval host plant families (NHF) and the mean forewing length (FWL) for each moth species to occupancy (i.e. proportion of the total number of sites at which a given moth species was recorded) for each of the two study sites.

		Intact forest			Harvested forest		
	Estimate	Standard Error	<i>p</i> -value	Estimate	Standard Error	<i>p</i> -value	
NHF	-0.0156	0.0302	0.606	0.140	0.0350	<0.001	
FWL	0.0240	0.0318	0.452	-0.0251	0.0278	0.367	



<u>Figure 3-1:</u> Species-area relationships of moth species in the intact boreal forest: (a) large moth species, (b) small moth species, (c) generalist moth species, and (d) specialist moth species. The curves are the fits of the power-law species-area model.



Figure 3-2: Species-area relationships of moth species in the harvested boreal forest: (a) large moth species, (b) small moth species, (c) generalist moth species, and (d) specialist moth species. The curves are the fits of the power-law species-area model.



Figure 3-3: Distance-decay of beta diversity for moth species in the intact (open circles) and harvested (open triangles) boreal forest sites fitted with simple linear regression: (a) large moth species, (b) small moth species, (c) generalist moth species, and (d) specialist moth species.

<u>Chapter 4</u>: Conclusion

In this study, I documented and compared spatial patterns of nocturnal moth species diversity between moth assemblages from an intact and a harvested forest located near the EMEND research site to determine the impacts of habitat loss and fragmentation caused by forest harvesting with aggregated green tree retention. Spatial patterns of species diversity revealed that the intact boreal forest supported a relatively abundant and diverse assemblage of nocturnal moth species where high levels of alpha-diversity were maintained. In contrast, the alphadiversity of moths, measured in terms of species richness, was relatively low within the harvested forest and it was shown to be strongly influenced by the amount of forest habitat surrounding a given light trap location. For example, relatively large patches of aggregated green tree retention within the harvested forest supported a greater abundance and richness of moth species than smaller sized patches. The amount of forest area surrounding light trap locations also had a strong influence on the pattern of nocturnal moth species beta-diversity in the harvested forest site (Figure 2-4). Ultimately, these findings provide further confirmation that intensive loss of forested habitat is detrimental to the maintenance of nocturnal boreal forest moth diversity (Thomas 2002; Schmidt and Roland 2006) regardless of spatial scale.

The loss and fragmentation of forested habitats caused by harvesting were especially detrimental to moth species with larvae that exhibit a narrow diet breadth. Diet specialist moth species occupied fewer trap locations within the

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harvested forest in relation to diet generalist species. Additionally, the diet specialist moth species from the harvested forest site exhibited spatial patterns of species diversity that are characteristic of species assemblages that contain species that are limited by the ability to establish local populations (Hovestadt and Poethke 2005). Local host plant biomass has been shown to be an important factor limiting the distribution Lepidopteran species (Yamamoto et al. 2007) and it is likely that the low level of occupancy exhibited by diet specialist moths species was related to a reduction in the abundance or biomass of their specific host plant species. This study showed that moth species with a narrow diet breadth have low abundance and limited spatial distribution, which would make them more susceptible to local extirpation from areas subject to habitat loss and fragmentation. Therefore, successful long-term conservation of nocturnal moth biodiversity in the boreal forest will strongly depend on management strategies that specifically focus on maintaining diet specialist moth species at both local and regional scales.

Overall, the results of this study suggest that aggregated green tree retention patches provide some benefits for maintaining nocturnal boreal forest moth species diversity within a harvested forest matrix but their overall value for the long-term conservation of moth species should be interpreted with caution. Large patches of aggregated green tree retention supported relatively abundant and diverse moth assemblages; however, most of the species that persisted in these patches were dietary generalists. Similarly, in other studies of moth species from temperate and boreal forests it has been shown that moth species

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representing functional groups that fed mainly on forbs or grasses were retained in areas with low forest cover while moth species with larvae that fed on woody plants declined in richness and abundance (Summerville 2004; Schmidt and Roland 2006). In this study, relatively small patches typically supported very low numbers of individual moths and many of these individuals were from moth species that were recorded at proportionally low abundances throughout the harvested forest site. The low abundance of moths in cleared habitats and small retention patches suggests that most moth species have low abilities to sustain viable local moth populations in these habitats. Therefore, there is a need to protect large areas for promoting the long-term persistence of species populations that are sensitive to the impacts of habitat loss (Stratford and Stouffer 1999). Providing large areas of relatively intact boreal forest adjacent to forest harvests is important to ensure the availability of forested habitats for specialists to recolonize harvested areas upon regeneration. At the scale of large harvested forests I suggest that it would be valuable to maintain equally large areas of intact and mature forests adjacent to the harvested areas so as to maintain a pool of specialist species for recolonization. This will be a more effective approach than attempting to maximize the representation of diversity (Economo 2011) by distributing relatively small patches of aggregated green tree throughout the harvested forest matrix.

Continuing research aiming to document the identities and spatial distribution of species throughout boreal forest habitats is essential to provide a more comprehensive understanding of the processes responsible for the response

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of boreal forest species assemblages to forest loss and fragmentation. This study focused on the effect of green tree retention on diversity patterns of moth assemblages, not the performance of individual moth populations. I would suggest it be helpful to further study the role of aggregated green tree retention patches in facilitating the dispersal of individual moths between local fragmented populations. Ultimately, the successful long-term conservation of nocturnal moth species diversity in the boreal forest will require further scientific knowledge regarding the species and population level responses of moths to habitat loss and fragmentation across multiple spatial scales.

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Genus species	Abundance (Intact)	Abundance (Harvest)	Mean Forewing Length	Larval Host Plant Specificity	Number of Known Host Plant Families	Author
Abagrotis placida	1	2	15	Polyphagous	4	(Grote, 1876)
Abrostola urentis	0	2	15	Oligophagous	1	Guenée, 1852
Acronicta fragilis	10	0	16	Polyphagous	4	(Guenée, 1852)
Acronicta grisea	30	3	17	Polyphagous	8	Walker 1856
Acronicta impleta	1	0	23	Polyphagous	8	Walker, 1856
Acronicta impressa	1	1	16	Polyphagous	7	Walker, 1856
Acronicta vulpina	1	0	22	Unknown	Unknown	Guenée, 1883
Aethalura intertexta	7	0	13	Polyphagous	10	(Walker, 1860)
Agrotis ruta	0	13	22	Unknown	Unknown	Eversmann, 1851
Amphipoea americana	4	1	15	Polyphagous	2	(Speyer, 1875)
Anaplectoides prasina	30	16	23	Polyphagous	8	([Denis & Schiffermüller], 1775)
Anaplectoides pressus	188	79	17	Polyphagous	6	(Grote, 1874)
Anathix puta	15	1	13	Monophagous	1	(Grote & Robinson, 1868)
Androlpolia contacta	22	23	22	Polyphagous	4	(Walker, 1856)
Antepirrhoe semiatrata	21	158	15	Monophagous	1	(Hulst, 1881)
Anticlea multiferata	5	2	12	Polyphagous	2	(Walker, 1863)
Anticlea vasiliata	4	4	15	Polyphagous	2	Guenée, [1858]
Apamea cogitata	38	78	18	Polyphagous	2	(Smith, 1891)

APPENDIX A: List of moth species captured with their abundance at each study site and associated life-history traits.

Apamea commoda	0	26	19	Unknown	Unknown	(Walker, 1857)
Apamea vultuosa	0	1	18	Oligophagous	1	(Grote, 1875)
Aplectoides condita	214	1	16	Polyphagous	3	(Guenée, 1852)
Autographa ampla	1	19	17	Polyphagous	6	(Walker, [1858])
Autographa bimaculata	3	3	18	Polyphagous	3	(Stephens, 1830)
Autographa californica	1	0	18	Polyphagous	26	(Speyer, 1875)
Autographa mappa	3	45	17	Polyphagous	4	(Grote & Robinson, 1868)
Autographa pseudogamma	0	1	21	Unknown	Unknown	(Grote, 1875)
Autographa rubidus	0	1	16	Unknown	Unknown	Ottolengui, 1902
Brachylomia algens	9	0	14	Polyphagous	5	(Grote, 1878)
Brachylomia discinigra	4	0	16	Unknown	Unknown	(Walker, 1856)
Cabera erythemaria	134	3	14	Oligophagous	1	Guenee (1858)
Cabera variolaria	30	6	12	Polyphagous	2	Guenée, [1858]
Callizzia amorata	44	0	9	Monophagous	1	Packard, 1876
Campaea perlata	471	210	18	Polyphagous	11	(Guenée, [1858])
Caradrina montana	0	46	15	Polyphagous	3	(Bremner, 1861)
Caripeta angustiorata	3	0	17	Oligophagous	1	Walker, [1863]
Caripeta divisata	214	2	19	Polyphagous	3	Walker, [1863]
Catocala briseis	0	1	31	Oligophagous	1	Edwards, 1864
Catocala semirelicta	14	3	36	Monophagous	1	Grote, 1874
Catocala unijuga	1	0	34	Oligophagous	1	Walker, 1858
Cerastis salicarum	5	0	15	Monophagous	1	(Walker, 1857)

Chytolita petrealis	8	2	13	Monophagous	1	Grote, 1880
Chytonix palliatricula	2	0	14	Polyphagous	1	(Guenée, 1852)
Cladara atroliturata	4	0	16	Polyphagous	3	(Walker, [1863])
Cladara limitaria	2	1	14	Polyphagous	6	(Walker, 1860)
Clostera albosigma	271	5	16	Polyphagous	2	Fitch, 1856
Clostera apicalis	12	0	14	Polyphagous	3	Walker 1855
Clostera brucei	44	3	13	Oligophagous	1	(Edwards 1885)
Coenophila opacifrons	29	5	16	Polyphagous	2	(Grote, 1878)
Colostygia circumvallaria	0	3	15	Oligophagous	1	(Taylor, 1906)
Cosmia praeacuta	0	1	16	Oligophagous	1	(Smith, 1894)
Cryptocala acadiensis	2	23	14	Polyphagous	7	(Bethune, 1870)
Ctenucha virginica	1	1	23	Polyphagous	3	(Esper, 1794)
Cyclophora pendulinaria	49	21	12	Polyphagous	7	(Guenée, [1858])
Dasychira plagiata	164	10	17	Polyphagous	11	(Walker 1865)
Diachrysia aereoides	2	16	18	Polyphagous	3	(Grote, 1864)
Digrammia rippertaria	16	0	14	Oligophagous	1	(Duponchel 1830)
Dodia albertae	0	1	16	Unknown	Unknown	Dyar, 1901
Drepana arcuata	6	2	17	Polyphagous	2	Walker 1855
Drepana bilineata	1	2	18	Polyphagous	4	(Packard, 1864)
Dysstroma brunneata	14	0	13	Monophagous	1	(Packard, 1867)
Dysstroma citrata	255	309	15	Polyphagous	8	(Linnaeus, 1761)
Dysstroma hersiliata	12	56	14	Monophagous	1	(Guenée, [1858])

Dysstroma truncata	5	24	16	Unknown	Unknown	(Hufnagel, 1767)
Dysstroma walkerata	12	10	15	Unknown	Unknown	(Pearsall, 1909)
Ecliptopera silaceata	47	5	14	Polyphagous	2	(Denis and Schiffermuller 1775)
Ectropis crepuscularia	30	0	17	Polyphagous	17	([Denis and Schiffermüller], 1775)
Egira dolosa	1	0	16	Polyphagous	3	(Grote, 1880)
Eilema bicolor	23	8	12	Polyphagous	3	(Grote, 1864)
Enargia decolor	10	0	20	Polyphagous	2	(Walker, 1858)
Enargia infumata	8	0	19	Polyphagous	2	(Grote 1874)
Entephria multivagata	0	2	18	Oligophagous	1	(Hulst, 1881)
Enypia griseata	0	31	17	Polyphagous	2	Grossbeck, 1908
Epirrhoe alternata	2	3	13	Monophagous	1	Müller, 1764
Epirrhoe sperryi	1	0	10	Monophagous	1	Herbulot, 1951
Eremobina claudens	1	0	15	Unknown	Unknown	(Walker, 1857)
Estigmene acrea	1	0	23	Polyphagous	23	(Drury 1773)
Eubaphe mendica	2	0	15	Polyphagous	3	(Walker, 1854)
Euchlaena tigrinaria	5	0	20	Polyphagous	8	(Guenée, [1858])
Eueretagrotis perattentus	7	1	15	Polyphagous	6	(Grote, 1876)
Eulithis destinata	5	1	18	Polyphagous	4	(Möschler, 1860)
Eulithis destinata	2	0	18	Polyphagous	4	(Möschler, 1860)
Eulithis explanata	17	11	15	Polyphagous	2	(Walker, 1862)
Eulithis flavibrunneata	8	4	17	Oligophagous	1	(McDunnough, 1943)

Eulithis propulsata	1	14	16	Polyphagous	3	(Walker, 1862)
Eulithis testata	18	10	16	Polyphagous	4	(Linnaeus, 1761)
Eulithis xylina	15	66	16	Polyphagous	8	(Hulst, 1896)
Euphyia intermediata	5	4	12	Polyphagous	3	(Guenée, [1858])
Eupithecia spp.	144	74	Not applicable	Not applicable	Not applicable	Not applicable
Euplexia benesimilis	1	0	15	Polyphagous	8	McDunnough, 1922
Eurois astricta	364	270	22	Polyphagous	8	(Morrison, 1874)
Eurois occulta	416	302	26	Polyphagous	13	(Linnaeus, 1758)
Euthyatira pudens	1	0	21	Polyphagous	2	(Guenée, 1852)
Euxoa campestris	0	2	16	Unknown	Unknown	(Grote, 1875)
Euxoa tessellata	2	0	16	Polyphagous	15	(Harris, 1841)
Gluphisia septentrionis	9	3	15	Polyphagous	6	Walker, 1855
Gluphisia severa	0	1	20	Unknown	Unknown	Edwards, 1886
Gnophaela vermiculata	0	2	22	Oligophagous	1	(Grote, 1864)
Grammia virgo	0	2	21	Polyphagous	6	(Linnaeus, 1758)
Graphiphora augur	187	52	19	Polyphagous	8	(Fabricius, 1775)
Hada sutrina	3	17	15	Unknown	Unknown	(Grote, 1881)
Hilla iris	29	0	16	Monophagous	1	(Zetterstedt, 1839)
Hydriomena furcata	189	40	16	Polyphagous	8	(Thunberg, 1784)
Hydriomena perfracta	3	5	15	Polyphagous	2	Swett 1910
Hydriomena renunciata	16	0	14	Polyphagous	3	Walker 1862
Hydriomena ruberata	39	0	15	Polyphagous	2	(Freyer, [1831])

Hypagyrtis piniata	1	0	15	Polyphagous	4	(Packard, 1870)
Hypena atomaria	12	0	14	Unknown	Unknown	Smith, 1903
Hypena edictalis	4	0	19	Unknown	Unknown	(Walker, 1859)
Hypenodes fractilinea	28	0	6	Unknown	Unknown	(Smith, 1908)
Hypocoena inquinata	0	2	12	Oligophagous	1	(Guenée, 1852)
Hyppa brunneicrista	1	1	18	Polyphagous	2	Smith, 1902
Hyppa contrasta	2	2	18	Polyphagous	12	McDunnough, 1946
Idia aemula	70	38	11	Polyphagous	3	Hübner, 1814
Idia americalis	11	1	12	Polyphagous	3	(Guenée, 1854)
Ipimorpha pleonectusa	8	21	16	Polyphagous	2	Grote, 1873
Iridopsis ephyraria	2	0	16	Polyphagous	Unknown	Walker, 1860
Iridopsis larvaria	27	1	16	Polyphagous	11	(Guenee [1858])
Lacanobia atlantica	0	4	17	Polyphagous	9	(Grote, 1874)
Lacanobia radix	2	51	17	Polyphagous	5	(Walker, [1857])
Lacinipolia anguina	0	1	13	Unknown	Unknown	(Grote, 1881)
Lacinipolia lorea	13	67	13	Polyphagous	8	(Guenée, 1852)
Lacinipolia lustralis	1	0	14	Unknown	Unknown	(Grote, 1875)
Lacinipolia olivacea	1	28	11	Polyphagous	5	(Morrison, 1874)
Lacinipolia renigera	0	2	12	Polyphagous	12	(Stephens, 1829)
Lasionycta secedens	45	12	13	Monophagous	1	(Walker, [1858])
Leucania dia	0	7	15	Oligophagous	1	(Grote, 1879)
Leucania multilinea	0	1	16	Oligophagous	1	Walker, 1856

Litholomia napaea	4	0	14	Polyphagous	4	(Morrison, 1874)
Lithomoia germana	14	0	20	Polyphagous	Unknown	Morrison, 1875
Lithophane innominata	1	0	18	Polyphagous	9	(Smith, 1893)
Lithophane pexata	1	0	16	Oligophagous	1	Grote, 1874
Lobophora nivigerata	6	5	13	Polyphagous	3	Walker, 1862
Lophocampa maculata	7	0	21	Polyphagous	14	Harris, 1841
Lycophotia phyllophora	205	424	15	Polyphagous	5	(Grote, 1874)
Macaria notata	3	2	15	Unknown	Unknown	(Linnaeus, 1758)
Macaria signaria	55	13	14	Oligophagous	1	(Hübner, [1809])
Malacasoma disstria	2	0	14	Polyphagous	16	(Hübner 1820)
Mesoleuca ruficillata	2	1	13	Polyphagous	2	(Guenée, [1858])
Metanema determinata	98	6	15	Polyphagous	4	Walker 1866
Metanema inatomaria	94	5	16	Polyphagous	4	Guenee [1858]
Mycterophora inexplicata	0	1	12	Unknown	Unknown	(Walker, [1863])
Mythimna oxygala	1	14	16	Unknown	Unknown	(Grote, 1881)
Nematocampa resistaria	15	9	12	Polyphagous	9	(Herrich-Schäff er, [1855])
Nycteola frigidana	11	3	11	Oligophagous	1	(Walker 1863)
Oligia illocata	1	0	17	Polyphagous	4	(Walker, 1857)
Oreta rosea	19	1	18	Polyphagous	2	(Walker 1855)
Orthofidonia tinctaria	10	0	14	Monophagous	1	(Walker, 1860)
Orthosia hibisci	5	3	17	Polyphagous	18	(Guenée, 1852)
Orthosia revicta	45	1	17	Polyphagous	9	(Morrison, 1876)

Orthosia segregata	6	0	16	Unknown	Unknown	(Smith, 1893)
Palthis angulalis	0	11	12	Polyphagous	10	(Hübner, 1796)
Panthea acronyctoides	90	1	18	Oligophagous	1	(Walker, 1861)
Paradiarsia littoralis	0	3	17	Polyphagous	5	(Packard, 1867)
Parastichtis suspecta	3	3	14	Polyphagous	2	(Hübner, 1856)
Perizoma basaliata	238	53	11	Unknown	Unknown	(Walker, 1862)
Pero morrisonaria	2	0	19	Polyphagous	9	(Edwards, 1881)
Phalaenostola metonalis	7	1	12	Polyphagous	4	(Walker, 1859)
Phalaenostola pyramusalis	4	14	12	Unknown	Unknown	(Walker 1859)
Pheosia rimosa	72	8	23	Oligophagous	1	Packard, 1864
Phlogophora periculosa	68	13	20	Polyphagous	11	Guenée, 1852
Phragmatobia assimilans	2	0	15	Polyphagous	6	Walker, 1855
Phyllodesma americana	87	13	17	Polyphagous	12	(Harris 1841)
Plagodis phlogosaria	12	0	16	Polyphagous	7	(Guenee [1858])
Plagodis pulveraria	112	15	16	Polyphagous	8	(Linnaeus 1758)
Platarctia parthenos	0	11	28	Polyphagous	6	(Harris, 1850)
Platypolia anceps	0	2	20	Unknown	Unknown	(Stephens, 1850)
Plemyria georgii	1	1	16	Polyphagous	5	(Hulst, 1896)
Plusia putnami	0	32	16	Polyphagous	4	Grote, 1873
Polia detracta	1	0	23	Polyphagous	6	(Walker, 1857)
Polia nimbosa	48	29	20	Polyphagous	5	(Guenée, 1852)
Polia purpurissata	0	4	19	Polyphagous	8	(Grote, 1864)

Polia rogenhoferi	6	1	22	Unknown	Unknown	(Möschler, 1870)
Polychrysia esmeralda	1	72	17	Monophagous	1	(Oberthür, 1880)
Probole alienaria	26	0	14	Polyphagous	12	(Herrich- Schäffer, [1855])
Prochoerodes lineola	1	0	22	Polyphagous	11	(Göze, 1781)
Protoboarmia porcelaria	22	11	14	Polyphagous	8	(Guenée, [1858])
Protodeltote albidula	79	1	11	Oligophagous	1	(Guenée, 1852)
Protolampra rufipectus	12	48	16	Polyphagous	4	(Morrison, 1874)
Pseudeustrotia carneola	1	0	11	Polyphagous	4	(Guenée, 1852)
Rheumaptera hastata	0	1	16	Polyphagous	7	(Linnaeus, 1758)
Rheumaptera undulata	1	0	18	Polyphagous	8	(Linnaeus, 1758)
Rivula propinqualis	252	52	10	Unknown	Unknown	Guenée, 1854
Schizura unicornis	6	0	17	Polyphagous	15	(Smith, 1797)
Scopula frigidaria	262	52	11	Oligophagous	1	(Möschler, 1860)
Scopula inductata	0	2	12	Polyphagous	3	(Guenée, [1858])
Selenia alciphearia	5	11	21	Polyphagous	5	Walker, 1860
Sicya macularia	10	23	16	Polyphagous	7	(Harris, 1850)
Smerinthus cerisyi	181	10	32	Polyphagous	3	Kirby 1837
Smerinthus jamaicensis	11	11	28	Polyphagous	8	(Drury 1773)
Spargania luctuata	66	27	13	Polyphagous	2	([Denis & Schiffermüller], 1775)
Spargania magnoliata	8	7	12	Polyphagous	2	Guenée, [1858]
Speranza bitactata	0	51	16	Unknown	Unknown	(Walker, 1862)

Speranza brunneata	22	10	12	Polyphagous	4	(Thunberg, 1784)
Speranza loricaria	91	36	14	Monophagous	1	(Hulst, 1837)
Sphinx poecila	0	1	29	Polyphagous	4	Stephens, 1828
Spodolepis substriataria	28	0	22	Polyphagous	2	Hulst, 1896
Sutyna privata	0	2	13	Oligophagous	1	(Walker, 1857)
Sympistis dentata	0	3	15	Oligophagous	1	(Grote, 1875)
Syngrapha alias	45	23	16	Polyphagous	2	(Ottolengui, 1902)
Syngrapha borea	0	1	17	Unknown	Unknown	(Aurivillius, 1890)
Syngrapha epigaea	0	2	20	Polyphagous	8	(Grote, 1875)
Syngrapha rectangula	0	4	17	Oligophagous	1	(Kirby, 1837)
Syngrapha viridisigma	21	121	20	Oligophagous	1	(Grote, 1874)
Trichodezia albovittata	0	2	13	Polyphagous	4	(Guenée, [1858])
Triphosa haesitata	4	0	20	Polyphagous	4	(Guenée, [1858])
Venusia cambrica	11	23	13	Polyphagous	4	Curtis 1839
Venusia pearsalli	2	0	12	Polyphagous	6	(Dyar 1906)
Virbia aurantiaca	1	0	13	Unknown	Unknown	(Hübner, [1831])
Virbia ferruginosa	9	6	13	Unknown	Unknown	(Walker, 1854)
Xanthia tatago	2	1	13	Unknown	Unknown	Lafontaine and Mikkola, 2003
Xanthorhoe abrasaria	127	162	13	Monophagous	1	(Herrich- Schäffer, [1855])
Xanthorhoe decoloraria	64	92	12	Unknown	Unknown	(Esper, [1806])
Xanthorhoe ferrugata	27	12	11	Polyphagous	6	(Clerck, 1759)
Xanthorhoe iduata	26	1	12	Polyphagous	2	(Guenée, [1858])

Xanthorhoe labradorensis	3	2	12	Oligophagous	1	(Packard, 1867)
Xanthorhoe lacustrata	61	0	13	Polyphagous	4	(Guenée, [1858])
Xanthorhoe ramaria	5	68	14	Unknown	Unknown	Swett and Cassino, 1920
Xestia atrata	0	9	19	Unknown	Unknown	(Morrison, 1874)
Xestia fabulosa	36	14	18	Monophagous	1	(Ferguson, 1965)
Xestia homogena	50	322	18	Oligophagous	1	(McDunnough, 1921)
Xestia imperita	20	4	17	Unknown	Unknown	(Hübner, [1831])
Xestia mixta	285	479	18	Polyphagous	6	(Walker, 1856)
Xestia normanianus	2	0	17	Polyphagous	4	(Grote, 1874)
Xestia oblata	1	13	16	Polyphagous	3	(Morrison, 1875)
Xestia perquiritata	54	14	18	Oligophagous	1	(Morrison, 1874)
Xestia praevia	11	0	16	Oligophagous	1	Lafontaine, 1998
Xestia smithii	170	308	16	Polyphagous	8	(Snellen, 1896)
Xylena curvimacula	2	0	22	Polyphagous	4	(Morrison, 1874)
Xylena thoracica	1	0	21	Polyphagous	5	(Putnam- Cramer, 1886)
Xylotype arcadia	13	2	20	Polyphagous	4	Barnes and Benjamin, 1922
Zenophleps alpinata	45	1	14	Polyphagous	2	Cassino, 1927

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Genus species	Growth Form	Site sampled	Author
Achillea millefolium	Forb	Intact	L.
Actaea rubra	Forb	Harvested	(Aiton) Willd.
Arnica cordifolia	Forb	Both	Hook.
Astragalus americanus	Forb	Intact	(Hook.) M.E. Jones
Chamerion angustifolium ssp. angustifolium	Forb	Both	(L.) Holub
Delphinium glaucum	Forb	Harvested	S. Watson
Dryopteris carthusiana	Forb	Harvested	(Vill.) H.P. Fuchs
Equisetum arvense	Forb	Both	L.
Equisetum pratense	Forb	Harvested	Ehrh.
Equisetum scirpoides	Forb	Harvested	Michx.
Equisetum sylvaticum	Forb	Both	L.
Fragaria virginiana	Forb	Both	Duchesne
Galium boreale	Forb	Both	L.
Galium triflorum	Forb	Both	Michx.
Geocaulon lividum	Forb	Intact	(Richards.) Fern.
Goodyera repens	Forb	Both	(L.) R. Br. ex Ait. f.
Lathyrus ochroleucus	Forb	Both	Hook.
Lathyrus venosus	Forb	Intact	Muhl. ex Willd.
Lycopodium annotinum	Forb	Both	L.
Maianthemum canadense	Forb	Both	Desf.
Mertensia paniculata	Forb	Both	(Aiton) G. Don
Mitella nuda	Forb	Both	L.
Moneses uniflora	Forb	Both	(L.) Gray
Orthilia secunda	Forb	Harvested	(L.) House
Petasites frigidus var. palmatus	Forb	Both	(Aiton) Cronquist
Platanthera obtusata	Forb	Both	(Banks ex Pursh) Lindl.
Platanthera orbiculata	Forb	Intact	(Pursh) Lindl.
Pyrola asarifolia	Forb	Both	Michx.
Pyrola chlorantha	Forb	Both	Sw.
Rubus chamaemorus	Forb	Harvested	L.
Rubus pubescens	Forb	Both	Raf.
Symphyotrichum ciliolatum	Forb	Both	(Lindl.) A. Löve & D. Löve
Taraxacum officinale	Forb	Harvested	F.H. Wigg.
Vicia americana	Forb	Intact	Muhl. ex Willd.
Viola renifolia	Forb	Both	A. Gray
Alnus viridis ssp. crispa	Shrub	Harvested	(Aiton) Turrill
Betula glandulosa	Shrub	Both	Michx.
Cornus canadensis	Shrub	Forb	L.
Ledum groenlandicum	Shrub	Both	Oeder
Linnaea horealis	Shrub	Both	L
Ribes olandulosum	Shrub	Harvested	C. Grauer
Ribes hudsonianum	Shrub	Harvested	Richards
Ribes lacustre	Shrub	Both	(Pers.) Poir
Ribes orvacanthoides	Shrub	Both	Ι.
Ribes triste	Shrub	Both	E. Pallas
Ruces Histe Posa acigularis	Shrub	Both	I and
KOSA ACICUIARIS	SILUD	DOUI	Linul.

APPENDIX B: List of plant species sorted by growth form.

Rubus idaeus	Shrub	Harvested	L.
Salix spp.	Shrub	Both	Not applicable
Shepherdia canadensis	Shrub	Both	(L.) Nutt.
Vaccinium vitis-idaea	Shrub	Both	L.
Vaccinium caespitosum	Shrub	Harvested	Michx.
Vaccinium oxycoccos	Shrub	Harvested	L.
Viburnum edule	Shrub	Both	(Michx.) Raf.
Abies balsamea	Tree	Harvested	(L.) Mill.
Betula papyrifera	Tree	Both	Marshall
Picea glauca	Tree	Both	(Moench) Voss
Picea mariana	Tree	Harvested	(Mill.) Britton, Sterns & Poggenb.
Pinus contorta	Tree	Both	Douglas ex Loudon
Populus balsamifera	Tree	Harvested	L.
Populus tremuloides	Tree	Both	Michx.