HABITAT ASSOCIATIONS OF RED SQUIRRELS (*Tamiasciurus hudsonicus*) AND THEIR IMPACT ON THE GRAY-CHEEKED THRUSH (*Catharus minimus minimus)* IN WESTERN NEWFOUNDLAND

by

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A Thesis submitted to

the School of Graduate Studies

in partial fulfillment of the requirements for the degree of

Master of Science

Cognitive and Behavioural Ecology Program

Memorial University of Newfoundland

April 2021

St. John's Newfoundland and Labrador

ABSTRACT

Introduced species are known for disrupting ecosystems and affecting endemic species. Red squirrels (*Tamiasciurus hudsonicus*) were introduced to Newfoundland during the 1960s and by the 1990s the Newfoundland Gray-cheeked Thrush (*Catharus minimus minimus*) had undergone a steep decline. It is hypothesized that nest predation by squirrels caused the thrush decline so during 2016 and 2017 I undertook point count surveys in the Long Range Mountains of western Newfoundland to compare the contemporary distributions and habitat use of these species. Squirrels and thrushes were strongly segregated, whereby thrushes were restricted to higher elevations (~340-600 m), while squirrels were abundant below 275 m, reaching an upper range limit at ~500 m. Gray-cheeked Thrushes were associated with harvested clearcuts, modified cuts, conifer forest, and tall scrub at the local scale, with only weak negative habitat associations at the landscape scale. Squirrels were associated with second-growth fir/spruce forest and old growth fir, while they avoided water, coniferous scrub, and regenerating fir/spruce forest. Gray-cheeked Thrushes have been historically abundant down to sea level, so this strong altitudinal segregation adds to the growing body of evidence that squirrels played an important role in the decline and range contraction of this species on Newfoundland.

GENERAL SUMMARY

Introduced species often impact native species. Red squirrels are predators of eggs and young songbirds. They were introduced to Newfoundland in the 1960s and have been implicated in the decline of the Newfoundland Gray-cheeked Thrush. I surveyed forests in western Newfoundland to compare the distributions of these two species. I found that squirrels and thrushes lived at different elevations, with thrushes occupying montane forests (~340-600 m), and squirrels being common below 275 m and not found above ~500 m. Habitat use also differed, with thrushes occupying strip cuts, clearcuts, coniferous forest, and tall scrub, and squirrels preferring 30-70 year-old fir/spruce or >70 year-old fir forests. Squirrels avoided water, scrub forest, and 10-30 year-old fir/spruce forest. In the past, the thrushes were common down to sea level, so my findings support the hypothesis that squirrels have restricted thrush populations to higher elevations.

ACKNOWLEDGEMENTS

My work on this thesis could not have been possible without the financial, intellectual, and emotional support of a whole host of people and organizations. This research was supported by funding from the Centre for Forest Science and Innovation, NSERC, Memorial University, and Gros Morne National Park. Additional support was provided by staff at Gros Morne National Park, especially Scott Taylor, who provided geomatics support. The Newfoundland and Labrador Wildlife Division generously allowed me to stay in The Roost for my two field seasons. Recordings of squirrel vocalizations that I used during my fieldwork were obtained from the Macaulay Library at the Cornell Lab of Ornithology and were collected by Wil Hershberger (ML 100916) and Matthew Medler (ML 136185).

Thank you to all my field technicians: Elora Grahame, Brendan Kelly, Noah Korne, Kathleen Manson, Anna Rodgers, Meaghan Tearle, and Benjamin West. They slogged through bogs, over slippery slash, broke free of alder thickets, and bashed through mountains of scrub without complaint, all while being frozen, rained and snowed upon, and eaten by countless biting insects. Thank you to Tina Leonard for being ready, unbidden, to enact a rescue mission from a forest fire and for just dropping in to visit in the field; my first social visit ever brought by helicopter!

I appreciated the CABE community in St. John's and the advice and questions provided by the faculty there including Dave Wilson, Carolyn Walsh, and Bill Montevecchi. A hearty thanks also goes out to Anne Storey, a member of my committee, for her comments and advice on all my manuscripts, and to Dan Kehler and David Schneider for their advice and assistance with statistical analyses. I'd also like to acknowledge the comments and reviews of April Robin Martinig and two anonymous reviewers during the peer review process, which led to me publishing the second chapter of my thesis in Canadian Journal of Forest Research (see published version: McDermott, J.P.B., Whitaker, D.M., and Warkentin, I.G. 2020. Constraints on range expansion of introduced red squirrels (*Tamiasciurus hudsonicus*) in an island ecosystem. Canadian Journal of Forest Research 50(10):1064-1073. doi: 10.1139/cjfr-2019-0369). A description of minor

changes to the published manuscript at the recommendation of my thesis examiners can be found in Chapter 2.1.

My family and friends from home deserve a special mention, for always being the most supportive of my goals and decisions, even when they take me to far-away lands. I'll always be appreciative of the "Ontario B'ys", Mahyar Garmsiri and Liang Zhu, for pushing me to work harder, and being my family while I was in St. John's. My endless appreciation also goes out to Darrian Washinger, my honorary lab-mate, who made sure I celebrated every win on the way, no matter how small, and kept me sane during all the times I thought I could never finish this.

Finally, I extend my sincere thanks and appreciation to my supervisors Ian Warkentin and Darroch Whitaker for their constant support and encouragement through tumultuous field seasons, seemingly endless analysis and writing, and personal upheaval (including when Darroch adopted my foster cat and saved me from endless heartache!). I can never thank them enough for guiding me towards the scientist I am today and for their unceasing efforts to find and provide opportunities for me.

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1 Introduction and overview

1.1 Introduced species effects on ecosystems

One of the defining ecological patterns of the Anthropocene has been the redistribution of species around the planet, creating the need to study the impacts of these newly arrived species on endemic biodiversity. Biological invasion has become widespread due to accidental and deliberate species introductions as well as changes in species' ranges in response to human-induced changes in the environment (Simberloff et al. 2013). The consequences of species introductions to novel environments are varied (Lockwood et al. 2007), but successful invasion can result in changes to the physical structure of an ecosystem, alter ecosystem processes and dynamics, and may even lead to range contraction, extirpation or extinction of native species and a broader loss of endemic biodiversity (Courchamp et al. 2003; Long 2003; Sax and Gaines 2008; Simberloff 2009). It can be difficult to assess the full effect of an invasive species on declining or extirpated species for many reasons. First among these is that species introductions typically cannot or should not be replicated through experimental approaches that could otherwise give strong inferential results. Instead, researchers often must rely on corroborating or correlative evidence such as: spatial and temporal correlations between invasive and endemic species' population trends; knowledge of the behaviour and ecology of the invasive species in other regions; presence of affected species in the diet of the new species; and decline of other members of the same prey guild (Fritts and Rodda 1998). In areas where much of the local biodiversity has remained undocumented, or when there has been an absence of systematic monitoring programs, it is not always simple or possible to fully assess the effects an introduced species has on a novel ecosystem.

Despite analytical challenges, introduced mammalian predators have been implicated in 58% of avian, mammalian, and reptilian species extinctions, and have played a role in the declines of hundreds of other species (Doherty et al. 2016). Ninety percent of bird species that are reported as having been imperiled or extirpated by the introduction of a mammalian predator are island endemics (Doherty et al. 2016), though it is not clear that endemic insular bird populations are at a higher risk of extinction from the introduction of a predatory mammal than mainland bird populations (see Blackburn et al. 2004; Medina et al. 2011; Doherty et al. 2016). Regardless, island endemics typically exist as relatively small, isolated populations that have evolved in less diverse ecosystems with simplified community structure, and so may have reduced competitive and anti-predator abilities in the face of invaders (Courchamp et al. 2003, Banks and Dickman 2007; Moser et al. 2018; Russell and Kaiser-Bunbury 2019). This "island tameness" is expected since native and endemic species did not co-evolve with the new threat (e.g., Fritts and Rodda 1998), and was illustrated by Campbell (1996) who found that an introduced species of gecko tended to flee from the threat of predation while a native island gecko did not. Additionally, islands are often lacking in whole guilds of species, and this reduced community diversity can make invasive species more likely to succeed (Simberloff 1995). While this may lead to range-wide declines of endemic populations, it may also be expressed in the form of reduced ecological niches, where endemic species become restricted to habitats to which invaders are poorly suited (Scheele et al. 2017; see also Parlato et al. 2015).

1.2 Tree squirrels as introduced species

Tree squirrels (family Sciuridae) possess biological traits that make the group particularly successful invaders of novel areas, including high vagility, high reproductive potential, and behavioural plasticity (Palmer et al. 2007; Wood et al. 2007). Species in this group also have broader community effects due to their omnivorous diets and generalist predatory behaviour, as well as through food hoarding that can modify forest dynamics and exacerbate interspecific competition for resources (Martin 1988; Vander Wall 2001). Consequently, studies of introduced, invasive populations of species in this group are important for understanding their potential ecological impacts and guiding management strategies (e.g., Gurnell et al. 2004). Numerous introductions in 14 countries have been documented, involving nine species of tree squirrels (Palmer et al. 2007). In reviewing these tree squirrel introductions, Palmer et al. (2007) documented consistent adverse ecological and economic impacts, including competition with native tree squirrels and other fauna, predation on native animals, alteration of forest structure and decreased forest regeneration, transmission of disease, and damage to human-made structures. Adverse impacts have become so pervasive in certain areas that management through hunts with bounties, nest eradications, fertility control, trapping, poisoning, and control through encouragement of native predation have all been tested or employed with varying success in an effort to curb their spread (Palmer et al. 2007; Sheehy et al. 2018).

Within the Sciuridae, North American red squirrels (*Tamiasciurus hudsonicus*, hereafter red squirrels) are notable for their far-reaching effects on boreal ecosystems. They can impose selection pressure on conifer cone morphology (e.g., *Pinus, Picea*; Smith 1970; Benkman 1989), limit forest regeneration through seed consumption (West 1989; English 1998), and are known to compete with seed-eating finches (e.g., *Spinus*, *Loxia*) and other granivores (e.g., *Tamias*, *Peromyscus*) for food (Smith and Balda 1979; Wren 2001; Benkman et al. 2009). Despite primarily consuming conifer seeds (Smith 1968), red squirrels are omnivorous predators and can account for up to 88% of the predation on songbird eggs, nestlings, and fledglings (Martin and Joron 2003; Willson et al. 2003; Haché et al. 2014), as well as predating the young of mammals including snowshoe hares (*Lepus americanus*) and even conspecifics (Callahan 1993; Steele 1998).

1.3 Red squirrels on Newfoundland

The island of Newfoundland has been subjected to numerous species introductions, including various amphibians, reptiles, birds, fish, invertebrates, and 13 species of mammals (e.g., Scott and Crossman 1964; South 1983; Montevecchi and Tuck 1987; Maunder 1997; Strong and Leroux 2014). The red squirrel is one of the most recent mammal introductions and is unique in that it arrived nearly simultaneously at widely separated locations through both sanctioned and unsanctioned translocations. During 1963 red squirrels were released at multiple locations on the Northern Peninsula by members of the public, and subsequently released to Camel Island by government officials (Payne 1976; Dodds 1983). The aesthetic appeal of red squirrels and their potential as a new fur source for trappers motivated these actions, while it was also hoped that red squirrels would augment the diet of the imperiled Newfoundland subspecies of American marten (*Martes americana atrata*; Goudie 1978). Since that time however, squirrels have not been found to comprise a substantial portion of the marten's diet (COSEWIC 2007). Through natural dispersal and additional translocations, red squirrels had colonized most of Newfoundland by the mid-1990s and are now likely found throughout the island in all suitable habitat (Goudie 1978; Minty 1976; Whitaker 2015). In other areas of their range across North America, red squirrel populations are thought to be naturally regulated by food supply rather than predation (Sullivan 1990; Stuart-Smith and Boutin 1995), suggesting that habitat quality may be the most important factor limiting any further expansion of the range of this species on Newfoundland.

Limited information is available on the contemporary distribution and abundance of red squirrels on Newfoundland, as well as any effects they may be having on the ecosystems they have colonized. Higher densities of red squirrels have been reported in central Newfoundland where black spruce (*Picea mariana*) stands dominate forest cover (0.4-5.8 squirrels/ha; West 1989; Reynolds 1997), compared to the balsam fir (*Abies balsamea*) or mixed coniferous stands (1.1-1.4 squirrels/ha; Wren 2001; Lewis 2004) that dominate forests in western Newfoundland and the Avalon Peninsula (Damman 1983). Benkman (1989) also stated that red squirrel densities in black spruce forests on Newfoundland could be twice as high as in comparable forests on the mainland, though no data were provided to support this suggestion. Other factors may also be important drivers of red squirrel distribution and habitat use on Newfoundland. For example, no red squirrels were observed during a three-year live trapping survey carried out in montane balsam fir forest at elevations between 450 m and 550 m (Shawn Gerrow, Parks Canada, unpublished report), suggesting that this species may be restricted to lower elevations on Newfoundland. However, sampling was not carried out at lower elevations and that study was not designed to identify an upper elevation limit on red squirrel occurrence. Thus, the limited number of studies, and incomplete knowledge on key factors such as elevation make it difficult to assess differences in red squirrel abundance between forest types or regions of Newfoundland or to identify key factors affecting red squirrel distribution. Though the extent of squirrel effects on Newfoundland ecosystems remains largely unstudied, red squirrels have been implicated as potential drivers of the decline of two endemic bird subspecies through predation of eggs and young (Newfoundland Gray-cheeked Thrush, *Catharus minimus minimus*; Whitaker et al. 2015; Fitzgerald et al. 2017) and/or interspecific competition for food (Newfoundland Red Crossbill, *Loxia curvirostra percna*; Benkman 1989; Environment Canada 2012).

1.4 Gray-cheeked Thrush on Newfoundland

The Gray-cheeked Thrush is a Neotropical migrant songbird that breeds in the northern boreal forest across Canada, Alaska, and into Siberia, and has been infrequently studied across their range and on Newfoundland (Whitaker et al. 2020). A limited understanding of the breeding biology and ecology of the Gray-cheeked Thrush can be attributed to a variety of factors, mostly linked to the remoteness of the habitats which it occupies during the breeding season. Understanding of this species was also limited by the fact that much of the early research attributed to it was actually carried out on another closely related species, the Bicknell's Thrush (*Catharus bicknelli*), which has a more southerly range and was only recognized as a distinct species during the 1990s (Ouellet 1993). It was only after the population on Newfoundland (*Catharus minimus minimus*; recently confirmed to be distinct from the mainland subspecies, *C. m. alicea*, via genetic research; FitzGerald et al. 2017) began to undergo substantial declines (SSAC 2010) that more detailed research on this relatively accessible population of the species was initiated. From the 1930s to the 1980s, the Newfoundland Gray-cheeked Thrush was reported as being a locally common, widespread, and abundant bird species (Peters and Burleigh 1951; SSAC 2010). During the 1970s it was the fifth most abundant landbird in Gros Morne National Park, being found in both the Long Range Mountains and throughout the coastal plains (Lamberton 1976). However, by late in the last century there was evidence of a dramatic drop in the number of individuals being detected and this subspecies was provincially listed as threatened in 2015 due to an apparent 95% decline between 1975 and 2005 (SSAC 2010). This estimate was based primarily on Breeding Bird Survey (BBS) data from 1974-2008, which was comprised of 23 routes around the island, where the average number of thrushes detected per route fell from 6.2 individuals in 1975-1984 to 0.4 individuals from 1999-2008 (SSAC 2010). These routes follow established roads, which generally avoid mountainous areas, and so are limited to elevations below 400 m ASL. As such, it is indicative only of population trends below this elevation. A follow-up survey in Gros Morne National Park in 1993 resampled the same plots as those sampled by Lamberton (1976) and found that Gray-cheeked Thrushes had completely disappeared from the coastal plains plots (Jacques Whitford Environment 1993). They did find, however, that the thrushes remained abundant in the Long Range Mountains. One BBS route in the park predominately samples coastal scrub habitat, and documented the complete disappearance of these thrushes; though more than 20 thrushes per year were observed along this route during the 1970s, none have been recorded since 1997 (Route 57021; SSAC 2010). Additionally, Fitzgerald et al. (2017) searched across areas of the island where Gray-cheeked Thrushes had been historically present, but found none in or near Terra Nova National Park in eastern Newfoundland, Grand Falls-Windsor in central Newfoundland, or in several areas in southwestern Newfoundland. However, it was known that some higher elevation areas of the Long Range Mountains in western Newfoundland still supported residual populations of Gray-cheeked Thrush in 2006 and 2007 (Whitaker et al. 2015). The apparent persistence of residual high elevation populations indicates that the 95% decline suggested from BBS data alone may be somewhat of an overestimate, and also suggests that montane areas could provide an important refuge for Gray-cheeked Thrush in Newfoundland. However, the extent, size, and elevational limits of these populations are largely unknown.

Across the Gray-cheeked Thrush's range in North America, they are associated with tall deciduous or coniferous shrub thickets in riparian, tundra, and treeline areas, as well as open canopy forests with a complex understory of woody shrubs (often deciduous like alder, *Alnus* spp. or willow, *Salix* spp.), montane areas, and also in stunted and mature coniferous stands (Di Corrado 2015; Whitaker et al. 2020). On the island of Newfoundland, descriptions of habitat use and occurrence have mostly been limited to casual observations, notes of presence within general bird surveys, or as part of a larger study focused on other topics (e.g., Marshall 2001). Generally, Gray-cheeked Thrushes in Newfoundland can be found in stunted conifer thickets, mature spruce (*Picea*) and fir

(*Abies*) forests (Marshall 2001), and in > 80 year-old, uncut fir forest (Thompson et al. 1999). The first comprehensive study done specifically relating to the habitat requirements of Gray-cheeked Thrush on Newfoundland was by Whitaker et al. (2015). They modelled habitat requirements at two different spatial scales and found that the occurrence of thrushes was positively related to tall scrub forest at both neighbourhood and landscape scales, with intermediate amounts of old growth forest at the landscape scale, and with clearcuts at the neighbourhood scale, but was negatively impacted by clearcuts at the landscape scale. Whitaker et al. (2015) also found elevation to be an important factor explaining Gray-cheeked Thrush distribution. The main difference between the Newfoundland Gray-cheeked Thrush and the mainland subspecies' habitat preferences appears to a weaker association with deciduous shrub thickets and stronger affinity for conifer scrub and forest on Newfoundland, which is reminiscent of the habitat affinities of Bicknell's Thrush (Marshall 2001). Questions remain surrounding the influence of some silvicultural methods including pre-commercial thinning, which negatively influence Bicknell's Thrush (Chisholm and Leonard 2008; McKinnon et al. 2014; Aubry et al. 2016), and strip cutting, as well as their use of different elevations, as the impact of these methods has not been given much consideration across the continental range of this species.

Various hypotheses have been proposed to explain the sudden, widespread decline of the Gray-cheeked Thrush on Newfoundland. These include deforestation and habitat degradation in their wintering grounds, forest management on their breeding grounds, adverse conditions or events during migration, potential competition with Swainson's

Thrushes (*Catharus ustulatus*), and the introduction of red squirrels to the island (SSAC 2010; Whitaker et al. 2015, 2018, 2020). Threats during migration and competition with Swainson's Thrushes have been dismissed as neither of these factors underwent striking changes during the period of major Gray-cheeked Thrush decline (see SSAC 2010; Whitaker et al. 2015). Additionally, Gray-cheeked Thrushes disappeared simultaneously from both managed and unmanaged forests on the breeding grounds, indicating that forest management was not a likely factor (Whitaker et al. 2015). At present, only habitat degradation on their wintering grounds and the introduction of red squirrels are still considered likely to have played a strong causal role in the population's decline.

1.5 Thesis objectives and outline

The principal goal of my research was to better understand whether introduced red squirrels have impacted the population of Gray-cheeked Thrushes on Newfoundland. I did this by collecting co-located survey data for the two species to evaluate Whitaker et al.'s (2015) hypothesis that they should now be strongly segregated by elevation. Other goals were to better understand the habitat needs of the Gray-cheeked Thrush and to improve the understanding of the distribution and ecology of red squirrels on Newfoundland. In Chapter 2, I describe the types of landcover which can be used to predict red squirrel occupancy in western Newfoundland, investigate their use of the landscape across an elevation gradient, and assess potential factors limiting their contemporary distribution on the island of Newfoundland. In Chapter 3, I compare the distributions of red squirrels and Gray-cheeked Thrushes across an elevation gradient to help better understand the likelihood and potential role that red squirrels may have played in the decline of the Newfoundland Gray-cheeked Thrush. I also endeavour to enhance our understanding of Gray-cheeked Thrush habitat use at different spatial scales. In Chapter 4, I discuss the potential for further expansion of red squirrels through the island, make several management recommendations for both red squirrels and Gray-cheeked Thrushes, and discuss future directions that should be taken to advance our understanding of both species on the island of Newfoundland, and more generally.

1.6 Co-authorship statement

This thesis has been prepared in manuscript style with the intention that Chapters 2 and 3 are stand-alone scientific articles to be submitted to peer-reviewed journals; as such, there is necessary repetition of some introductory material and methods in Chapters 1 – 3. I published Chapter 2 in the Canadian Journal of Forest Research in 2020 with Darroch Whitaker and Ian Warkentin (my graduate supervisors) as co-authors, and so I use plural rather than singular first-person pronouns. Copyright remains with me and my co-authors; it is available in an Open Access format, and can be referenced as "McDermott, J.P.B., Whitaker, D.M., and Warkentin, I.G. 2020. Constraints on range expansion of introduced red squirrels (*Tamiasicurus hudsonicus*) in an island ecosystem. Canadian Journal of Forest Research 50(10):1064-1073. doi: 10.1139/cjfr-2019-0369". Additionally, Chapter 3 is intended for submission to a peer-reviewed publication with my graduate supervisors as co-authors and is formatted for Biological Conservation, and so I again use plural rather than singular first-person pronouns.

The work presented in this thesis is my own and I conducted this research independently, with contributions and collaborations from others, especially my graduate supervisors (Drs. Ian Warkentin and Darroch Whitaker) who provided advice and editorial support throughout. Identification of the research topic originated with Darroch Whitaker and Ian Warkentin. I was heavily involved with design of the research related to my thesis chapters and I planned my field work with the assistance of Darroch Whitaker and Ian Warkentin. We hired field technicians as a cohesive hiring committee, and I collected my data with the help of these field technicians who were under my supervision while in the field (Elora Grahame, Brendan Kelly, Noah Korne, Kathleen Manson, Anna Rodgers, Meaghan Tearle, and Benjamin West). I conducted all data analysis, with input and advice from Darroch Whitaker, Ian Warkentin, Dan Kehler, and Dave Schneider. I wrote the initial and subsequent manuscript drafts for all chapters, incorporating edits and suggestions from Ian Warkentin and Darroch Whitaker, and Anne Storey (committee member). I also incorporated suggestions and edits in Chapter 2 from April Robin Martinig and two anonymous reviewers during the peer-review process for publication in the Canadian Journal of Forest Research.

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2 Constraints on range expansion of introduced red squirrels (*Tamiasciurus hudsonicus*) in an island ecosystem

2.1 Co-authorship Statement

I published this chapter in the Canadian Journal of Forest Research in 2020 with my graduate supervisors (Ian Warkentin and Darroch Whitaker) as co-authors. As such, I use plural rather than singular first-person pronouns throughout, and formatting of the references section matches the journal's requirements. Copyright has remained with me and my co-authors; it is available in an Open Access format, and can be referenced as "McDermott, J.P.B., Whitaker, D.M., and Warkentin, I.G. 2020. Constraints on range expansion of introduced red squirrels (*Tamiasicurus hudsonicus*) in an island ecosystem. Canadian Journal of Forest Research 50(10):1064-1073. doi: 10.1139/cjfr-2019-0369". There are various small changes to the published manuscript that I incorporated based on the reviews of my thesis examiners. These include the incorporation of a short statistical analysis on the fine-scale vegetation data, for which I added a small paragraph of methodology, reported statistical findings in the results section, and minor alterations of the discussion; the addition of a map of my study area (Figure 2-1); the indication of significant variables in Figures 2-3 and 2-4; and the inclusion of minor wording changes to increase clarity.

Conception of the research idea was by Darroch Whitaker and Ian Warkentin, who provided advice and suggestions throughout the research, but the work described in this chapter is my own. I planned and executed the data collection with their assistance. I conducted data analysis independently, with input and advice from Darroch Whitaker, Ian

Warkentin, Dan Kehler, and Dave Schneider. I prepared the manuscript, incorporating edits and suggestions from Ian Warkentin and Darroch Whitaker, and Anne Storey (committee member). I also incorporated suggestions and edits from April Robin Martinig and two anonymous reviewers during reviews for publication.

2.2 Abstract

Limitations on range expansion of introduced species can offer insights into their basic ecology and inform conservation of associated endemics. North American red squirrels (*Tamiasciurus hudsonicus*) were recently introduced to the island of Newfoundland, where they have been implicated in the decline of two endemic bird subspecies. We conducted 1960 point count surveys with playback to assess red squirrel distribution and habitat use across a 257 km^2 montane landscape in western Newfoundland during the summers of 2016 (following conifer masting) and 2017 (after non-masting). We used Generalized Additive Models with stepwise model selection to assess the annual relationship between land cover and red squirrel occurrence. Red squirrels were most common at low elevations and not detected above ~ 500 m elevation. They were negatively associated with water, coniferous scrub and 10-30 year old fir/spruce, but positively associated with 30-70 year old fir/spruce and > 70 year old fir. Red squirrel presence was related to more land cover variables in 2016, after a masting year. Absence of red squirrels from higher elevation forests apparently resulted from lack of suitable habitat rather than incomplete range expansion. Climate or silviculture-induced changes in vegetation may alter mid and upper elevation habitat suitability.

Key words: North American red squirrel (*Tamiasciurus hudsonicus*), elevation, habitat, introduced species, range expansion

2.3 Introduction

Biological invasion is widespread due to accidental and deliberate introductions as well as the shifting or expansion of species' ranges in response to human-induced changes in the environment (Simberloff et al. 2013). While the consequences of species introductions to novel environments are varied (Lockwood et al. 2007), island ecosystems have typically been more vulnerable due to such factors as simplified community structure, dispersal barriers, and lower ecosystem diversity, as well as typical traits of endemic island species such as small populations and reduced competitive and anti-predator abilities (e.g., Wood et al. 2017; Russell and Kaiser-Bunbury 2019). Successful invasion can result in altered community dynamics and may even lead to the extirpation or extinction of native species and a broader loss of endemic biodiversity (Courchamp et al. 2003; Sax and Gaines 2008).

Tree squirrels (family Sciuridae) possess biological traits that make the group particularly rapid and successful invaders of novel areas, including high vagility, high reproductive potential, and behavioural plasticity (Palmer et al. 2007; Wood et al. 2007). Species in this group also have broader community effects due to their omnivorous diets and generalist predatory behaviour, as well as through food hoarding that can modify forest dynamics and exacerbate interspecific competition for resources (Martin 1988; Vander Wall 2001). Consequently, studies of introduced, invasive populations of species in this group are valuable for understanding their potential ecological impacts and guiding management strategies (e.g., Siepielski 2006). In reviewing tree squirrel introductions, Palmer et al. (2007) documented consistent adverse ecological and economic impacts, including competition with native tree squirrels and other fauna, predation on native animals, alteration of forest structure and decreased forest regeneration, transmission of disease, and damage to human-made structures. Within the Sciuridae, North American red squirrels (*Tamiasciurus hudsonicus*, hereafter red squirrels) are notable for their far-reaching effects on boreal ecosystems. They can impose selection pressure on conifer cone morphology (e.g., *Pinus, Picea*; Smith 1970; Benkman 1989), limit forest regeneration through seed consumption (West 1989; English 1998), and are known to compete with seed-eating finches (e.g., *Spinus*, *Loxia*) and other granivores (e.g., *Tamias*, *Peromyscus*) for food (Smith and Balda 1979; Wren 2001; Benkman et al. 2009). Despite primarily consuming conifer seeds (Smith 1968), red squirrels are also predators and can account for up to 88% of the predation on songbird eggs and fledglings occurring during a season (Martin and Joron 2003; Willson et al. 2003; Haché et al. 2014), as well as predating the young of mammals including snowshoe hares (*Lepus americanus*) and even conspecifics (Callahan 1993; Steele 1998).

Red squirrels are a relatively new addition to the fauna of Newfoundland, Canada, having been introduced to the island in 1963 and 1964 (Payne 1976; Whitaker 2015). Members of the public carried out the initial unsanctioned introductions, though government officials followed this with a series of translocations aimed at accelerating the spread of the species. The aesthetic appeal of red squirrels and their potential as a new fur source for trappers motivated these actions, while it was also hoped that red squirrels would augment the diet of the imperilled Newfoundland subspecies of American marten (*Martes americana atrata*; Goudie 1978). Though Newfoundland is the largest island in the circumpolar boreal biome (>108,000 km^2), rapid dispersal and translocations resulted in red squirrels becoming widespread and abundant across the island by the mid-1990s (Minty 1976; Goudie 1978; Whitaker 2015). The extent of their effects on Newfoundland ecosystems remains largely unstudied, but red squirrels have been implicated as potential drivers of the decline of two endemic bird subspecies through nest predation (Newfoundland Gray-cheeked Thrush, *Catharus minimus minimus*; Whitaker et al. 2015; Fitzgerald et al. 2017) and/or interspecific competition for food (Newfoundland Red Crossbill, *Loxia curvirostra percna*; Benkman 1989; Pimm 1990). Red squirrels are also known to harvest up to 96% of available black spruce (*Picea mariana*) cones in poor cone years on Newfoundland (West 1989), though it is unlikely this would impact longer-term forest growth.

Despite their successful introduction to various islands off continental North America, (Payne 1976; Long 2003; Martin and Joron 2003), there has been little quantitative study of red squirrel habitat associations, distribution, or abundance in these settings. Balsam fir (*Abies balsamea*) and black spruce dominated forests of Newfoundland provide novel, but lower quality, habitat compared to the white spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta*) stands in western North America where red squirrels have more often been studied (Brink and Dean 1966). To our knowledge, few studies have focussed on habitat associations of red squirrels in forests with a comparable balsam fir/black spruce composition (e.g., Allard-Duchêne et al.

2014); Riege (1991) worked in a forest with only 29% fir and an abundance of seeds and nuts available from deciduous forests, while Kemp and Keith (1970) conducted their study in a black spruce stand that lacked balsam fir. Likewise, these systems were not comparable to Newfoundland where the widespread conifer cover combines a masting species of relatively lower lipid content with a species that more consistently offers moderate amounts of higher lipid content cones (balsam fir and black spruce, respectively; Wren 2001). Conifers on Newfoundland have also evolved in the absence of a terrestrial granivore. Consequently, cones on Newfoundland may have thinner scales compared to those on the mainland, making them more accessible to red squirrels (Benkman 1989). Similarly, limited information is available on the distribution and abundance of red squirrels on Newfoundland, especially during periods of high and low cone availability. Higher densities of red squirrels have been reported in central Newfoundland where black spruce stands dominate forest cover (0.4-5.8 squirrels/ha; West 1989; Reynolds 1997), compared to the balsam fir or mixed coniferous stands (1.1-1.4 squirrels/ha; Wren 2001; Lewis 2004) that dominate forests in western Newfoundland and the Avalon Peninsula (Damman 1983). Benkman (1989) also stated that red squirrel densities in black spruce forests on Newfoundland could be twice as high as in comparable forests on the mainland, though provided no data supporting this suggestion. Other factors may also be important drivers of red squirrel distribution and habitat use on Newfoundland. For example, no red squirrels were observed during a three-year live trapping survey carried out in montane balsam fir forest at elevations between 450 and 550 m (Shawn Gerrow, Parks Canada, unpublished report), suggesting that this species may be restricted to lower elevations on Newfoundland. However, sampling was not carried out at lower elevations and they did not attempt to identify an upper elevation limit on red squirrel occurrence. Thus, the limited number of studies, and failure to address key factors such as elevation make it difficult to assess differences in red squirrel abundance between forest types or regions of Newfoundland or, more importantly, to identify key factors affecting red squirrel distribution and abundance.

We studied the occurrence of introduced red squirrels across an elevation gradient in a montane, balsam fir-dominated forest landscape of western Newfoundland. Our primary objective was to assess the habitat use and distribution of red squirrels where the available conifer species differ from those in other areas where this species has been studied. Since black spruce retains cones for multiple years and provides a more reliable food source than balsam fir, we expected habitat use to vary between years that did or did not follow large balsam fir cone crops (i.e., masting) (Minty 1976; Farrar 1995). Newfoundland has only been colonized by red squirrels in the past ~50 years, so we then used our findings on factors limiting the species' distribution to evaluate the potential for further range expansion on Newfoundland. This information may be important to conservation of endemic biota, as unoccupied habitats may be serving as short- or long-term refugia for native species that are impacted by introduced red squirrels.

2.4 Materials and Methods

2.4.1 Survey area

We collected our data across a 257 km^2 study area in the upper Humber River and Main River watersheds (centered at 57° 16′ W, 49° 40′ N) on the eastern slope of the

Long Range Mountains of western Newfoundland, Canada (Figure 2-1; see Whitaker et al. 2015 for a detailed description of the study area). The study area spanned a 75 m to 608 m elevation gradient with land cover dominated by wet balsam fir forests (Thompson et al. 2003; McCarthy and Weetman 2006). For context, the highest point on Newfoundland is 814 m. All mountains exceeding 600 m, which account for just 1% of the island (1 010 km^2), occur in western Newfoundland and are dominated by Arctic-alpine barrens and windswept krummholz (Damman 1983). Forests below 450 m elevation and in deep valleys are characterized by a matrix of mixed and single-species stands of productive forest dominated by balsam fir or black spruce along with bogs, heaths, rock barrens, and other natural openings (Damman 1983; McCarthy and Weetman 2006). Other secondary tree and shrub species in the region include white birch (*Betula papyrifera*), eastern larch (*Larix laricina*), white spruce (*Picea glauca*), mountain ash (*Sorbus* sp.), alder (*Alnus* sp.), and serviceberry (*Amelanchier* sp.). Above 450 m, open areas and non-productive scrub forest become increasingly prevalent due to increased wind exposure, deep and late snow cover, low nutrient availability, and saturated soils (Damman 1983). Between 1990 and 2004, 19.7% of the landscape in the surveyed area was logged in cutblocks ranging from 0.30 ha to 217.7 ha, with a mean size of 21.6 ± 31.8 ha. Most cutblocks occur between 300 m and 500 m elevation, and two ~100 ha experimental strip cuts, which were harvested during 2001 and 2003, span elevations of 419-564 m (see Whitaker et al. 2015). Harvesting since that time has been limited to the creation of a 60 m-wide electricity transmission corridor through a northern section of the study area in 2016 and 2017. Periodic stand-killing outbreaks of defoliating insects are the primary form of large natural forest disturbance in the region, but are uncommon above ~400 m due to climate severity (McCarthy and Weetman 2006). Red squirrels were present in the region by the mid-1980s and have been widespread and common since at least the mid-1990s (Whitaker 2015).

2.4.2 Field methods

We conducted point count surveys (Buckland et al. 2001; Chavel et al. 2017) from 8 June to 17 July in 2016 and 2017. Red squirrels are ~ 1.5 times more likely to call in response to a broadcast of vocalizations compared to calling rates before the broadcast, often approaching the broadcaster (Shonfield 2010), and respond twice as frequently to the call of a stranger compared to a neighbour (Price et al. 1990). Consequently, we employed an 11-minute point count protocol that consisted of six minutes of silent watching and listening followed by a broadcast of two minutes of Gray-cheeked Thrush songs and calls (for a related study), one minute of silence, a one-minute broadcast of red squirrel vocalizations, and one final minute of silent observation. During each of the time blocks in the 11 minutes of the point count, we recorded each red squirrel that was heard or seen. The red squirrel broadcast was created from archived recordings of red squirrel rattles and chucks from Nova Scotia and Quebec (Macaulay Library of Bioacoustics, Cornell Lab of Ornithology; Catalogue numbers: 100916 and 136185), which are known to elicit territorial responses from red squirrels (Price et al. 1990; Siracusa et al. 2017). The volume of broadcasting units (FoxPro model FX3 or Crossfire game callers; FoxPro Incorporated, Lewistown, PA 17044, USA) was set at a constant level for all point counts. When measured 1 m from the speaker the average volume of red squirrel vocalizations was 53.7 dB, with peak volumes of 73.9 dB.

We spaced point count locations 500 m apart in a grid, leading to a systematic assessment of red squirrel distribution across our survey landscape each year. During 2016, which followed a conifer masting year in the region (Robineau-Charette and Whitaker 2017), the grid encompassed 991 point count locations, while in 2017 (a non-masting year; Robineau-Charette and Whitaker 2017) we shifted the grid 250 m north and east within the same area and sampled 969 locations. Thus, over the two sampling years that followed winters of differing cone availability, we collected point count data during a single visit to each of 1 960 point count locations. Surveys were conducted between 05:40 h and 14:30 h by single observers (4 individuals during 2016, 5 individuals during 2017: 1 individual common to both years), sampling a series of 5-12 adjacent point count locations each day. Sampling alternated between low, mid, and high elevation portions of the study area on consecutive days across the season. Observers recorded categorical assessments of wind (Beaufort scale), precipitation (none, rain, drizzle, fog), and cloud (0-5) during each point count, and surveys were not conducted when high winds (Beaufort scale >5: >29 km/h), or persistent precipitation, and/or fog might have impaired visual or auditory detections of red squirrels. In 2017, following completion of each point count, we tallied the number of >1.3 m tall stems of each tree or shrub species along a 2 m × 22.6 m transect running North-South and centered on the survey point (total 45.2 m^2), to obtain a measure of stand composition and tree distribution at a point count level across the study area.

2.4.3 Data management and analysis

We extracted land cover data in the area surrounding each point count location from the provincial forest resource inventory Geographic Information System (GIS) database, which was created using high-resolution (sub 10 cm pixel) 3D aerial photographs taken in 2007. Land cover types were mapped in accordance with the standard forest resource inventory scheme used by the Province of Newfoundland and Labrador, with landscape elements assigned to cover types (e.g., forest, bog, barren, water) and forest stands classified according to 20-year age classes and dominant tree species composition. Stands of scrub forest were classified into eight height classes (breaks at 3.5 m, 6.5 m, 9.5 m, 12.5 m, 15.5 m, 18.5 m, and 21.5 m). Using ArcGIS 10.4.1 (ESRI 2002), we extracted this land cover information within a 52.3 m radius of each survey point (i.e., 0.86 ha circular plot). This distance was based on maximum red squirrel home range size estimates reported by LaMontagne et al. (2013) from white spruce forests in the Yukon under conditions of low cone availability. Broader spatial-scale habitat cover was not considered because red squirrels are highly territorial and vigorously defend their territories (Smith 1968; Price et al. 1990; Reynolds 1997). Red squirrels detected at one location could potentially have been the same as those found at neighbouring locations, though this seems unlikely because of the distance between points and because off-territory forays, while undertaken by both males and females, are limited (Benhamou 1996; Lane et al. 2009). Even so, knowing the individual identity of a red squirrel at the point count location was not essential for our study; rather we were simply interested in knowing whether red squirrels used the area. We then aggregated land cover types into categories that would be more relevant based on our understanding of red squirrel habitat needs. We grouped the eight deciduous and coniferous scrub categories into two height classes (<6.5 m and >6.5 m) based on previous work in our study area (Whitaker et al. 2015), and because this is the approximate height where canopy becomes closed (Allard-Duchêne et al. 2014). To account for the time lag between the collection of the aerial photographs and this study, we added 10 years to the age class for each forest stand, and we then grouped 20-year stand classifications into three broader age classes: regenerating stands (10-30 years old), second growth stands (30-70 years old), and mature stands (70+ years old). Stands younger than 30 years are not yet mature and so produce few, if any, cones, while on average more cones should be produced with increasing age (Viereck 1983, Viereck and Johnston 1990, Viglas et al. 2013). Finally, the elevation of each survey point was extracted from a digital elevation model from Natural Resources Canada's CanVec geospatial database (available under the Government of Canada's Open Government License [https://open.canada.ca/en]). The resolution of this data varies from 1:10,000–1:50,000 scale.

We analysed data (red squirrel presence-absence at a point) for each year separately as we expected that red squirrels could be using habitat differently following winters of high (2016) and low cone availability (2017). As a first step, we conducted a two-sample Kolmogorov-Smirnov test to compare the elevation distribution of red squirrels between 2016 and 2017. We then developed a global linear model to explain variation in squirrel occurrence, and used backwards stepwise variable selection to identify land cover features associated with red squirrel occurrence each year (all data analyses completed using R statistical software, version 3.3.1; R Core Team 2016). We did not detect any red squirrels above 515 m elevation in either 2016 or 2017, so we excluded survey locations above 515 m elevation from these analyses to lessen confounding effects of land cover and elevation, resulting in a total of 844 and 823 point count locations in 2016 and 2017, respectively.

We measured land cover variables as the proportion of area within the 52.3 m radius circle they accounted for (range 0-1) and tested for independence with a Spearman's correlation matrix (i.e., $r < 0.5$; Dormann et al. 2013). To limit variables to those having minimally adequate explanatory power, we then eliminated land cover variables from further analyses if fewer than 5% of the total points surveyed included that cover type. The remaining variables (Table 2-1) included a mixture of land cover types which we expected red squirrels would select or avoid. We expected that open habitat, water, and scrub habitat would be less used by red squirrels as they provide little or no food or cover, while forests, specifically mature fir or fir/spruce stands, would be selected by red squirrels. Examination of the distribution of red squirrels across the study area suggested that elevation could be correlated with red squirrel occurrence, so elevation was also included in our models. To account for factors that might affect detectability of red squirrels, we included wind, cloud, and precipitation as fixed categorical variables, observer as a random categorical variable, and ordinal date (day of year) and time of day as continuous variables in our global model each year. Though these variables were included in our analyses and reported in our results to account for some variation that could be attributed to differences in detection, we did not discuss them further.

We fit our global model for each year using a Generalized Additive Model (GAM) with red squirrel presence/absence as the response variable (R package mgcv version 1.8-31; Wood 2011). When fitting models, we specified a binomial error distribution with a clog-log link function, which performs better for datasets having an unequal ratio of absences and presences (Zuur et al. 2009). Each continuous explanatory variable was fit as a smoothed nonparametric spline to allow for non-linear relationships. All terms except wind and cloud were set to a default number of knots, which are used to calculate the maximum degrees of freedom for an individual smoothed term. For wind and cloud, we specified a maximum kernel of k=3 to allow the model to run based on limitations of degrees of freedom for these terms. We also specified a maximum likelihood (ML) smoothness selection criterion, which is recommended when manually dropping terms. We then simplified the global model by removing variables in a stepwise fashion in order of least significance based on their p-values: if the resulting model had a lower Akaike's Information Criterion (AICc; corrected for small sample sizes) compared to the previous model, that factor was considered unimportant and dropped from the model. The final model was accepted when dropping any of the remaining terms would lead to an increase in model AICc, as the model with the lowest AICc value is presumed to be the most parsimonious (Burnham and Anderson 2002). Finally, for ease of comprehension and to illustrate the nature and strength of the relationship, we plotted each continuous variable in our final model against their predicted fitted values of red squirrel probability of presence when all other variables were held constant at their mean.

To assess the suitability of habitat for red squirrels within different elevation zones, we calculated the proportion of land cover across our study area for each of the variables that appeared in either of our final annual models. Elevation ranges were determined *a posteriori* as below 275 m (low), between 275 m and 499 m (mid), and above 500 m (high). The zone below 275 m encompasses the area where we detected the majority of red squirrels in both 2016 and 2017. The upper elevation threshold is the elevation below which 99% of red squirrels were detected in 2016 and 2017.

We investigated the presence/absence of each vegetation species or grouping found in our point count locations (alder [*Alnus* sp.], serviceberry [*Amelanchier* sp.], balsam fir, black spruce, eastern larch [*Larix laricina*], no trees/shrubs [open habitat], cherry [*Prunus* sp.], snag, mountain ash [*Sorbus* sp.], white birch [*Betula papyrifera*], white spruce [*Picea glauca*]) along a continuous elevation gradient by creating a Generalized Linear Model (GLM) for each one. These models had a binomial error distribution, used a clog-log link function, and included vegetation presence/absence as the response variable using the function "glm" (R package lme4 version 1.1-26; Bates et al. 2015). Note though that when plotting differences in the distribution of these fine-scale (point count location level) vegetation features across elevations we visualized them with elevation split into categories that matched those mentioned above, but with the upper boundaryset instead at 450 m to match the transition between vegetation zones identified by Damman (1983).

2.5 Results

During 2016, we saw or heard 241 red squirrels at a total of 184 point count locations (18.6% of point counts), whereas during 2017 only 47 red squirrels were detected at 46 locations (4.7% of point counts). In both years, the rate of red squirrel encounter at a location was inversely related to elevation, with proportion of locations where red squirrels were detected within elevation intervals below 275 m ranging from 0.60 – 1.00 during 2016 versus 0.10 – 0.30 in 2017; the highest elevations at which we detected a red squirrel were 515 m and 513 m during 2016 and 2017, respectively (Figure 2-2). The proportion of point count locations below 275 m occupied by red squirrels was 3.8 times higher than above 275 m in 2016, while during 2017 the proportion of occupied locations below 275 m was 5.7 times higher than above 275 m (Figure 2-2). However, the distribution of red squirrels across the elevation gradient was not significantly different between years (Kolmogorov-Smirnov test: $D = 0.196$, $p = 0.11$).

For 2016, after a masting year, the best model explaining red squirrel presence/absence retained nine variables and explained 38.9% of the deviance in the data. Variables influencing detection rates that were retained included ordinal date (day of year; $\chi^2_{1.5,828.4} = 4.83$, $P = 0.149$), precipitation ($\chi^2_{1,828.4} = 0$, $P = 1$), and time of day ($\chi^2_{1,828.4} = 8.09$, $P = 0.004$). Graphical analysis of the model fit for ordinal date indicated that in 2016 the probability of a red squirrel being detected remained very similar through the first half of our sampling season, and increased slightly in the later half (Figure 2-3A). The probability of a red squirrel being detected decreased later in the day (Figure 2-3B). The importance of elevation was evident through the strong inverse trend in the probability of a red squirrel being present with increasing elevation ($\chi^2_{2.6,828.4} = 113.95$, $P < 0.0001$; Figure 2-3C). Land cover variables retained in the 2016 model were mature balsam fir, regenerating fir/spruce, second growth fir/spruce, water, and low scrub (< 6.5 m). Mature balsam fir had a positive association with the probability of a red squirrel being present, though this relationship was not strong ($\chi^2_{1,828.4} = 2.12$, $P = 0.145$; Figure

2-3D). Similarly, though regenerating fir/spruce was retained in the best model and had an inverse relationship with the probability of red squirrel being present (Figure 2-3E), this association was weak ($\chi^2_{1,\ 828.4} = 2.10$, $P = 0.148$). As such, mature fir and regenerating fir/spruce are likely not particularly important predictors of red squirrel occurrence. The relationship of red squirrels with second growth fir/spruce was curvilinear, where the probability of a red squirrel being present increased up to approximately 50% cover of second growth fir/spruce, but decreased at higher amounts of this cover type ($\chi^2_{2.47,828.4} = 27.83$, $P < 0.0001$; Figure 2-3F). By comparison, water and low scrub were inversely related to the probability of a red squirrel being observed (water: $\chi^2_{1,\ 828.4} = 7.00$, $P = 0.008$, Figure 2-3G; low scrub: $\chi^2_{1,\ 828.4} = 11.69$, $P < 0.001$, Figure 2-3H).

For 2017, after a non-mast year with far fewer red squirrel detections, the best model only included five variables and explained just 17.7% of the deviance in the data. The probability of a red squirrel being detected decreased through the season ($\chi^2_{1.95,813.8} = 7.81$, $P = 0.035$; Figure 2-4A). Observer ($\chi^2_{2.23,813.8} = 6.76$, $P = 0.018$) and time of day ($\chi^2_{2.05,813.8} = 4.15$, $P = 0.155$) were also retained, though the effect of time of day on squirrel detections appeared to be limited (Figure 2-4B). The importance of elevation was again evident through the negative trend in the probability of a red squirrel being present with increasing elevation ($\chi^2_{1,813.8} = 14.65$, $P < 0.001$; Figure 2-4C). Low scrub was the only land cover variable that was retained for 2017 and increased cover decreased the probability of observing a red squirrel ($\chi^2_{1,813.8} = 4.33$, $P = 0.037$; Figure 2-4D).

We graphed the proportion of total land area in our survey area for each land cover variable that was retained in either the 2016 or 2017 model at low (<275 m), mid (275-499m), and high elevations (>500 m; Figure 2-5). Short coniferous scrub stands (inversely related with red squirrel presence) made up only 4% of cover in low elevations but became increasingly dominant at higher elevations, where they accounted for 33% of land cover. Second growth balsam fir/black spruce (the only significant positive predictor of red squirrel presence) decreased with elevation and was unavailable above 500 m. Mature balsam fir had a non-significant positive association with red squirrel presence, but increased in availability with increasing elevation. Surface water and regenerating fir/spruce peaked at intermediate elevations.

Our stem counts from the 2017 vegetation surveys revealed that higher elevation sites had slightly different tree and shrub species composition than lower elevation sites (Figure 2-6). Some deciduous tree and shrub species such as alder, mountain ash, and cherry were less common between 275 m and 450 m compared to lower elevations, and were not observed above 450 m elevation. This change in occurrence with elevation was significant for alders ($z_{1,960} = -6.86$, $P < 0.001$), but not for mountain ash ($z_{1,960} = -1.43$, $P = 0.15$) or cherry ($z_{1,960} = -1.11$, $P = 0.27$). Similarly, the incidence of white spruce, white birch, and eastern larch declined significantly as elevation increased (white spruce: $z_{1,960} = -3.01$, $P < 0.01$; white birch: $z_{1,960} = -3.34$, $P < 0.001$; eastern larch: $z_{1,960} = -3.62$, $P < 0.001$). Conversely, a higher proportion of points above 450 m had snags and open habitat, and these positive trends with elevation were significant (snags: $z_{1,960} = 2.89$, $P < 0.01$; open: $z_{1,960} = 2.37$, $P = 0.02$).

2.6 Discussion

Given the high capacity for invasion among introduced tree squirrel species (Wood et al. 2007) and the success of North American red squirrels in colonizing other oceanic islands and even isolated continental forests (Long 2003; Martin and Joron 2003; Siepielski 2006), documenting their distribution on the island of Newfoundland is an important step towards understanding their potential to impact such ecosystems. Despite a large difference in number observed between years, the relative abundance of red squirrels was consistently higher at low elevations compared to higher elevations, and they reached an elevation limit at approximately 500 m in both years. This upper limit to their current distribution suggests that red squirrels may not be able to expand further upslope on the island without climate or forest management driven changes in high-elevation vegetation. Within the elevation range they did occupy, in 2016 after a masting year red squirrels avoided habitats that provide limited food or shelter, including coniferous scrub, 10-30 year old mixed conifer, and where surface water became more prevalent in the immediate landscape around a location. Instead, they were associated most strongly with 30-70 year old mixed conifer stands. In 2017, after a non-masting year, red squirrels were found in much lower numbers but within the same elevation range as the year before. We expected that important or more beneficial habitats would be strongly selected in 2017, as we presumed that red squirrels occupying the highest quality territories would have been more likely to survive through winter following a low mast crop. Instead, the model for 2017 contained far fewer land cover predictors of red squirrel presence, with only coniferous scrub – an inverse predictor of squirrel presence – appearing important. It is possible that this lack of model complexity resulted at least in part from reduced statistical power as a result of having observed fewer red squirrels in 2017, even though survey effort was similar in both years. This reduced statistical power in 2017 could also have accounted for inconsistent patterns in the influence of ordinal date and time between years, though it is also possible that daily seasonal patterns in squirrel activity or detectability are density dependent and should be taken into consideration when implementing survey protocols.

Red squirrel encounter rate differed considerably between years, being more than five times higher in 2016 compared to 2017, which followed high and low cone production years, respectively. While some variability between years could be attributed to visiting different point count locations in each year, we sampled >950 points each year and points sampled in the second year were interspersed midway between those sampled the previous year and covered the same study area. In addition, this inter-annual difference is consistent with the major fluctuations typical of red squirrel populations across the rest of their range, commonly linked to availability of conifer seeds (Wheatley et al. 2002; Martin and Joron 2003; Boutin et al. 2006). The magnitude of this inter-annual population fluctuation was also comparable to nearby Gros Morne National Park, where red squirrel encounter rates are on average four times higher during winters that follow abundant cone crops than during winters that follow sparse cone crops, and were 6.5 times higher during winter 2016 than winter 2017 (Robineau-Charette and Whitaker 2017). Interestingly, while we observed far more red squirrels in 2016, their relative distribution across the elevation gradient was similar following both masting and non-masting years. Direct impacts of red squirrels via predation on native wildlife would be expected to be stronger in high population years, and also at lower elevations where squirrels consistently occupy a higher proportion of the landscape (e.g., Martin and Joron 2003; McFarland et al. 2008). However, competitive impacts via cone predation may be higher in non-mast years, when red squirrels can harvest most or all of the limited cone crop during fall (West 1989) and preferentially select larger cones that contain a higher number of large, viable seeds (COSEWIC 2016). This can leave few viable, nutrient-rich seeds available as food for other granivores during winter (e.g., Benkman et al. 2009).

Large changes in red squirrel population size between years could affect the proportion of red squirrels using or occupying different elements of the available habitat. Based on the findings of others (Minty 1976; Farrar 1995; Allard-Duchêne et al. 2014), we expected that red squirrels would be more abundant in black spruce stands during 2017, following a year of low balsam fir cone production, as black spruce maintains cones on the tree for up to 30 years, whereas balsam fir cones rarely persist from year to year. However, in 2017 no habitat factors were found to be positively associated with red squirrel presence. This could in part be due to the low number of red squirrel detections, and the consequent reduction in statistical power when modeling habitat relationships in an area having a mosaic of land cover types. Still, black spruce forest was not included in either the 2016 or the 2017 model, indicating that may not be an important predictor of red squirrel distribution in western Newfoundland. Instead, we found that red squirrel presence was positively associated with the extent of cover of second growth balsam fir/black spruce stands in 2016, but that this land cover was not as important in 2017. Selection of this stand age is consistent with findings from Thompson and Curran (1995) in Newfoundland, where red squirrels were found significantly more often in fir stands 40-60 years old compared to other stand age classes. Balsam fir in this age class produces large cone crops during masting events but is effectively barren otherwise (Messaoud et al. 2007). The presence of black spruce in these mixed species stands would presumably buffer the severity of low fir cone crops, creating a more reliable and consistent overall food source across years. However, if there was a reliable food supply between years, and other drivers of red squirrel population dynamics (predation, migration, etc.) were relatively consistent between years, we would expect that red squirrel occurrence would be relatively stable, which is not what we observed. The large difference in encounter rate of red squirrels across our study area between years could be explained by a difference in the number of red squirrels found in fir-dominated stands between years. Similar trends have been seen in other systems during years with white spruce (a high-quality masting species) cone failure (Wheatley et al. 2002). Red squirrel density in white spruce stands that had limited cone production dropped to levels that matched the typically lower densities seen in mixed conifer and lodgepole pine stands, whereas red squirrel density remained stable in mixed and pine stands (Wheatley et al. 2002).

The retention of both positive and negative land cover predictors of red squirrel occurrence in our models may offer insight into the absence of red squirrels at higher elevations. High elevation portions of our study area, particularly above 500 m where there is an increased prevalence of coniferous scrub cover and no second growth fir/spruce forest (Figure 2-5), appear to be sub-optimal habitat for red squirrels. In cold, windswept areas like the upper reaches of the Long Range Mountains, black spruce reproduces asexually through adventitious rooting rather than by seed dispersal (Roberston 1993) often resulting in little cone production in these scrub spruce stands. Wind also causes high elevation fir and spruce stands to be stunted with extremely dense, low canopies, and very little understory vegetation. We did not detect cherries (*Prunus* spp.) or mountain ash (*Sorbus* spp.) above 450 m, yet seeds and fruit from these species, which were present at very low numbers in low elevation areas, might help red squirrels persist in years of low cone production (Steele 1998). Additionally, white spruce, though also uncommon at lower elevations, was absent at higher elevations. Unfortunately, our survey season did not coincide with optimal phenology for mushrooms, an important alternate food source (Fletcher et al. 2010), so we cannot comment on the availability of mushrooms at higher elevations. Further, snow pack at these higher elevations takes on average three weeks longer to melt in the spring (Damman 1983), and is often present well into June, delaying leaf-out of shrubs and production of flowers and berries or other growing season foods. This may be a critical period for red squirrels, as food stores cached the previous autumn could be depleted, especially if they have cached fewer cones than required to last the winter (Fletcher et al. 2010), rendering these areas uninhabitable or at least sub-optimal. Apart from limited availability of food, scrub forest may also be structurally unsuitable, as it has branches that are tightly intertwined, potentially impeding movement for squirrels, while narrow trunks would offer few natural cavities large enough for nesting (Vahle and Patton 1983). As such, it seems unlikely that red squirrels will expand further upslope on the island, barring climate or forest management driven changes to mid- and high-elevation forests. Changes in climate could alter the intensity and frequency of insect outbreaks, windthrow, or wildfire at these elevations, thereby altering forest age structure and habitat suitability for red squirrels. Similarly, forest management has already altered the age structure of forests at these elevations. Logging that occurred between 1990 and 2005 in our study area has created large regenerating stands that may become favourable for red squirrels in less than two decades. Thus, while significant range expansion of red squirrels above 500 m elevation seems unlikely, both changes in the natural disturbance regime as a result of climate change and forest harvesting may augment the amount of suitable red squirrel habitat between 300 m and 500 m elevation. Consequently, while the upper elevation limit of red squirrel distribution may remain relatively stable, we suggest that there is potential for red squirrels to become more abundant at intermediate elevations in our study area, and to use different age classes of regeneration depending on the cause of disturbance (Allard-Duchêne et al. 2014).

In conclusion, red squirrels have recently been introduced into forest ecosystems on the island of Newfoundland that are different from those where red squirrels have typically been studied across the remainder of their range. White spruce, the most important masting species in western North America, is present in low numbers in most areas away from human settlement on Newfoundland, and is replaced by balsam fir and black spruce, which produce less energy rich cones (Brink and Dean 1966; Wren 2001). In our study area, red squirrels were most common after a masting year in 30-70 year old mixed coniferous forest stands. If they remained present in these stands from year-to-year, trees in these mixed stands could provide food more consistently during both balsam fir masting and non-masting years than for squirrels present in stands comprised of only balsam fir. They were also most common at low elevations and were absent from montane forests above ~500 m in both years, whereas in other portions of their range they are frequently present above 2000 m (Hamer 2016). This elevation limit may be vital to the persistence of endemic biodiversity on Newfoundland, where just 4% of the island (4 260 km^2) exceeds 500 m in elevation. For example, the Newfoundland Gray-cheeked Thrush, which was once common at all elevations on the island, has become largely restricted to montane forests above ~450 m since the introduction of red squirrels (Whitaker et al. 2015; McDermott, unpublished data). Both thrushes and squirrels are rare in the narrow zone of overlap from ~450-500 m, so the two species are now effectively allopatric on Newfoundland. Given the diversity of known and suspected impacts of introduced red squirrels to the endemic biota of Newfoundland, future research should also investigate the mechanism(s) behind their elevation range limit and better document the impacts that red squirrels may be having on forest ecosystems.

2.7 Acknowledgements

Many thanks to Elora Grahame, Brendan Kelly, Noah Korne, Kathleen Manson, Anna Rodgers, Meaghan Tearle, and Benjamin West, who assisted with data collection, and to Scott Taylor for geomatics support. We gratefully acknowledge the reviews by April Robin Martinig, Anne Storey, and two anonymous reviewers on earlier versions of the manuscript, and Dan Kehler for advice regarding statistical analyses. The Newfoundland and Labrador Department of Fisheries and Land Resources, Forestry and Wildlife Branch provided use of a cabin and other logistical support. Funding and other support was supplied by the Centre for Forest Science and Innovation (Newfoundland and

Labrador Department of Natural Resources), the Natural Sciences and Engineering Research Council of Canada, and Gros Morne National Park of Canada. Research was conducted under a scientific research permit from the Newfoundland and Labrador Department of Environment and Conservation, Parks and Natural Areas Division, as well as a research permit from the Department of Fisheries and Land Resources, Forestry and Wildlife Branch, and animal care approval (16-16-IW) from the Memorial University of Newfoundland Institutional Animal Care Committee.

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2.9 Tables and Figures

Table 2-1: Land cover variables included in global models to explain presence of red squirrels (*Tamiasciurus hudsonicus*) in the upper Humber and Main River watersheds, Newfoundland in 2016 and 2017. Elevation was also included in model for each year.

Land cover class	Code	Description	Mean cover within 52.3 m [range]
Low scrub	cs1	Scrub forest < 6.5 m tall	13.3% [0.0-100%]
Tall scrub	cs2	Scrub forest > 6.5 m tall	12.9% [0.0-100%]
Open	open	Bogs and barrens	7.3% [0.0-100%]
Water	water	Standing water (rivers, ponds, lakes)	2.4% [0.0-81.6%]
Regenerating fir	bf1	10-30 year old balsam fir forest	4.6% [0.0-100%]
Mature fir	bf3	> 70 year old balsam fir forest	11.1% [0.0-100%]
Regenerating fir/spruce	bfbs1	10-30 year old forest with ~50% each balsam fir and black spruce	5.2% [0.0-100%]
Second growth fir/spruce	bfbs2	30-70 year old forest with ~50% each balsam fir and black spruce	6.5% [0.0-100%]
Mature fir/spruce	bfbs3	> 70 year old forest with ~50% each balsam fir and black spruce	17.9% [0.0-100%]
Mature spruce	bs3	> 70 year old black spruce forest	4.2% [0.0-100%]
Mixed forest	mix	Forest with both deciduous and coniferous trees (all ages)	5.6% [0.0-100%]
Harvested forest	areaharv	Forest harvested between 1990 and 2004	17.4% [0.0-99.8%]

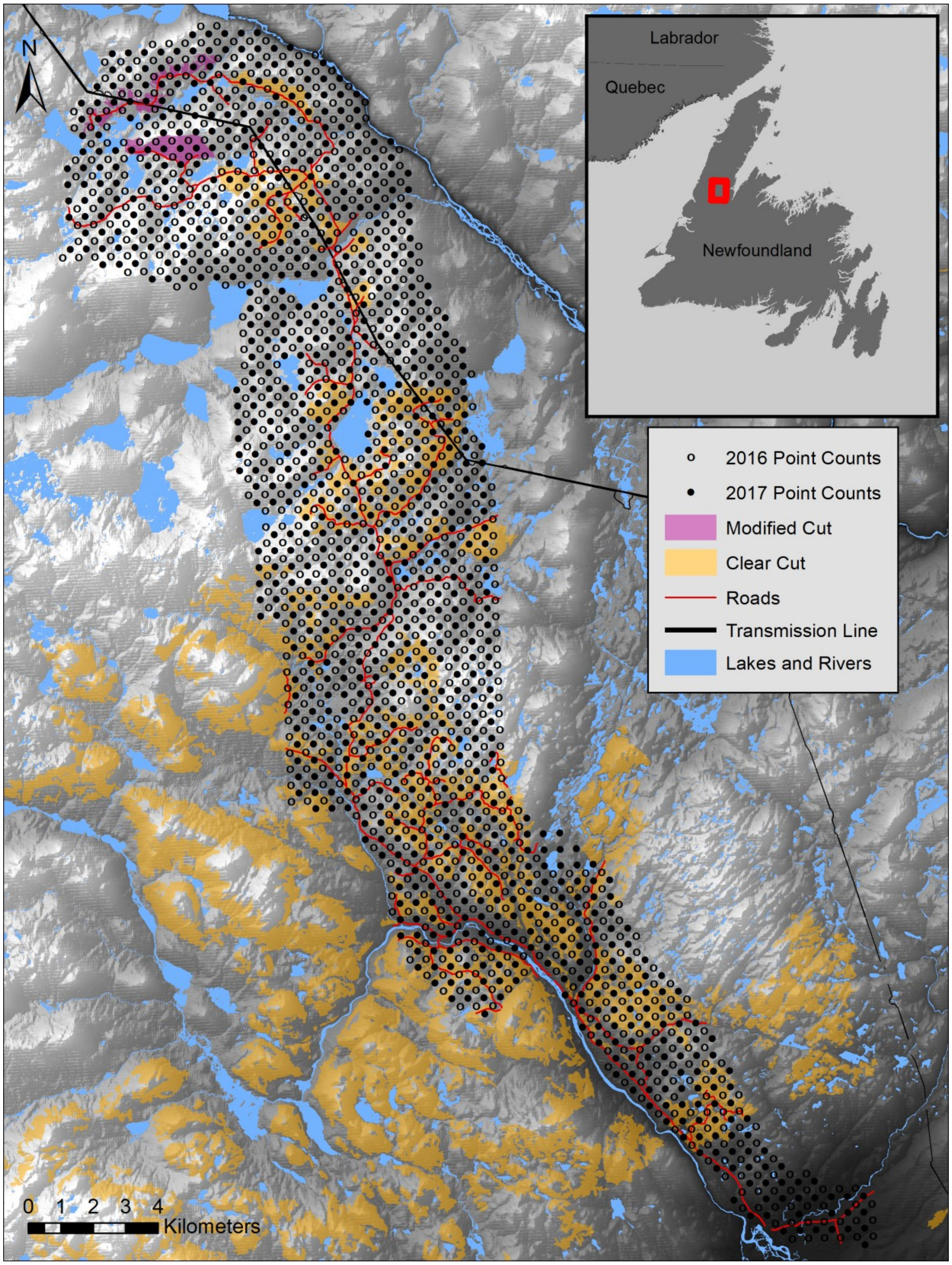

Figure 2-1: Study area in the upper Humber River and Main River watersheds of western Newfoundland. The location of the study area on Newfoundland is shown with the red rectangle on the inset map.

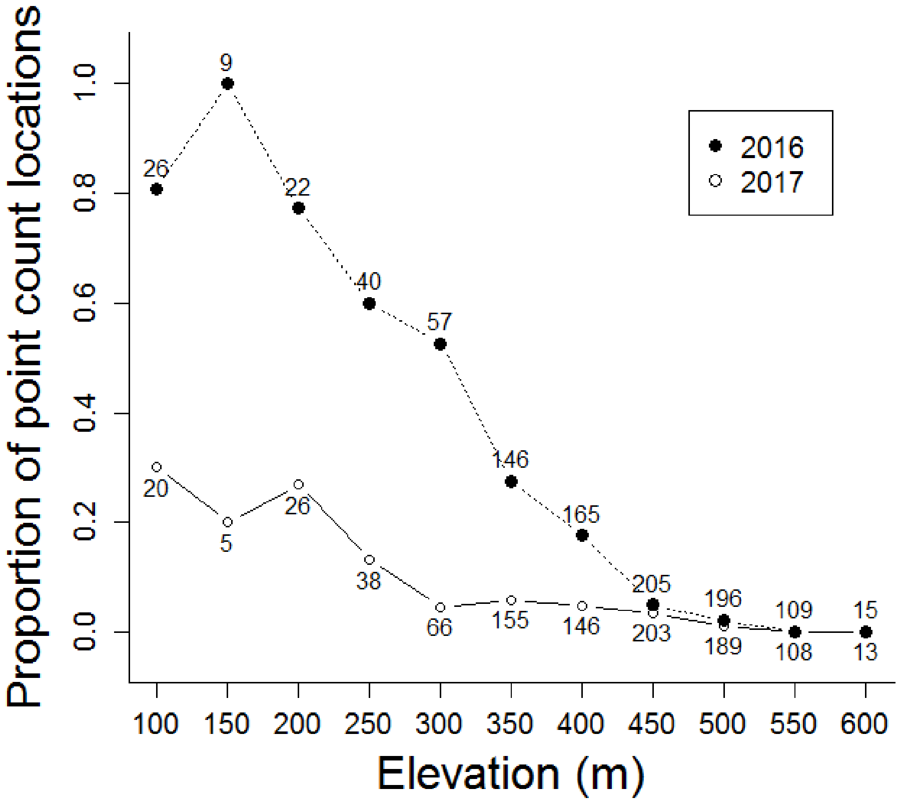

Figure 2-2: Elevation distribution of red squirrels (*Tamiasciurus hudsonicus*) in the Main River and upper Humber River watersheds of western Newfoundland in 2016 and 2017. The proportion of point count locations are based on 50 m elevation intervals. Data labels indicate number of point count locations (total n = 1 960) in each elevation category, with values for 2016 indicated above the dotted line and values for 2017 appearing below the solid line.

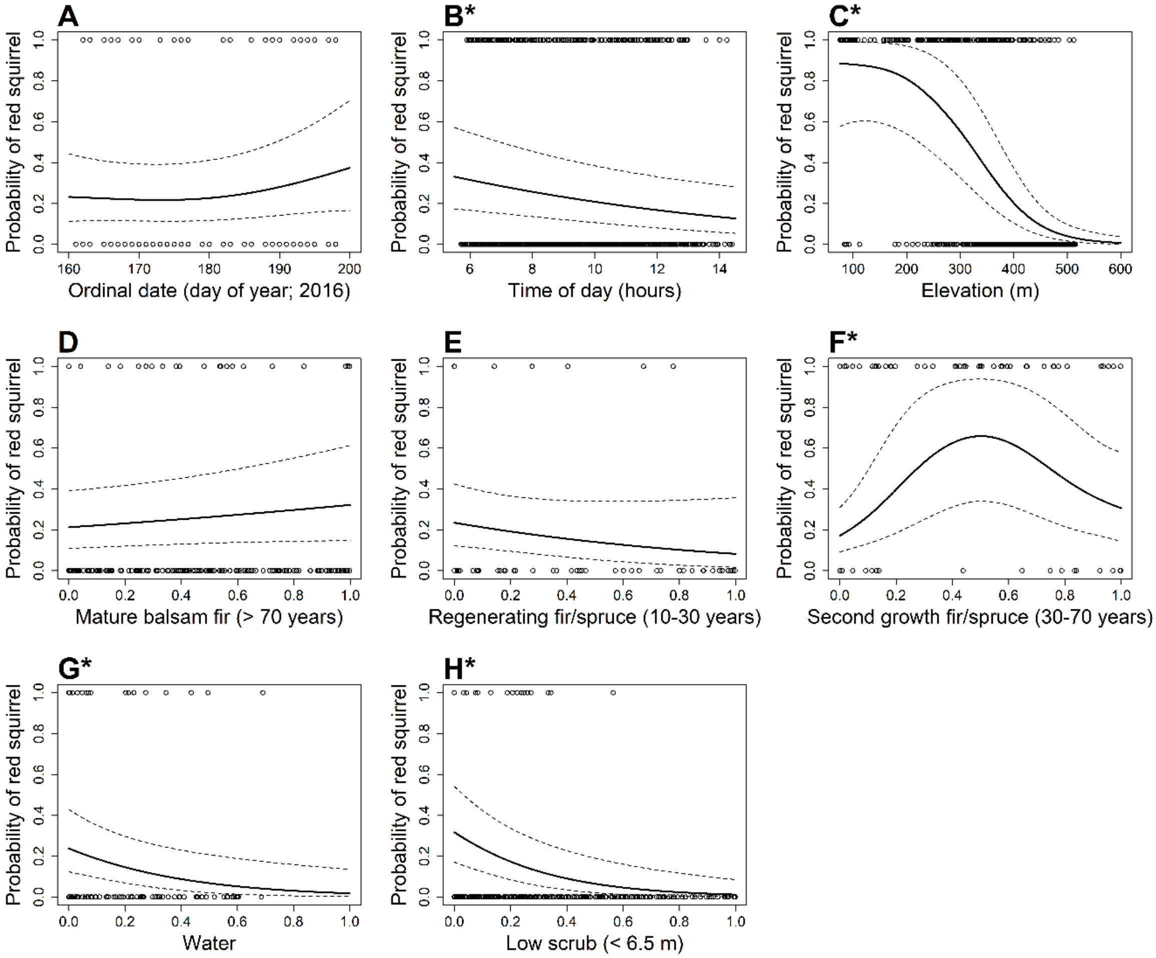

Figure 2-3: Predicted probabilities of red squirrel (*Tamiasciurus hudsonicus*) presence in the Main River and upper Humber River watersheds in western Newfoundland in 2016 for factors retained from the global model after stepwise model reduction. Each variable plot was generated from predicted fitted values while holding all other variables constant at their means. Dotted lines indicate 95% confidence intervals and individual observations (n = 844) are shown as presences and absences (1 or 0). Significant variables are indicated with an *.

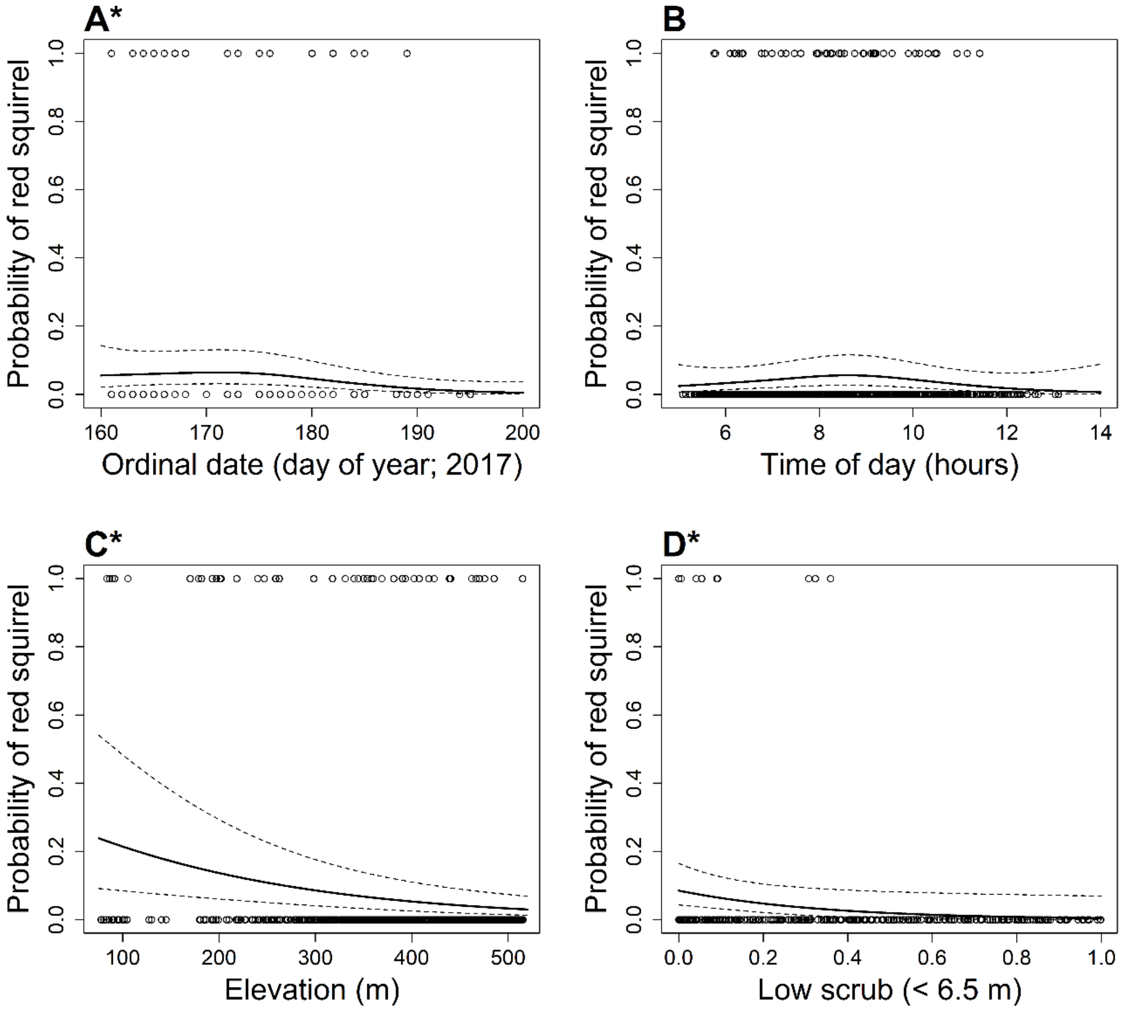

Figure 2-4: Predicted probabilities of red squirrel (*Tamiasciurus hudsonicus*) presence in the Main River and upper Humber River watersheds in western Newfoundland in 2017 for factors retained from the global model after stepwise model reduction. Each variable plot was generated from predicted fitted values while holding all other variables constant at their means. Dotted lines indicate 95% confidence intervals, and individual observations (n = 823) are shown as presences and absences (1 or 0). Significant variables are indicated with an *.

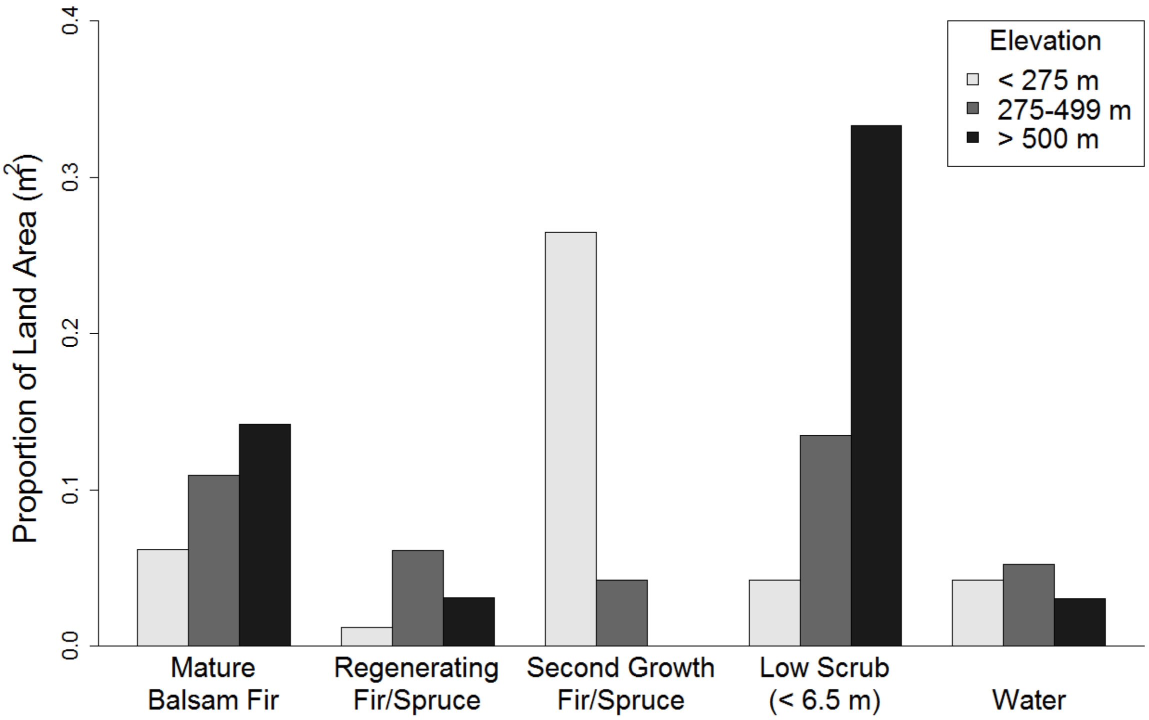

Figure 2-5: Proportion of total land within our 257 km^2 study area accounted for by land cover classes included in our best models predicting red squirrel (*Tamiasciurus hudsonicus*) occurrence in the Main River and upper Humber River watersheds in western Newfoundland in 2016 and 2017. Elevations <275 m indicate areas where red squirrels were abundant, 275-499 m where red squirrels were present but uncommon, and >500 m where red squirrels were absent.

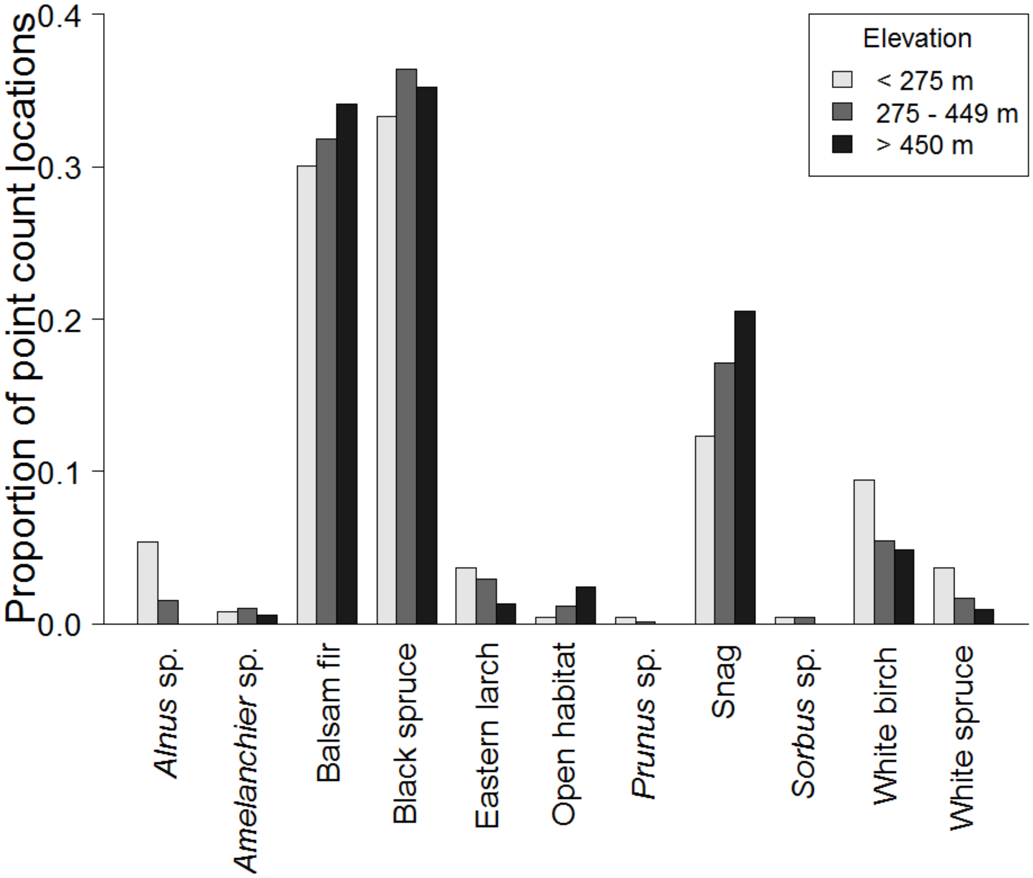

Figure 2-6: Proportion of point count locations containing individual tree or shrub species within a 2 m × 22.6 m transect running North-South and centered on the survey point (total 45.2 m^2) at elevations <275 m, 275-450 m, and >450 m in the Main River and upper Humber River watersheds in 2017. Note the disappearance of *Alnus* sp. (alder), *Sorbus* sp. (mountain ash), and *Prunus* sp. (cherry) as elevation increased.

3 Apparent range contraction by Gray-cheeked Thrushes (*Catharus minimus mimimus*) in response to introduced red squirrels (*Tamiasciurus hudsonicus*)

3.1 Co-authorship Statement

This chapter is intended for submission to a peer-reviewed publication with my graduate supervisors (Ian Warkentin and Darroch Whitaker) as co-authors, and so I use plural rather than singular first-person pronouns throughout. However, the work found in this chapter is my own. Conception of the research idea was by Darroch Whitaker and Ian Warkentin, who provided advice and suggestions throughout the research. I planned and executed the data collection with their assistance. I conducted data analysis independently, with input and advice from Darroch Whitaker, Ian Warkentin, Dan Kehler, and Dave Schneider. I prepared the manuscript, incorporating edits and suggestions from Ian Warkentin and Darroch Whitaker, and Anne Storey (committee member).

3.2 Abstract

Introduced species are well known for their disruption of ecosystems and impacts on endemic species. Red squirrels (*Tamiasciurus hudsonicus*) were introduced to the island of Newfoundland during the 1960s and have been hypothesized as a cause of the precipitous decline of the Newfoundland Gray-cheeked Thrush (*Catharus minimus minimus*). We undertook a series of 1960 point count surveys over two years (2016 and 2017) in the Long Range Mountains of western Newfoundland in order to compare the contemporary distributions of red squirrels and Gray-cheeked Thrushes across an elevation gradient. We also evaluated local and landscape scale habitat use of thrushes, with particular attention to harvested forest stands, using landcover data from a provincial forest resource inventory. Red squirrels and Gray-cheeked Thrushes were strongly segregated across the elevation gradient, with thrushes occupying a restricted range at higher elevations (~340-600 m), and red squirrels being abundant below 275 m and reaching an upper range limit at ~500 m. Gray-cheeked Thrushes were positively associated with harvested forest, conifer forest, and tall scrub at the local scale, and negatively associated with tall scrub, regenerating forest, and second growth forest at the landscape scale. Both clearcuts and modified strip cuts were selected by thrushes. Breeding Bird Survey data indicate that Gray-cheeked Thrushes were historically abundant down to sea level, so our finding of strong elevational segregation adds to the growing body of evidence that red squirrels played an important role in the decline and range contraction of the Gray-cheeked Thrush on Newfoundland.

Keywords: species introduction, invasive species, Newfoundland, elevation, habitat, boreal, forest management

3.3 Introduction

Threats such as habitat loss, climate change, harvesting, and alien species introductions are affecting endemic populations of species all over the world, often resulting in geographic range and niche reductions (Scheele et al. 2017) or even extirpation or extinction (Long 2003; Sodhi et al. 2008; Sánchez-Bayo and Wyckhuys 2019). Introduced mammalian predators have been implicated in 58% of avian, mammalian, and reptilian species extinctions, and have played a role in declines of hundreds of other species (Doherty et al. 2016). Ninety percent of bird species that are reported as having been imperilled or extirpated by the introduction of a mammalian predator are island endemics (Doherty et al. 2016), though it is not clear that insular bird populations are at a higher risk of extinction from introduced predatory mammals than mainland bird populations (see Blackburn et al. 2004; Medina et al. 2011; Doherty et al. 2016). Regardless, island endemics typically exist as relatively small, isolated populations that have evolved in less diverse ecosystems, and so may have reduced competitive and anti-predator abilities in the face of introduced mammals (Courchamp et al. 2003, Banks and Dickman 2007; Russell and Kaiser-Bunbury 2019). While this may lead to range-wide declines of endemic populations, impacts may also be expressed in the form of reduced ecological niches, where an endemic species becomes restricted to refugial habitats to which invaders are poorly suited (Scheele et al. 2017).

While introduced species can affect naturally occurring communities and the associated ecosystem processes, native wildlife populations may also suffer additive effects from other stressors such as habitat degradation or loss, and climate change. For example, boreal forests are often subject to forest harvesting, silviculture (e.g., thinning or planting), suppression of natural disturbance agents such as wildfire and outbreaks of defoliating insects, and the construction of resource roads (Burton et al. 2003). When managed properly, timber harvesting may mimic natural disturbances such as fire, windthrow, or insect outbreaks, and result in a mosaic of stands at various stages of succession within a larger forested area (Bergeron et al. 2002). However, if sufficient attention is not given to maintaining natural age composition and structure of forest landscapes, many old growth or disturbance specialist species may lack the attendant landscape elements or mosaic necessary to survive and thrive (Niemelä 1999; Thompson et al. 1999; Bergeron et al. 2002). At the same time, climate change may be leading to range shifts into more northerly ecosystems or higher elevations for many species (Lehikoinen and Virkkala 2016; Kirchman and Van Keuren 2017; Whitaker 2017; Rushing et al. 2020). These and other threats can cause synergistic negative effects on a species' ability to persist in an area, and may exacerbate the stresses that introduced species place on endemic populations.

The island of Newfoundland, Canada is the largest island in the circumpolar boreal biome. Due to the contemporary oceanic barrier and the existence of an Atlantic shelf refugium during the Pleistocene, the island supports numerous endemic subspecies of more widely distributed boreal species (Dodds 1983; Montevecchi and Tuck 1987; Pielou 1991; Fitzgerald et al. 2019). For example, the Newfoundland Gray-cheeked Thrush (*Catharus minimus mimimus*), genetically distinct from the Northern Gray-cheeked Thrush (*C. m. alicea*) which occurs across the rest of the species' continental distribution, was historically abundant throughout much of the island and occurred in suitable habitat at all elevations (Lamberton 1976; SSAC 2010; Fitzgerald et al. 2017, 2019). However, Breeding Bird Survey data suggest a decline of ~95% between 1975 and 2005, and the Newfoundland subspecies was listed provincially as threatened in 2015 (SSAC 2010). Since then, Whitaker et al. (2015) reported that a large residual population persists but is restricted to montane forests in western Newfoundland. This limited distribution was surprising given that during the 1970s and 1980s the species had been abundant at low elevations, and led to their hypothesis that the species had been restricted to higher elevations as a result of the introduction of red squirrels (*Tamiasciurus hudsonicus*) to the island (Whitaker et al. 2015). However, no co-located data were available at the time to make a rigorous comparison of the distributions of thrushes and squirrels.

Red squirrels were introduced to Newfoundland in 1963 and 1964 (Payne 1976; Dodds 1983) and, aided by a series of translocations, became widespread and pervasive by the mid-1980s (Whitaker 2015). Red squirrels are functional granivores but opportunistic omnivores (Steele 1998) and so have the potential to negatively impact bird populations on the island through both competition for food and predation on eggs and young (Willson et al. 2003; Benkman et al. 2009). Indeed, research has shown that red squirrels can have pervasive impacts that dramatically alter reproductive success and the composition of avian assemblages on islands and in isolated "insular" patches of continental forest (Martin and Joron 2003; Siepielski 2006). Predation of eggs and nestlings by red squirrels is known to cause near complete nesting failure in populations of the closely related Bicknell's Thrush (*Catharus bicknelli*; McFarland et al. 2008), and since their arrival, red squirrels have become the dominant nest predator on the island of Newfoundland (Lewis 2004).

Gray-cheeked Thrush are reported to use broadly similar habitat across the species range, but on Newfoundland most such data were collected before red squirrels became widespread, and habitat use may have been altered as thrushes adapted to this novel threat. Generally Gray-cheeked Thrushes are found in areas having dense regenerating stands of coniferous or deciduous saplings and shrubs, dense willow (*Salix spp.*) and alder

(*Alnus spp.*) thickets, or old growth coniferous forest having complex understories, though there are localized differences (Whitaker et al. 2020). Historically on the island of Newfoundland, Gray-cheeked Thrushes were less likely to be found in deciduous shrub thickets and instead were more likely to occur in coastal windswept coniferous scrub habitat (Marshall 2001) and old growth (> 80 years) balsam fir (*Abies balsamea*) forest, while avoiding second growth (40-80 years) stands (Thompson et al. 1999). Most recently, Whitaker et al. (2015) described habitat use by Gray-cheeked Thrushes at neighbourhood and landscape scales (respectively within 115 m and 1250 m radius areas) in populations above 300 m elevation in western Newfoundland. They found broad similarities with previous assessments of habitat requirements but also identified a large influence of elevation on the occurrence of Gray-cheeked Thrushes and a curvilinear relationship with old growth forest, peaking at intermediate amounts. Forest harvesting has been little studied in relation to the Gray-cheeked Thrush habitat use, but for the Bicknell's Thrush provides important regenerating habitat, particularly in 11-13 year old harvested stands in New Brunswick (Chisholm and Leonard 2008), and in stands 20 years post-harvest or older in Quebec (Aubry et al. 2018). Whitaker et al. (2015) found a general increase in Gray-cheeked Thrushes with amount of harvested forest, but the exact nature of the relationship was unclear. There has also been no study on the optimal harvesting method or age of harvested areas with respect to Gray-cheeked Thrush occurrence.

We evaluated Whitaker et al.'s (2015) hypothesis that introduced red squirrels may have excluded Gray-cheeked Thrushes from lower elevation habitats in western

Newfoundland. In a related study we assessed the distribution and habitat associations of red squirrels (McDermott et al. 2020; Chapter 2), and here we compare the distributions of squirrels and thrushes using co-located surveys across an elevation gradient. Due to the presumed predation pressure on eggs and young by squirrels, we predicted that red squirrels and Gray-cheeked Thrushes would show strong spatial segregation, with thrushes occupying a restricted range at higher elevations than squirrels. We also assessed habitat use by thrushes to better describe the contemporary pattern of habitat use at local and landscape scales and to evaluate the use of harvested stands by this refugial population of the thrushes. We predicted that forest harvesting would have a positive effect on Gray-cheeked Thrush occurrence, and that this relationship would be strongest for stands 11-13 years or > 20 years post-harvest, as this has been reported for Bicknell's Thrush (Chisholm and Leonard 2008; Aubry et al. 2018).

3.4 Materials and Methods

3.4.1 Study Location

We conducted our research across a 257 km^2 study area that spans an elevation gradient from 75 m to 608 m ASL in the upper Humber River and Main River watersheds (57° 16´ W, 49° 40´N) of the Long Range Mountains of western Newfoundland, Canada (Figure 3-1). The study area is dominated by wet balsam fir forests, and climatic conditions in the region limit the extent of natural disturbances such as large-scale fires or outbreaks of defoliating insects, particularly at higher elevations (Thompson et al. 2003; McCarthy and Weetman 2006; Arsenault et al. 2016). Locations below 450 m elevation and in valleys support mixed and single-species stands of productive forest composed primarily of balsam fir or black spruce (*Picea mariana*) within a matrix of bogs, barrens, and other natural openings (Damman 1983; McCarthy and Weetman 2006). Additional tree and shrub species include white birch (*Betula papyrifera*), tamarack (*Larix laricina*), trembling aspen (*Populus tremuloides*), pin cherry (*Prunus pensylvanica*), white spruce (*Picea glauca*), mountain ash (*Sorbus* sp.), alder (*Alnus* sp.), and serviceberry (*Amelanchier* sp.). At locations above 450 m elevation, factors such as increased wind exposure, deep and late snow cover, low nutrient availability, and saturated soils lead to an increasing prevalence of bogs, barrens, and non-productive scrub forest (Damman 1983). Between 1990 and 2004, 19.7% of the landscape in the surveyed area was logged in cutblocks ranging from 0.30 ha to 217.7 ha, with a mean size of 21.6 ± 31.8 ha. In addition, two ~100 ha experimental strip cuts were harvested during 2001 and 2003, and spanned 419 - 564 m elevation (see Whitaker et al. 2015). Forest clearing since that time has largely been limited to the creation of a 60 m-wide high voltage electricity transmission corridor during 2016 and 2017 that passes through the northern end of the study area. Introduced red squirrels likely colonized the region between ~1985 and 1990 (Whitaker 2015).

3.4.2 Data collection and variable creation

To assess the co-distribution of thrushes and squirrels throughout our study area, we conducted surveys from early June to mid-July in 2016 and 2017 across a grid of points spaced 500 m apart. During 2016 the grid encompassed 991 survey points; we then shifted the grid 250 m north and east during 2017 to enhance coverage of the study area, and sampled 969 points. When possible, we alternated surveys between low, medium, and high elevation portions of the study area on consecutive days. Solitary observers (four individuals during 2016, five individuals during 2017; one common to both years) each typically sampled a series of 5-12 adjacent points per day between 05:40 h and 14:30 h. We did not conduct surveys when high winds (> 5 Beaufort scale; 29 km/h), precipitation, and/or fog would have impaired visual or auditory detections of thrushes or squirrels.

During the visit to each point, we followed an 11-minute unlimited distance point count protocol. This included the following sequence of time blocks: an initial six minutes of silent listening; a two-minute broadcast of a Gray-cheeked Thrush singing and calling (same broadcast as used by Whitaker et al. 2015); one minute of silence; a one-minute broadcast of red squirrel vocalizations (taken from the Macaulay Library, Cornell Lab of Ornithology: catalogue numbers ML100916 and ML136185); and one final minute of silent observation. We set broadcast units (FoxPro model FX3 or Crossfire game callers; FoxPro Incorporated, Lewistown, PA 17044, USA) at a constant volume for all surveys; when measured 1 m from the speaker the average volume of vocalizations was 57.7 dB, with peak volumes of 82.6 dB, where the intention was to mimic natural sound production, and volumes were similar to Whitaker et al. (2015). During each of the time blocks within the 11-minute point count, we recorded each bird and red squirrel that was seen or heard.

We obtained land cover data from the Newfoundland and Labrador forest resource inventory Geographic Information System (GIS) database, which was developed from high resolution (sub 10 cm pixel) 3D aerial photography collected in 2007. Using ArcGIS 10.4.1 (ESRI 2002), we extracted this land cover data within 132 m and 1250 m of each survey point, which we interpret as representing local and landscape scale habitat for Gray-cheeked Thrushes, respectively. We assessed habitat needs at multiple scales, as passerines in the boreal forest use the land in different ways within local vs. landscape scales. Avian activities at the local or territory level are typically focused on nesting and territorial defence, while at the landscape scale they typically include foraging and extra-pair mate acquisition (sensu Mayr 1935; Leonard et al. 2008; Whitaker and Warkentin 2010). Gray-cheeked Thrushes have also been shown to select different landcover types between these two scales (see Whitaker et al. 2015). Breeding season space use has never been studied for Gray-cheeked Thrush, so our local scale (132 m radius or 5.5 ha) approximates the maximum female territory size and minimum male territory size of the Bicknell's Thrush (Collins 2007), while 1250 m (490.8 ha) reflects a landscape scale that has the potential to influence space use by individuals (Leonard et al. 2008; see also Whitaker et al. 2015). At each scale, we aggregated similar cover types into generalized categories to enhance the biological relevance of the land cover information and for greater consistency with Whitaker et al. (2015). We grouped conifer scrub into two height classes (< 6.5 m and > 6.5 m). We accounted for the time between collection of the aerial photography data and our field work by adding 10 years to the age class for each forest stand, and then grouped the 20-year age classes into three broader successional categories: regenerating stands 10-30 years old; second growth stands 30-90 years old; and mature stands 90+ years old. These three age classes represent broad forest successional stages having distinct, characteristic stand structure and biotic communities (Thompson et al. 2003; Table 3-1). Stands were also classified into forest cover types based on tree species composition, with classes consisting of ≥ 75% coniferous, ≥ 75%

deciduous, or mixed species (25-50% deciduous with coniferous). Composite successional stage/composition variables were then created by merging age class with forest cover type, resulting in nine composite variables at each scale (Table 3-1). Other land cover classes included open habitat (bogs, barrens, and other natural openings), and harvested forest (including both clearcuts and modified strip cuts; Table 3-1). All land cover variables were quantified as the proportion (0 to 1) of the area they accounted for within the 132 m or 1250 m local and landscape radius circles around each survey point. We also included length of shoreline within 132 m or 1250 m, which was measured as the total length in metres and was rescaled to fall within a range of 0 to 1 relative to the length of the largest observed shoreline value. We calculated a squirrel probability of occurrence value for each survey point using the *predict* function in R, based on a red squirrel habitat model we developed from our data (see Chapter 2). That habitat model was created through an analysis of red squirrel occurrence data for each year of the study, using stand age classes which are pertinent to squirrels measured within a 52.3 m radius of each survey point (a scale relevant to squirrel space use). The main positive predictors included the proportion of 30-70 year old fir/spruce (moderate cone production) and > 70 year old fir (good cone production), while negative predictors included elevation, water, coniferous scrub, and 10-30 year old fir/spruce (poor cone production). Finally, we obtained the elevation of each survey point using a digital elevation model from Natural Resources Canada's CanVec geospatial database (available under the Government of Canada's Open Government License [https://open.canada.ca/en]).

3.4.3 Data analyses

a) Comparisons between the occurrence of Gray-cheeked Thrushes and red squirrels

To broadly address our question regarding the effect of red squirrels on Gray-cheeked Thrushes, we first assessed whether the occurrence of each species was independent of one-another each year using a Chi-square test. We also used Kolmogorov-Smirnov tests to test for differences between the elevation distributions of Gray-cheeked Thrushes and red squirrels each year. This and all other statistical analyses were completed using R statistical software (version 3.3.1 and 3.6.2; R Core Team 2019).

b) Red squirrel and habitat influence on Gray-cheeked Thrush occurrence

Whitaker et al. (2015) reported that Gray-cheeked Thrushes were associated with higher elevations in our study area, and during our surveys thrushes were not detected below 317 m. Consequently, we truncated our dataset to include only points above this elevation ($n = 1670$ points) to lessen any confounding effect of correlations with elevation on our results. All candidate variables were tested for independence using a Spearman correlation matrix (i.e., $r < 0.6$ indicating independence; Dormann et al. 2013). Elevation and red squirrel probability of occurrence were highly correlated (Spearman's rho = -0.69, $p < 0.001$), which is not surprising given that elevation was included in the model we used to predict squirrel probability of occurrence (see Chapter 2). To resolve this, we eliminated elevation as a candidate variable and retained red squirrel probability of occurrence as it was of greater biological interest. Further, we assumed that elevation *per se* does not drive Gray-cheeked Thrush distribution since this species was previously common throughout Newfoundland at elevations down to sea level (Lamberton 1976;

SSAC 2010; Fitzgerald et al. 2017). Land cover variables were also eliminated if they were present at < 5% of survey points.

We created nine candidate linear models that included year, red squirrel probability of occurrence, and various combinations of forest successional stage and composition at the local and landscape scales as explanatory variables. These nine candidate models (Table 3-2) were developed to evaluate the importance of: 1) red squirrels, and forest composition at both the local and landscape scales, 2) red squirrels, and forest composition at the local scale and forest successional stage at the landscape scale, 3) red squirrels, and forest successional stage at the local scale and forest composition at the landscape scale, 4) red squirrels, and forest successional stage at both the local and landscape scales, 5) red squirrels, and composite successional stage/composition variables at the local scale and forest successional stage at the landscape scale, 6) red squirrels, and forest successional stage at the local scale and composite successional stage/composition variables at the landscape scale, 7) red squirrels, and forest composition at the local scale and composite successional stage/composition variables at the landscape scale, 8) red squirrels, and composite successional stage/composition variables at the local scale and forest composition at the landscape scale, and 9) red squirrels, and composite successional stage/composition variables at both the local and landscape scales.

Before fitting our candidate models, we first fit each land cover variable in a univariate Generalized Additive Model (GAM) using the function “gam” (R package mgcv version 1.8-33; Wood 2011) with occurrence of thrushes as the response variable.

This was done to assess the likely nature (shape) of the relationship between thrush occurrence and that variable. In these exploratory models the land cover variables were fit as smoothed nonparametric splines to allow for nonlinear relations, and we specified a clog-log link function, which typically performs better when the ratio of presence to absence is not approximately equal (Zuur et al. 2009). Land cover variables which appeared to be non-linear were generally parabolic, and so were also given a second order polynomial term in each of the nine candidate models where they were specified. Within each candidate model only one variable was included from any pair of correlated variables (Booth et al. 1994).

We then fit each of our nine candidate models using a Generalized Linear Model (GLM) having a binomial error distribution, a clog-log link function, and Gray-cheeked Thrush presence/absence as the response variable using the function “glm” (R package lme4 version 1.1-26; Bates et al. 2015). We then simplified each of these nine models through manual backwards step-wise selection to eliminate unimportant variables. At each step, the explanatory variable having the lowest explanatory power was assessed, and if removing it yielded an improvement in model fit ($p < 0.05$ or a reduction in Akaike’s Information Criterion adjusted for small sample sizes [ΔAICc] > 2), then it was dropped from the model. Once all unimportant variables had been eliminated the resulting nine best models were compared using AICc (R package MuMIn version 1.43.15; Bartoń 2020) to decide which of the nine combinations of red squirrel probability of occurrence, successional or compositional aspects of the forests, and other land cover variables, had the most explanatory power. The model having the lowest AICc was assumed to be the most parsimonious model explaining the distribution of Gray-cheeked Thrushes, and any other models having a ΔAICc < 2 were considered competing models (Burnham and Anderson 2002; Symonds and Mousalli 2011).

c) Silviculture analyses: Age and proportion of harvest forest

We conducted a separate analysis to assess relationships between Gray-cheeked Thrush occurrence and the age and proportion of harvested forest within a 132 m radius circle. For this analysis, we retained all points at elevations above 317 m which had a cutblock present within 132 m (n = 664). Age (years since harvesting) was calculated for each of these cutblocks based on the year (2016 or 2017) when we visited that survey point. Where multiple cutblocks of different ages were present within 132 m, we took a weighted average of the ages of harvested stands to calculate a representative cut age for the point. This occurred at 67 of 664 points, and most (72%) of these had cuts that were only one or two years apart in age. Proportion of harvested forest within a 132 m radius and age of cutblocks were fit as continuous variables. We created five candidate GLMs (R package lme4 version 1.1-26; Bates et al. 2015) having all possible univariate, additive and multiplicative combinations of cutblock age and proportion harvested, along with a null model containing no explanatory variables. Models were fit using a binomial error distribution and a clog-log link. Using MuMIn (R package MuMIn version 1.43.15; Bartoń 2020), we ranked the models based on AICc, to identify the most parsimonious model, and considered all models having a ΔAICc < 2 to be competing models (Burnham and Anderson 2002; Symonds and Mousalli 2011).

d) Silviculture analyses: Harvesting method

We assessed the importance of harvesting method (clear cut or modified [strip] cut) on Gray-cheeked Thrush occurrence. Modified cuts were present only between 419 and 564 m elevation (1039 points), so we restricted the comparison to points in this elevation range. We fit four GAMs (R package mgcv version 1.8-33; Wood 2011) including a null model and all additive combinations of the proportions of clear cut and modified cut within a 132 m radius circle around each point. Models were fit using binomial error distributions and clog-log link functions, and continuous variables were fit as splined, non-parametric terms. “k” values of each term were specified *a posteriori* as instructed by Wood (2017). Models were then compared using AICc (R package MuMIn version 1.43.15; Bartoń 2009), where the model having the lowest AICc value was considered the best model and any models having ΔAICc < 2 were considered as competing models (Burnham and Anderson 2002; Symonds and Mousalli 2011).

3.5 Results

In total, we collected single visit data over two years at 1960 survey points. During 2016 we saw or heard a total of 142 Gray-cheeked Thrushes at 117 of the 991 survey points (11.8% of points), while in 2017 we detected a total of 123 Gray-cheeked Thrushes at 100 out of 969 survey points (10.3% of points). During 2016, we saw or heard 241 red squirrels at a total of 184 point-count locations (18.6% of point counts), whereas during 2017, only 47 red squirrels were detected at 46 locations (4.7% of point counts). In 2016 no Gray-cheeked Thrushes were observed at elevations below 340 m (representing 18.5% of points), while in 2017 only one thrush was observed below 317 m (representing 14.9% of points). The proportion of survey points within 50-m elevation increments where thrushes were observed steadily increased above these elevations and peaked at 525-575 m, where thrushes were detected at 29% and 22% of points during 2016 and 2017, respectively (Figure 3-2). In 2016 we were 13 times more likely to observe a thrush at points where squirrels were not seen compared to those where squirrels were seen ($\chi^2 = 23.69$, $p < 0.001$), while in 2017 after a large drop in squirrel occurrences (see Chapter 2), we were only 1.7 times more likely to see a thrush at points without squirrels than with ($\chi^2 = 0.02$, $p = 0.902$). Although the elevation distribution of squirrels and thrushes overlapped from 340-515 m in 2016 and 317-513 m in 2017, the distributions of red squirrels and Gray-cheeked Thrushes were significantly different in both years (2016: $D = 0.81$, $p < 0.001$; 2017: $D = 0.68$, $p < 0.001$; Figure 3-2). The two species were only detected at the same points on six occasions across the two years: two in 2016 and four in 2017. These sites of co-occurrence fell between 370 - 470 m elevation, near the lower elevation limit of thrushes and the upper limit of squirrels. For more detailed information on red squirrel distribution and abundance in our study area, see Chapter 2.

Each of the nine best Gray-cheeked Thrush occurrence models retained red squirrel probability of occurrence as a predictor, along with a suite of land cover variables at the local and landscape scales (see Table 3-3 for model summaries). When we ranked these simplified models according to AICc, Model 2 performed better than the rest (Table 3-4 and Figure 3-3). This best model indicated that year was important, with lower thrush occurrence in 2017 than 2016. Red squirrel probability of occurrence had a strong negative association with Gray-cheeked Thrush occurrence, matching our observations of the relative distribution of thrushes and squirrels along the elevation gradient and infrequent co-occurrence at point count locations. Predicted probability of thrush occurrence fell to zero when the probability of red squirrel occurrence exceeded 40% (Figure 3-3A). Proportion of tall scrub was retained at the local scale in the highest-ranked model, having a weak positive relationship with thrush occurrence (Figure 3-3B). At the local scale Gray-cheeked Thrush presence was positively related to the proportion of harvested forest (Figure 3-3C). Shoreline length had a quadratic relationship with predicted thrush occurrence at the local scale, peaking at the local scale when ~ 495 m of shoreline was present within 132 m (Figure 3-3D). At the local scale, Gray-cheeked Thrush presence was also positively related to two terms that quantified forest composition rather than successional stage: (1) thrush presence was positively associated with proportion of coniferous forest (Figure 3-3E); and (2) predicted thrush presence increased with up to 30% cover of mixed forest, but was weakly negatively associated with higher proportions of mixed forest (Figure 3-3F). At the landscape scale thrush presence was negatively associated with tall scrub, regenerating forest, and second growth forest (Figure 3-3G-I).

With respect to the importance of forest harvesting at survey points > 317 m elevation that contained a cutblock (n = 664), an additive model including both cutblock age and proportion of harvested forest was more informative than univariate models that included only cutblock age or proportion of harvested forest, or a model that included an interaction between the two (Table 3-5). The multiplicative model was within 2 AICc of the best model but had a nearly identical log likelihood and was more complex, so the interaction between cutblock age and proportion of harvested forest is likely uninformative (Leroux 2019). In the best model, proportion of harvested forest was positively associated with Gray-cheeked Thrush occurrence, as was seen in the more general habitat analysis (Figure 3-4B). Gray-cheeked Thrush occurrence was also highest in 12 year-old cutblocks (the youngest age in our study area), and decreased steadily with increasing cutblock age (Figure 3-4A). However, cutblocks ≥ 19 years old were only present below 428 m, an elevation range where thrushes were less common (Figure 3-4C), raising the concern that the observed negative relation between cutblock age and thrush occurrence was an artefact of this non-random distribution of older cutblocks. To explore this possibility, we carried out a *post hoc* analysis using our best model but in which we truncated the range of age of cuts to 12 to 18 years-old. This indicated that thrush occurrence was not related to age for 12-18 year-old cutblocks (Figure 3-4D).

For the harvesting method analysis, which was restricted to elevations between 419 and 564 m, the model including additive effects of both clearcuts and modified strip cuts had the most power to explain Gray-cheeked Thrush occurrence, compared to the null and univariate models (Table 3-6). Occurrence of thrushes was positively influenced by the amount of both clearcuts and modified (strip) cuts in a linear manner (Figure 3-5).

3.6 Discussion

Our findings are consistent with the hypothesis that introduced red squirrels may be a stressor constraining the contemporary distribution of Gray-cheeked Thrushes on the island of Newfoundland. Squirrels appear to now limit these thrushes to higher elevation areas of the Long Range Mountains where squirrels have not yet colonized, likely due to ecological limits on their distribution (see Chapter 2). This creates nearly allopatric distributions of the two species, with a zone of overlap at intermediate elevations in which both species are rare. Although we have no historical data on the distribution of thrushes in our study area prior to the arrival of squirrels, Breeding Bird Survey data and other historical reports indicate that Gray-cheeked thrushes were common at low elevations (i.e., below 400 m ASL) throughout Newfoundland until the 1980s (Lamberton 1976; Marshall 2001; SSAC 2010). Historical survey data for higher elevation areas on the island of Newfoundland are limited, but Lamberton (1976) reported that they were abundant in the highlands of the Long Range Mountains in Gros Morne National Park, just ~15 km from our study area, and this is consistent with their occurrence in high elevation habitats across the southern portion of the species' range (Whitaker et al. 2020).

Other aspects of red squirrel population ecology may also have important consequences for Gray-cheeked Thrushes. We found no difference between years in the elevation range distribution of squirrels but did observe a four-fold change in squirrel abundance between 2016 and 2017. This is consistent with squirrel population dynamics elsewhere and is largely driven by annual variation in masting of conifer trees (Chapter 2). Red squirrels are known to negatively impact songbird nesting success throughout their range (e.g., Darveau et al. 1997; Martin and Joron 2003; Mahon and Martin 2006), and are the most important nest predator on Newfoundland, especially of ground or low-lying nests (Lewis 2004). Consequently, their substantial annual population fluctuations (Wheatley et al. 2002; Martin and Joron 2003; Boutin et al. 2006) mean that the predation pressure and potential impact that they have on Gray-cheeked Thrushes and other songbirds could vary substantially from year-to-year. In agreement with this, the drop in Gray-cheeked Thrush detection rate that we observed in 2017 may have reflected poor recruitment during 2016, when we recorded higher red squirrel populations. Similar population fluctuations caused by cyclical fluctuations in red squirrel abundance and nest predation have been reported in Bicknell's Thrushes (McFarland et al. 2008; Hill et al. 2019), Brown Creepers (*Certhia americana*; Poulin et al. 2010), and American Redstarts (*Setophaga ruticilla*; Sherry et al. 2015).

Our study examined correlations between species distributions but did not assess direct fitness consequences of squirrel presence on Gray-cheeked Thrushes. Therefore, this study does not provide direct evidence that red squirrels caused the collapse of the Newfoundland thrush population over the past four decades (SSAC 2010) or precipitated the restriction of thrushes to their contemporary montane range. However, our findings do add strong support to a growing body of evidence pointing to this conclusion. There is a close temporal correlation between the rapid colonization of Newfoundland by red squirrels during the 1970s and 1980s (Whitaker et al. 2015) and the collapse of the Gray-cheeked Thrush population in the 1980s (SSAC 2010). A lack of monitoring data between the mid-1980s when the thrushes were still common in many areas, and the early 2000s by which time they had disappeared from much of the island (SSAC 2010), makes it difficult to relate local declines to the precise timing of squirrel colonization. However, the first squirrel was reported in Gros Morne National Park in 1975 (Minty 1976), when Gray-cheeked Thrushes were still extremely common in lowland regions of the park (Lamberton 1976). Indeed, in 1974 and 1975 an average of 24 thrushes was counted along a 50-stop Breeding Bird Survey (BBS) route in the park (Route 57021; SSAC 2010). However average counts on that BBS route dropped by 68% from 1981-1985 (mean = 7.75 thrushes per year) and the thrushes had virtually disappeared from park lowlands by 1992 (Jacques Whitford Environment 1993). An average of just one thrush per year was detected along this BBS route from 1992-1997 and no Gray-cheeked thrushes have been detected since 1997 (SSAC 2010). Gray-cheeked Thrush nests are often on the ground or relatively low in trees (< 2 m; Whitaker et al. 2020), which could leave them at high risk of squirrel depredation (Lewis 2004). Another recent study for which surveys were conducted widely across Newfoundland indicated that Gray-cheeked Thrushes were greater than three times more likely to be detected at sites where no red squirrel was detected (Fitzgerald et al. 2017). Additionally, Gray-cheeked Thrushes are still apparently common at low elevations on some coastal islands in the Newfoundland archipelago that have not been colonized by red squirrels (Fitzgerald et al. 2017; Whitaker and Warkentin, unpublished data). The negative relationship between red squirrel probability of occurrence and Gray-cheeked Thrush detection that we found is strongly consistent with these other observations. The fact that low elevation populations disappeared while high elevation ones have remained abundant suggests that not all Gray-cheeked Thrushes on the island of Newfoundland were affected equally by the stressor(s) that caused the population to collapse. Certain populations of these thrushes could also have been impacted by changes in climate that have been seen in western Newfoundland, such as increased temperature and precipitation (Government of Canada historical data: https://climate.weather.gc.ca) which could vary altitudinally. However, the near allopatry between squirrels and thrushes provides evidence that squirrels were a contributor to the different fates of high and low elevation populations. Thus, there are multiple lines of evidence suggesting that red squirrels contributed to the rapid decline of the Gray-cheeked Thrush on Newfoundland.

While range restriction of Gray-cheeked Thrushes is clearly important, a second important finding is the use of managed forests by Gray-cheeked Thrushes. This pattern is reminiscent of the habitat associations of Bicknell's Thrush, which make use of regenerating stands (Chisholm and Leonard 2008). These findings and past research (Whitaker et al. 2015) suggest that the levels of timber harvest and silvicultural techniques used on Newfoundland may benefit Gray-cheeked Thrushes. However, while increased harvesting at the local scale led to greater likelihood of Gray-cheeked Thrush occurrence, at the landscape scale habitat that was regenerating from either harvesting or natural disturbances did have negative influences on thrush occurrence. This suggests that there is a limit in the extent to which harvesting across the broader landscape benefits Gray-cheeked Thrushes. A closer look at harvested forest suggested that Gray-cheeked Thrushes were more common in larger, 12-year-old regenerating cutblocks that were either clearcut or produced through modified strip cuts, but that the value of harvested areas declined linearly with age. However, this latter pattern may have been skewed by the non-random distribution of cutblock ages across our study area. The majority of harvested areas $\geq$ 19 years old occurred below 428 m elevation where thrushes were generally uncommon, possibly due to the presence of squirrels. Younger cuts (12-18 years old) spanned a broader elevation range and were common in higher elevation areas, where thrushes were also more common and squirrels were rare or absent. Because of this, we ran a post-hoc test on a truncated dataset that only included 12-18 year-old cuts to assess whether there was support for the linear decline in use of cuts with age, as suggested in our initial analysis. This indicated that cut age was unimportant in the best model, suggesting that cuts ranging in age from 12-18 years post-harvest were equally important to the thrushes. Further study is needed to assess the value of younger (< 12 years) and older (> 18 years) cuts for Gray-cheeked Thrush.

Based on previous findings of Gray-cheeked Thrush habitat use (Lamberton 1976; Marshall 2001; Whitaker et al. 2015; Fitzgerald et al. 2017), we would have expected to find a strong positive relationship with coniferous scrub. As with Whitaker et al. (2015), we found a positive though weaker association between thrush occurrence and the amount of tall scrub at the local scale. That study also reported that thrushes were most common in areas having intermediate amounts of scrub at the landscape scale, whereas we found that thrush occurrence was negatively associated with tall scrub at this scale. Thus, while findings are inconsistent regarding landscapes which have low and intermediate amounts of tall conifer scrub, both studies suggest that landscapes dominated by this habitat type are poorly suited for Gray-cheeked Thrushes. A possible explanation for these findings is that, for this reclusive species, tall conifer scrub provides a safe location to nest and display because of the tight, dense weave of branches, but at the landscape scale the thrushes select different habitats for foraging or other needs. On the other hand, coniferous scrub is not a suitable habitat for red squirrels (Chapter 2). Previous assessments of habitat use also found Gray-cheeked Thrushes solely in old growth forest (Thompson et al. 1999) or using moderate amounts of old growth forest (Whitaker et al.

2015). From this, we would have expected a strong positive or curvilinear relationship with old-growth forest. However, old-growth forest was not included in our best model. As our results are inconclusive, and counter previous knowledge of the species, we recommend further study to clarify Gray-cheeked Thrush's use of old-growth forest.

Other habitat associations matched those of Whitaker et al. (2015) for the same study area and may reflect foraging activity. Gray-cheeked Thrushes feed primarily on insects like beetles (Carabidae), ants (Formicidae), and spiders (Aranae), as well as fruit particularly during migration (Whitaker et al. 2020). Tall conifer scrub generally grows in low productivity areas, which supports few fruiting shrubs and trees and may not provide a very productive community of arthropods to feed on. As such, it is perhaps not surprising to find that Gray-cheeked Thrushes were less common in landscapes dominated by this habitat. The negative relationship with increasing proportion of regenerating forest and second growth forest at the landscape scale has also been seen in work by Thompson et al. (1999) and Whitaker et al. (2015). This may indicate that a landscape containing a mosaic of smaller tracts of many forest ages is preferred, especially because a rich and abundant selection of arthropods would likely be associated with all successional stages of productive forest (Niemela et al. 1996; Buddle et al. 2006; Blanchet et al. 2013). Shoreline length appeared important in predicting thrush occurrence at the local scale and it was also found to be important by Whitaker et al. (2015) at the landscape scale. It is not entirely clear why shoreline length is important, as this thrush species is not widely known to be associated with riparian or aquatic habitats, other than a brief mention of this in British Columbia (Di Corrado 2015). However, riparian zones, like many ecotones, may be relatively productive and present more diverse foraging opportunities; they have been shown to support higher abundance, richness, and diversity of birds than non-riparian areas (LaRue et al. 1995).

Differences in habitat selection that we saw at the local and landscape scales may be explained by differences in the behaviours that Gray-cheeked Thrushes engage in at a particular spatial scale. Avian activities at the landscape scale typically include foraging and extra-pair mate acquisition, while activity at the local or territory level activity is typically focused on nesting and territorial defence (sensu Mayr 1935; Leonard et al. 2008; Whitaker and Warkentin 2010). However, little is known about the breeding system of the Gray-cheeked Thrush, though two closely related *Catharus* thrushes show evidence of polygynandry (Bicknell's Thrush, Goetz et al. 2003; and Veery [*C. fuscescens*], Halley et al. 2016). If Gray-cheeked Thrushes also employ a polygynandrous mating system, their use of space in relation to extra-pair copulations and territory or nest defense may differ from that of most Neotropical migrants. This could result in different sizes or overlap of territories as a result of conspecific aggregations such as lekking, loose colonies, or territory clusters. There have been various reports of larger numbers of Gray-cheeked Thrushes being present within a small area, which could provide support for this idea (Marshall 2001; Whitaker et al. 2020). It could be possible that the Gray-cheeked Thrush selects habitat at the landscape scale for food availability, and at the local scale for both food availability and, additionally, safety from predation.

Since we found an increase in probability of thrush occurrence with increasing cover of coniferous forest, and with mixed forest up to ~30% cover at the local scale, it seems plausible that thrushes might use hierarchical top-down habitat selection (Kristan III 2006). This would involve first selecting for a matrix of smaller tracts of different habitats at a landscape scale, and then for continuous forest habitat like coniferous or mixed forest at a local scale. Alternatively, we may only see positive landcover associations at the local scale because landcover at the landscape scale is likely to be similar no matter where they settle, since the landcover in these mountains is a naturally complex matrix. It is also possible that our 1250 m radius landscape scale could overestimate the space requirements of a Gray-cheeked Thrush. Two studies on spatial use by Bicknell's Thrush (Aubry et al. 2011; Wilson 2020) found that their average home range size was 40 ha, which would correspond with a circle of radius 355 m (Wilson 2020); much smaller than the scale which we used.

Findings of this study add to the body of evidence suggesting that the introduction of red squirrels to Newfoundland was a key stressor that led to the near extirpation of the Newfoundland Gray-cheeked Thrush population at lower elevations. Higher elevation areas apparently now act as a refugia allowing Gray-cheeked Thrushes to persist free of the threat of red squirrels. With this is mind, we believe that any description of Gray-cheeked Thrush habitat in western Newfoundland should be changed to include "high-elevation". Terrain exceeding ~400 m ASL, above which Gray-cheeked Thrush seem to regularly occur now, is restricted to western Newfoundland and represents < 14% of the island (~15 595 km^2). Much of this is also covered by arctic/alpine barrens where Gray-cheeked Thrushes do not occupy, leaving very little area for the thrushes to persist. Within these montane forests of western Newfoundland, regenerating clearcuts and strip cuts that are not affected by browsing of hyper-abundant moose support high numbers of thrushes, possibly because they offer a preferred combination of dense cover and high productivity. If future circumstances arise which allow squirrels to colonize these montane forests, Gray-cheeked Thrush populations could be placed at further risk. This could happen as natural regeneration after forest harvesting creates tracts of 30-70 year-old stands, which are favoured by red squirrels in masting years (Chapter 2), but which are currently rare at higher elevations (McCarthy and Wheetman 2006). In much the same way, if climate change allows large scale disturbances such as insect outbreaks which are currently limited by harsh climate (McCarthy and Wheetman 2006), to occur, we could see a short-term benefit to these montane thrushes, but with a longer-term impact if post-disturbance forests regenerate into stands of an age that red squirrels can expand into and occupy.

3.7 References

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3.8 Tables and Figures

Table 3-1: Variables included in models to explain presence of Gray-cheeked Thrush in the upper Humber and Main River watersheds, Newfoundland in 2016 and 2017. All are present at the local (132 m) and landscape (1250 m) scale, except mt3, which is only present at the landscape scale.

Variable	Code	Description
Probability of red squirrel	predictresq	Predicted probability of a red squirrel being present (range 0-1)
Year	year	Year of survey (2016 or 2017)
Low scrub	lowscrub	Coniferous scrub forest < 6.5 m tall
Tall scrub	tallscrub	Coniferous scrub forest > 6.5 m tall
Open	open	Bogs and barrens
Water	shoreline	Length of shoreline (m)
Harvested forest	harv	Forest harvested between 1990 and 2004
Conifer forest	conifer	Forest stands where ≥ 75% of trees are coniferous
Mixed forest	mix	Forest stands with 25-50% deciduous trees among the coniferous trees
Regenerating forest	regen	10-30 year old forest; very dense, overstocked stands with up to 40K stems/ha
Second growth forest	secgf	30-90 year old forest; second growth and mature stands having closed canopies and increasingly open understories as stands mature
Mature forest	oldgf	> 90 year old forest; mature stands having canopy gaps, large snags, and relatively complex and biodiverse understories
Regenerating conifer	ct1	Regenerating (10-30 years old) coniferous forest
Second growth conifer	ct2	Second growth (30-90 years old) coniferous forest
Mature conifer	ct3	Mature (90+ years old) coniferous forest
Regenerating mixed forest	mt1	Regenerating (10-30 years old) mixed forest
Mature mixed forest	mt3	Mature (90+ years old) mixed forest

Table 3-2: *A priori* habitat models showing composition, successional stage, and composite succession/composition variables used to describe the occurrence of Gray-cheeked Thrush in the upper Humber River and Main River watersheds in 2016 and 2017. All nine models also included year and predicted probability of red squirrel presence (see Chapter 2). See Table 3-1 for variable name descriptions.

Model	**Local scale (132 m)**				**Landscape scale (1250 m)**			
	Composition	**Successional stage**	**Successional stage/ Composition**	**Other**	**Composition**	**Successional stage**	**Successional stage/ Composition**	**Other**
1	conifer, mix			open, lowscrub, tallscrub, shoreline	conifer, mix			open, lowscrub, harv, shoreline
2	conifer, mix			open, lowscrub, tallscrub, shoreline, harv		regen, secgf, oldgf		open, lowscrub, tallscrub, shoreline
3		regen, secgf, oldgf		open, lowscrub, tallscrub, shoreline	conifer, mix			open, lowscrub, harv, shoreline
4		secgf		open, lowscrub, tallscrub, shoreline, harv		regen, secgf, oldgf		open, lowscrub, tallscrub, shoreline
5			ct2, mt1	open, lowscrub, tallscrub, shoreline, harv		regen, secgf, oldgf		open, lowscrub, tallscrub, shoreline
6		secgf		open, lowscrub, tallscrub, shoreline, harv			ct1, ct2, ct3, mt1, mt3	open, lowscrub, tallscrub, shoreline
7	conifer, mix			open, lowscrub, tallscrub, shoreline, harv			ct1, ct2, ct3, mt1, mt3	open, lowscrub, tallscrub, shoreline
8			ct1, ct2, ct3, mt1, mt2	open, lowscrub, tallscrub, shoreline	mix		ct1, ct2, ct3, mt1, mt3	open, lowscrub, tallscrub, shoreline, harv
9			ct2, mt1	open, lowscrub, tallscrub, shoreline, harv				open, lowscrub, tallscrub, shoreline

Table 3-3: Comparison of the best 9 land cover and red squirrel models explaining Gray-cheeked Thrush occurrence in 2016 and 2017 in the upper Humber River and Main River watersheds of western Newfoundland (n = 1670). Variables retained in each model have a coefficient under the model column, and otherwise were dropped from the model. See Table 3-1 for variable name descriptions.

			Model 2	**Model 7**	**Model 5**	**Model 4**	**Model 9**	**Model 6**	**Model 1**	**Model 8**	**Model 3**	**null**
		Intercept	-1.74	-2.47	-2.41	-2.41	-1.69	-1.71	-5.03	-5.35	-5.05	-1.9
		year	+	+	+	+	+	+	+	+	+	+
		predictresq	-5.43	-5.01	-4.15	-4.13	-5.89	-6	-6.21	-6.22	-6.14	
Local (132 m) Land Cover	**Composition**	conifer	0.9	0.8					0.89			
		mix	5.7	5.73					6.58			
		mix^2	-9.63	-9.88					-10.95			
	Successional stage	regen						1.63			1.56	
		secgf				2.34		2.6				
		oldgf						0.89			1.05	
	Successional stage/ Composition	ct1					1.68			1.67		
		ct2			2.51		2.46					
		ct3					0.81			1.01		
	Other	harv	1.25	1.24	1.47	1.47			1.15			
		shoreline	3.27	3.31	3.48	3.48	3.07	2.99	3.5	3.12	3.08	
		shoreline^2	-4.17	-4.22	-4.53	-4.54	-4.12	-3.95	-4.41	-4.15	-4.09	
		tallscrub	0.88				0.84	0.85				
Landscape (1250 m) Land Cover	**Composition**	conifer							7.08	7.5	6.8	
		conifer^2							-5.73	-6.2	-5.85	
		mix							-3.45		-3.73	
	Successional stage	regen	-1.46									
		secgf	-7.56		-9.3	-9.18						
		oldgf			1.46	1.46						
	Successional stage/ Composition	ct1		-1.37								
		ct2		-7.59			-9.09	-10.26				
		ct3		3.94								
		ct3^2		-4.78								
	Other	harv								3.6	3.94	
		harv^2								-7.09	-7.27	
		lowscrub			1.3	1.3			3.22	3.42	3.25	
		tallscrub	-6.32	-5.08	-5.04	-5.04	-5.77	-6.14				
Model Comparisons		df	13	14	11	11	11	11	13	12	13	2
		logLik	-565.71	-566.5	-572.5	-572.71	-574.23	-574.93	-576.2	-582.39	-581.98	-642.54
		AICc	1157.65	1161.25	1167.17	1167.57	1170.63	1172.02	1178.63	1188.96	1190.18	1289.09
		ΔAICc	0	3.6	9.52	9.92	12.98	14.37	20.98	31.32	32.54	131.44
		weight	0.85	0.14	0.01	0.01	0	0	0	0	0	0
		Pseudo-R^2	0.165	0.163	0.151	0.151	0.147	0.146	0.143	0.131	0.132	0.001

Table 3-4: Summary of parameter estimates for the best model explaining Gray-cheeked Thrush occurrence based on land cover and red squirrel predicted values in the upper Humber River and Main River watersheds of western Newfoundland in 2016 and 2017 (n = 1670; see Table 3-3). See Table 3-1 for variable name descriptions.

	Estimate	SE	z value	p value
Intercept	-1.74	0.24	-7.27	3.50E-13
predictresq	-5.43	1.49	-3.63	< 0.0001
tallscrub.132	0.88	0.58	1.53	0.126
harv.132	1.25	0.26	4.84	< 0.0001
shoreline.132	3.27	1.04	3.14	0.002
shoreline.132^2	-4.17	1.98	-2.11	0.035
conifer.132	0.90	0.27	3.32	0.001
mix.132	5.70	2.29	2.49	0.013
mix.132^2	-9.63	4.71	-2.04	0.041
tallscrub.1250	-6.32	1.42	-4.45	< 0.0001
regen.1250	-1.46	0.67	-2.17	0.030
secgf.1250	-7.56	2.67	-2.83	0.005
year2017	-0.33	0.14	-2.33	0.020

Table 3-5: Comparison of models assessing the influence of forest harvesting (cutblock age and proportion of harvested forest [size]) on Gray-cheeked Thrush occurrence in Main River and upper Humber River watersheds in western Newfoundland in 2016 and 2017 (n = 664).

Model	Intercept	age	size	age*size	df	logLik	AICc	ΔAICc	weight
age + size	-0.609	-0.108	0.966		3	-266.371	538.778	0	0.605
age*size	-1.199	-0.07	2.125	-0.074	4	-266.265	540.59	1.812	0.245
size	-2.275		0.874		2	-269.022	542.063	3.285	0.117
age	-0.414	-0.092			2	-270.601	545.22	6.442	0.024
null	-1.868				1	-272.573	547.152	8.374	0.009

Table 3-6: Comparison of Generalized Additive Models investigating the influence of proportion of modified cut (MC) and clearcut (CC) on Gray-cheeked Thrush occurrence in Main River and upper Humber River watersheds in western Newfoundland (n = 1039).

Model	Intercept	s(CC)	s(MC,k=3)	df	logLik	AICc	ΔAICc	weight
CC + MC	-1.71	+	+	3	-464.90	936.43	0	0.98
CC	-1.69	+		2	-470.10	944.21	7.78	0.02
MC	-1.68		+	2	-473.60	951.26	14.83	0.00
null	-1.67			0	-477.40	956.81	20.38	0.00

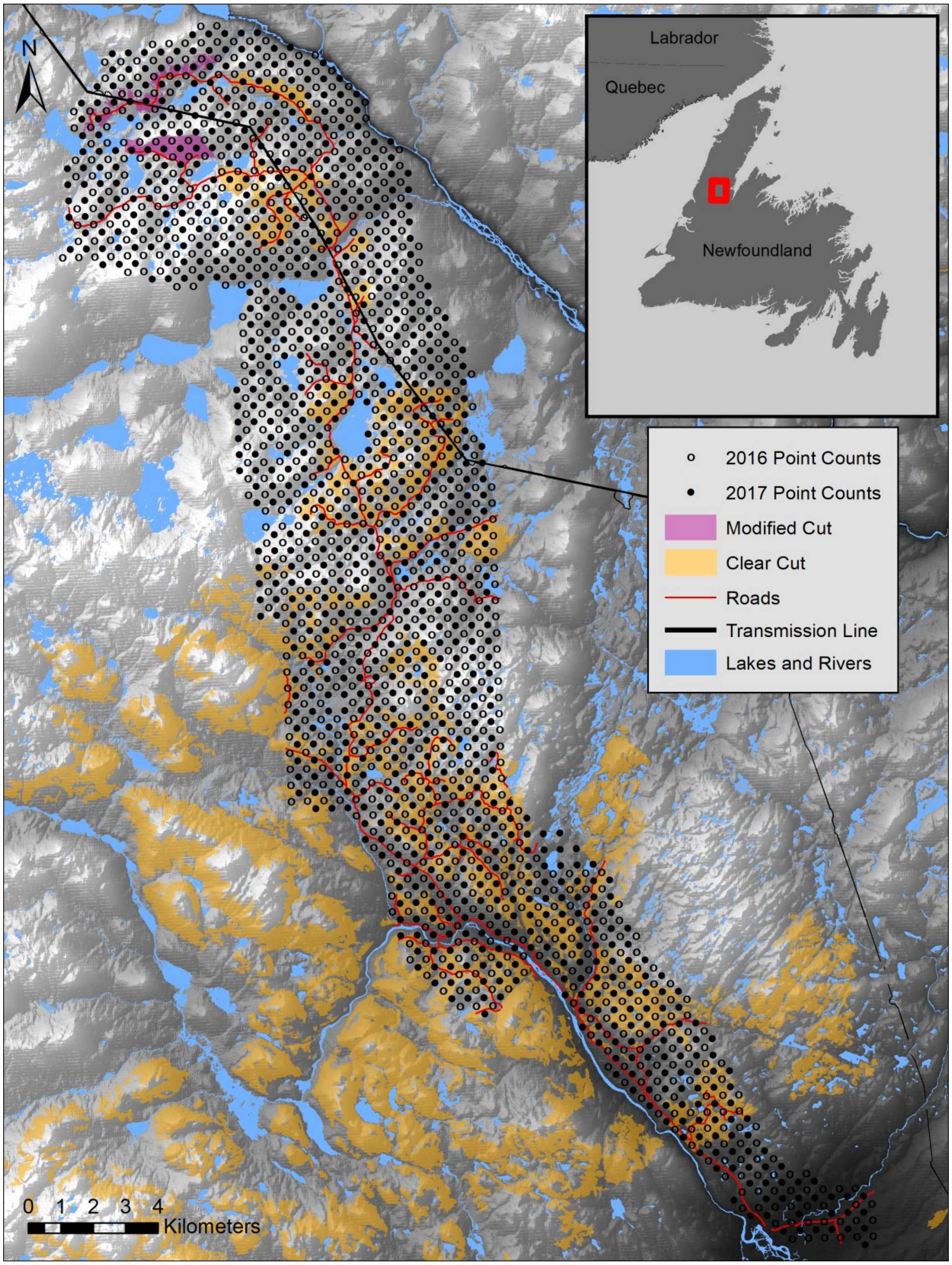

Figure 3-1: Study area in the upper Humber River and Main River watersheds of western Newfoundland. The location of the study area on Newfoundland is shown with the red rectangle on the inset map.

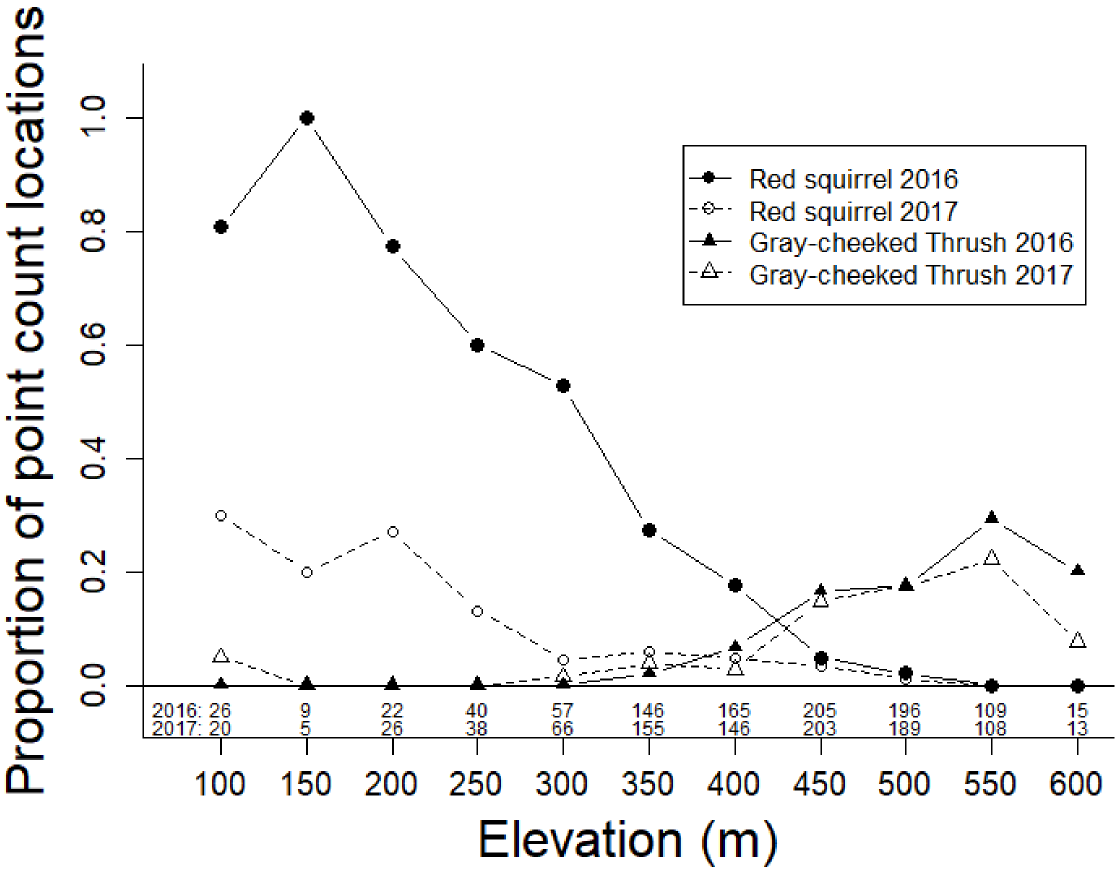

Figure 3-2: Elevation distribution of Gray-cheeked Thrushes and red squirrels in the Main River and upper Humber River watersheds in 2016 and 2017. Red squirrels were common at lower elevations, decreasing as elevation increased, whereas Gray-cheeked Thrushes were almost exclusively detected at elevations higher than 375 m. Data labels above x-axis indicate number of point count locations (total n = 1960) in each elevation category.

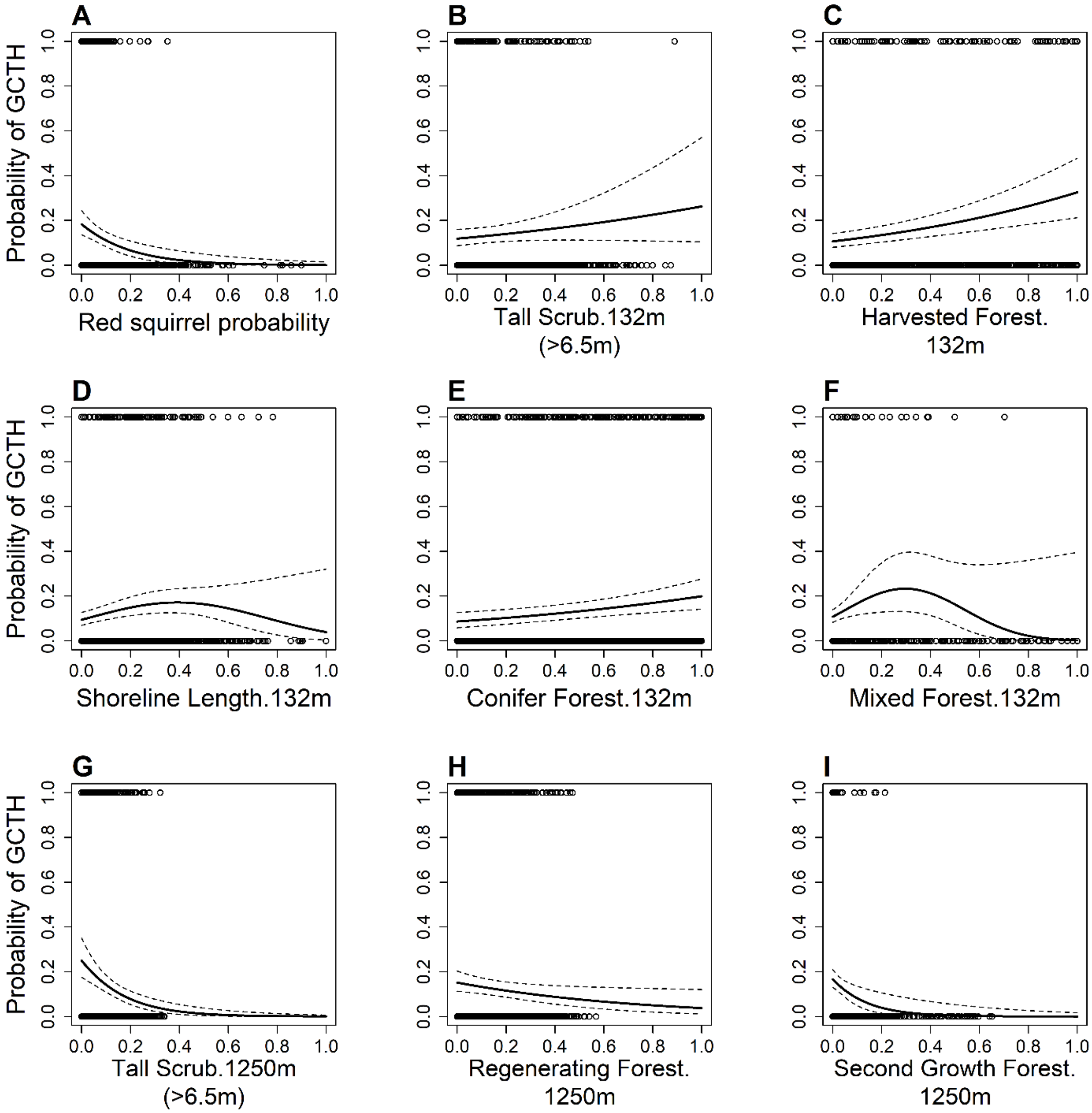

Figure 3-3: Predicted probabilities of Gray-cheeked Thrush presence in the Main River and upper Humber River watersheds in western Newfoundland in 2016 and 2017 for factors retained from the best model. Each variable plot was generated from predicted fitted values while holding all other variables constant at their means. Dotted lines indicate 95% confidence intervals and individual observations (n = 1670) are shown as presences and absences (1 or 0). All variables except for tall scrub (132 m) are statistically significant.

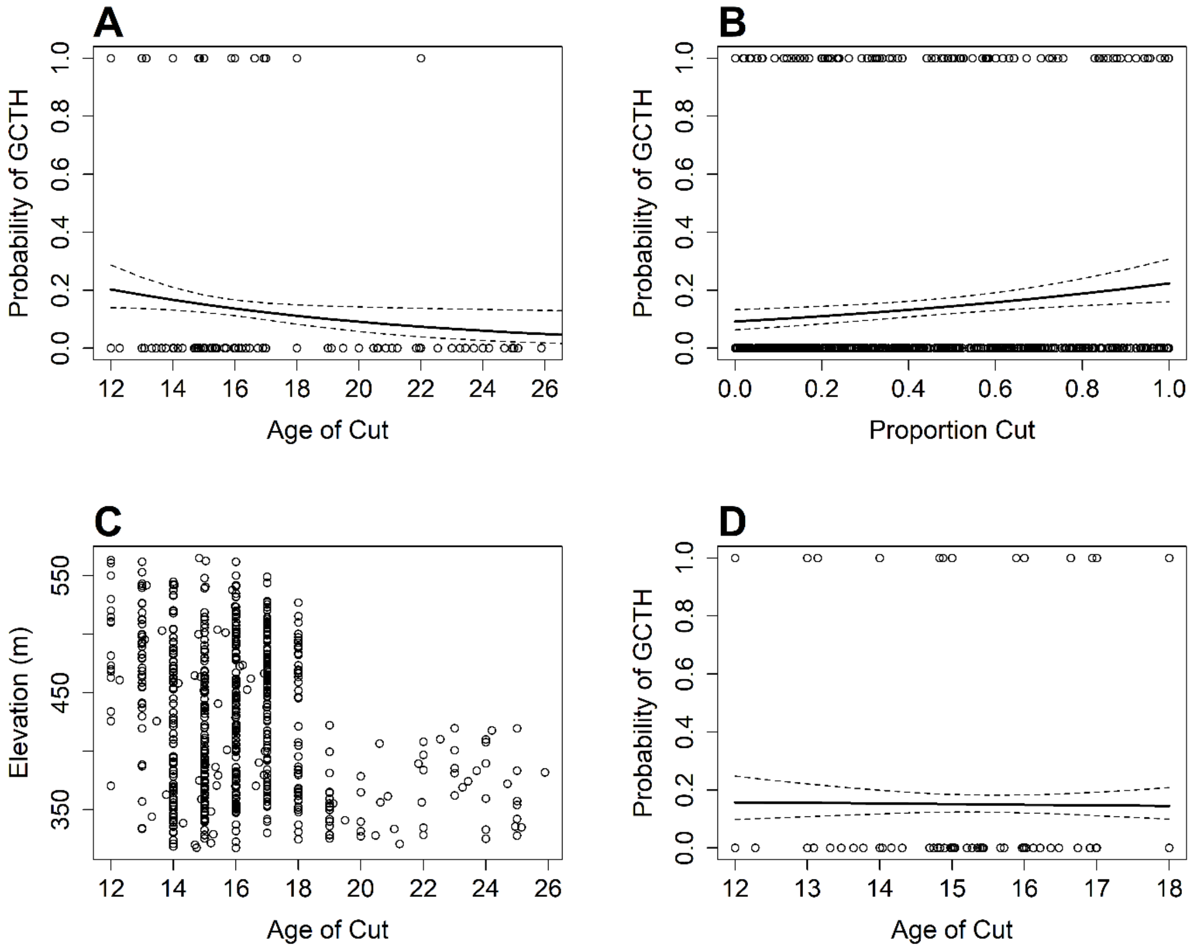

Figure 3-4: **A**, **B**, and **D** show predicted probabilities of Gray-cheeked Thrush presence in the Main River and upper Humber River watersheds in western Newfoundland in 2016 and 2017 based on the age of harvested areas, and proportion that was cut. Data in **A** and **B** was limited to elevations above 317 m and each variable plot was generated from predicted fitted values while holding the other variable constant at its mean. **C** included data from all elevations, and the plot was generated from predicted fitted values. Dotted lines indicate 95% confidence intervals and individual observations (**A** & **B**: n = 664, **D**: n = 601) are shown as presences and absences (1 or 0). **C** shows the distribution of harvested sites along an elevation gradient (n = 1960).

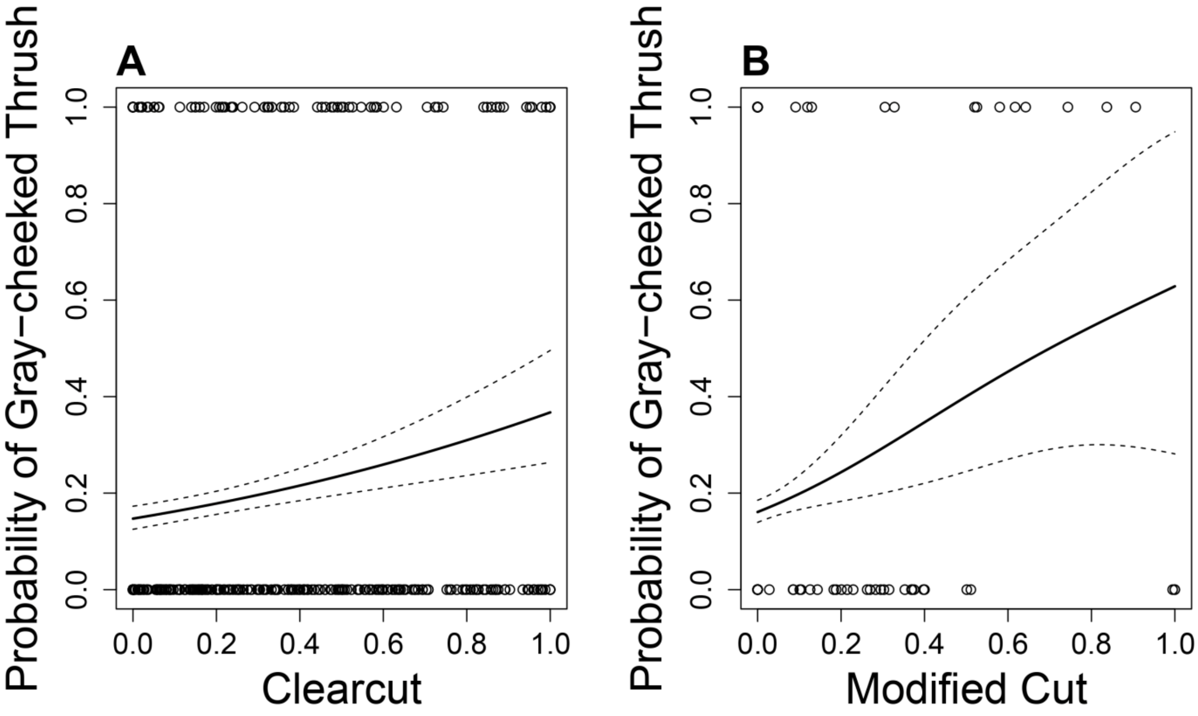

Figure 3-5: Predicted probabilities of Gray-cheeked Thrush presence as a function of the proportion of clearcut or modified cut within 132 m. Data includes only elevations between 419-564 m, in the Main River and upper Humber River watersheds in western Newfoundland in 2016 and 2017 (n = 1039). Each variable plot was generated from predicted fitted values while holding the other variable constant at its mean. Dotted lines indicate 95% confidence intervals and individual observations are shown as presences and absences (1 or 0).

4 Discussion

4.1 Overview

Gray-cheeked Thrushes (*Catharus minimus minimus*) have historically been present and abundant throughout the island of Newfoundland, but disappeared from most locations in eastern, central, and especially coastal Newfoundland when they experienced a 95% population decline beginning in the 1970s (SSAC 2010; Fitzgerald et al. 2017). Following this decline, residual populations remain, unstudied and poorly documented, in montane regions of western Newfoundland (Whitaker et al. 2015). The timing of these thrush disappearances coincided with the spread of red squirrels (*Tamiasciurus hudsonicus*) which were introduced to the island beginning in the 1960s. Red squirrels, as members of the Sciuridae family, are well known for their high level of invasiveness and diverse effects on the boreal ecosystem, including their detrimental effects on the recruitment of nesting songbirds (Martin and Joron 2003; Palmer et al. 2007). These thrush population declines are of conservation concern because the Newfoundland Gray-cheeked Thrush is a distinct subspecies found only on the island of Newfoundland and in south-eastern Labrador (SSAC 2010; Fitzgerald et al. 2017). During my thesis research, I found that Gray-cheeked Thrushes and red squirrels occupy nearly allopatric altitudinal ranges in my study area. Thrushes occupy high elevations and squirrels occupy low elevations, with a narrow range of overlap between ~300-500 m. The two species appear to make use of the landscape in different ways. Red squirrels in conifer masting years are most likely to occupy locations with moderate amounts of cover by fir/spruce forests between 30-70 years of age and avoid coniferous scrub, while Gray-cheeked Thrushes are most likely to occupy locations with coniferous forests, coniferous scrub, and stands that have been harvested in the previous 2-3 decades. In this final chapter I provide a series of recommendations regarding forest and wildlife management that arise from my thesis findings, and discuss ongoing knowledge gaps and future research needs.

4.2 Future expansion of red squirrels

Red squirrels were limited in their elevation distribution in western Newfoundland to areas below ~500 m ASL, with the majority of individuals occurring at much lower elevations. Nevertheless, to support conservation planning, it is important to assess the potential for future expansion upslope by squirrels to determine if high elevation areas will remain a refuge from this introduced nest predator for Gray-cheeked Thrush and other similar songbird species. We assessed the proportion of total area covered by landcover types which were selected (positive) or avoided (negative) by red squirrels (see Chapter 2) at low (< 275 m), mid (275-499 m), and high elevations (> 500 m). Coniferous scrub, which was associated with low squirrel occurrence, made up only 4% of cover in low elevation areas of our study area but became increasingly dominant at higher elevations, where it accounted for > 30% of landcover (Figure 2-4). Conversely, second growth forest was associated with high squirrel occurrence up to ~50% cover around a point, but was rare at intermediate elevations and absent above 500 m (Figure 2-4). This suggests that squirrels have likely expanded their range to the extent which they are able, given contemporary habitat availability.

Northward or upslope treeline shifts and expansion of shrub vegetation into otherwise open habitat as a response to climate change are projected to continue in the future (Weijers et al. 2018). Given the response documented for wildlife at the boreal-tundra ecotone (Wheeler et al. 2018), these changes may have important implications for the altitudinal distribution of red squirrels in Newfoundland and elsewhere on the continent. Shrubification has been well documented throughout much of the Arctic (e.g., Ju and Masek 2016; Myers-Smith and Hik 2018), but studies across a range of environments suggest variability in the extent of treeline shifts altitudinally or latitudinally, with only 52% of studies documenting an advance northward or to higher elevations (Harsch et al. 2009). This variability in treeline response to climate change is likely dependent on several factors including the amount of warming, level of soil moisture, and on whether the treeline boundary is diffuse, abrupt, or has a krummholz (stunted and windswept) form (Harsch et al. 2009; Myers-Smith et al. 2015; Ackerman et al. 2017). In particular, where vegetation changes to a stunted krummholz form, it is less likely that conifers will expand upslope due to limitations on their survival associated with harsh winter conditions (e.g., high wind or desiccation of exposed stems), rather than growing season temperatures (Harsch et al. 2009). In Newfoundland, there is limited mountainous terrain higher than 500 m for red squirrels to invade. Though localized productive old growth forest occurs in sheltered valleys (Damman 1983, McCarthy and Weetman 2006), most of these upper elevation areas are prone to high wind which has led to alpine tundra, or the development of this krummholz landcover type. These cover types have limited potential to become productive forest even as climate changes, unless the impacts of wind on montane vegetation, particularly during winter, are significantly reduced (Damman 1983). Consequently, these high elevation areas in Newfoundland where wind-driven krummholz forests dominate may remain poorly suited to further expansion by red squirrels, leaving higher areas as refuges for native species in the foreseeable future.

However, alterations to the natural disturbance regime, including natural succession after forest harvesting, or changes in climate, could provide other means by which red squirrels might expand upslope. Historically, mid-elevation productive forest in this region of Newfoundland existed as gap-dynamic old growth stands due to climate conditions that limited large-scale forest disturbances such as fire or insect outbreaks (McCarthy and Weetman 2006). However, forest harvesting from 1990-2004 created clearcuts and modified (strip) cuts at elevations up to 560 m, introducing large-scale disturbance to the landscape. Assuming low enough levels of moose browsing, these large swathes of harvested areas will mature in the next 10-50 years to become second growth forest, increasing the ~5% current second growth forest landcover up to ~25% of the area between 275-300 m. These stands may be suitable for red squirrels, possibly allowing them to increase in numbers at intermediate elevations and expand into higher elevation montane forests that are currently unoccupied. Similarly, second growth forest could also be produced at higher elevations if climate change alters the natural disturbance regime by increasing the frequency or extent of defoliating insects or wildfire. There is, however, considerable uncertainty in model predictions related to future forest pest outbreaks, which also produces uncertainty in predicting movement of other wildlife after these events (Boulanger et al. 2016).

4.3 Current determinants of Gray-cheeked Thrush distribution in Newfoundland

One of the main findings I report in this thesis is that red squirrels appear to constrain the contemporary occurrence of Gray-cheeked Thrushes. The elevation distributions of thrushes and squirrels across the study area were nearly mutually exclusive in both years, with squirrels occupying lower elevation sites and Gray-cheeked Thrushes occupying higher elevation sites. These observations suggest that thrushes and squirrels are now largely restricted in elevation range and strongly segregated, to the point of near allopatry, in western Newfoundland. Out of 1960 points surveyed in either 2016 or 2017, we only detected both a red squirrel and a Gray-cheeked Thrush at six locations (0.3% of survey sites). There have, however, been reports of a handful of localized pockets of Gray-cheeked Thrushes that persist in an approximately 25 km length of coastline on the Avalon Peninsula of Newfoundland (from Bay Bulls south to Brigus South, with a particularly dense pocket around La Manche; Fitzgerald et al. 2017; also see Gray-cheeked Thrush sightings map of that area in eBird)) along with some squirrel-free offshore islands in the region (Fitzgerald et al. 2017). This raises questions about whether thrushes and squirrels may co-exist at some locations on Newfoundland, or whether lowland areas on the Avalon act as a population sink where Gray-cheeked Thrushes only persist through immigration by individuals from nearby squirrel-free areas. The occurrence of these lowland populations certainly does not nullify the hypothesis that red squirrels have strongly influenced the broader distribution of the thrushes on Newfoundland. Localized montane populations appear in other areas of the Gray-cheeked Thrush's continental range, where they have co-existed with squirrels for much longer periods of time. In western Canada, for example, thrushes are found in high elevation mountains and plateaus, but there is evidence of localized breeding in smaller numbers down to sea level (Höhn and Marklevitz 1974; Di Corrado 2015).

4.4 Future directions and management recommendations

Since it appears likely that red squirrels will continue to restrict Gray-cheeked Thrushes to the upper reaches of the mountain ranges of western Newfoundland, management prescriptions should be developed for Gray-cheeked Thrushes in their contemporary niche, rather than referring back to their more extensive historical range on Newfoundland (Scheele et al. 2017). However, the extent to which Gray-cheeked Thrushes persist on squirrel-free offshore islands should be assessed, and conservation planning should include an examination of islands within their historical range. A key action for managing offshore islands with possible Gray-cheeked Thrush populations would be to prevent squirrel introductions, through public education to limit translocations, and with a reporting system where the public could report squirrels on islands where they had previously been absent. Further, if islands are identified where red squirrels have been introduced and have apparently extirpated thrushes, these islands could be used as experimental locations to assess if red squirrel eradications at smaller scales could be a useful restoration technique. There are numerous examples where this type of intensive invasive mammal eradication has been successful in enabling the restoration of insular populations of extirpated and imperilled landbirds, among other benefits (see review by Jones et al. 2016). At the larger scale of the main island of Newfoundland, red squirrels are too numerous and firmly established to eradicate, so other management options should be investigated to limit or at least reduce future range expansion into montane forests. Potential management options include updating land management strategies to discourage red squirrel success and encourage increased natural predation (Doherty et al. 2016), especially in forest types that are needed by at-risk endemic species. This could come in the form of supporting greater development of predator populations through recovery of the Newfoundland marten (*Martes americana atrata*), or providing supplementary nest locations for squirrel predators like the Great Horned Owl (*Bubo virginianus*) or Northern Goshawk (*Accipiter gentilis*). Alternatively, creating a perceived predation risk for squirrels through broadcasting predator calls and establishing a "landscape of fear" (Zanette and Clinchy 2019) could lead to reduced predation pressure by squirrels on nesting songbirds. This sort of natural, top-down control has promoted/increased success in controlling other invasive squirrel species and restoring a more natural ecosystem balance (Twining et al. 2020). However, relying solely on a predation-based red squirrel management program should be undertaken with some reservations, as red squirrels in other parts of their range have been found to be food-limited rather than predation-limited (Sullivan 1990; Stuart-Smith and Boutin 1995). If this holds true in Newfoundland, then management in this way would not be as effective as expected. However, it is worth investigation, as Sullivan (1990) saw very strong population effects of food supplementation but did not study predation, and Stuart-Smith and Boutin (1995) were not able to study predation effects from marten or avian predators, both of which would be present in Newfoundland.

Likewise, Gray-cheeked Thrush habitat requirements should be considered when managing forests. Since thrushes are positively associated with larger cutblocks up to 7 ha in size based on the spatial scale of our assessment (Chapter 3), forest harvesting could be used to create either clear cuts or modified strip cuts at elevations above 375 m. These forest harvesting methods would provide habitat preferred by Gray-cheeked Thrushes. However, this management strategy must be used with caution as forest harvesting could reduce the red squirrel predator community (Lõhmus 2005), and red squirrels are likely to be found in fir/spruce forests that are 30-70 years old (Chapter 2). Provided future timber harvest rotation remains at 50-60 years in Newfoundland (Sturtevant et al. 1997), it is likely that red squirrels could have 20 years or so of regenerated stands of an appropriate age before they would be cut again. It would thus be advisable for researchers to study the potential upslope movement by red squirrels as regenerating stands age and become available in these areas. This could be most easily achieved by repeating the red squirrel surveys I carried out in high elevation regenerating clearcuts once these stands have reached second growth stage (i.e., in ~10-50 years) to see if forest harvesting has enabled the up-slope expansion of red squirrels. Another important question would be to assess whether clearcuts and modified cuts are equally suitable for red squirrels. The knowledge that thrushes appear to benefit from both clearcut and modified strip cuts (Chapter 3) could provide greater flexibility in forest management techniques should one be more preferred by these upslope-dispersing red squirrels. Additionally, one harvesting technique may be more beneficial to another species at risk, or for maintaining the gap-dynamic old-growth forest structure similar to that found naturally in montane forests of western Newfoundland. The current forest management strategy in Newfoundland is comprehensive and addresses the benefits of matching silviculture practices (size and age maintenance of stands) to natural ecological disturbances like fire, windthrow, and insect outbreaks (Government of Newfoundland and Labrador 2014; see also Bergeron et al. 2002). However, these management policies are unlikely to come into effect as there is currently very little commercial forest harvesting occurring in the montane forests of western Newfoundland due to a downturn in market rates for the pulp and paper industry.

Forest management should also seek to limit further upslope expansion of red squirrels by striving to maintain the current small-scale gap dynamics (McCarthy and Weetman 2006), even as climate change may encourage larger-scale disturbances. As climate changes, defoliating insect outbreaks such as spruce budworm are likely to become temporally longer and effect larger areas (Gray 2008). Upon regeneration, these larger-scale disturbances could provide more second growth forest in mid-elevations that may benefit red squirrel expansion. In order to maintain the current disturbance regime, and thus conserve Gray-cheeked Thrushes by limiting large areas of squirrel-friendly land, the suppression of large-scale insect outbreaks, or fire, could be considered, with full consideration of its effect on other species in the community, and using ecologically-sound methods that match the historical disturbance regime.

Pre-commercial thinning is another forest management technique of interest in conservation planning for Gray-cheeked Thrushes as it has been found to adversely affect the closely related Bicknell's Thrush (*Catharus bicknelli*; Chisholm and Leonard 2008; Aubry et al. 2016). However, all the forest stands that were pre-commercially thinned in our survey area fell at elevations well below the current range of Gray-cheeked Thrushes, so we could not evaluate the effects of this silvicultural practice. Additionally, though widely applied in the 1980s and 1990s to offset a wood supply shortfall, pre-commercial thinning has been little used in Newfoundland since 1998 and has been almost completely phased out since 2014 (Government of Newfoundland and Labrador 2014). Consequently, this management technique has little bearing on thrush population management on Newfoundland for the foreseeable future, but may be important in other parts of the Gray-cheeked Thrush's range where pre-commercial thinning is a widely used silvicultural technique, or if it once again becomes widely applied on Newfoundland.

Studies that compare the distribution of red squirrels and Gray-cheeked Thrushes in other regions, including coastal islands, mountains along the southern edge of the species' range, and near the boreal-tundra ecotone throughout North America, would help us more fully understand if and how squirrels affect and constrain thrush populations more generally. It is also important that studies be undertaken to assess the direct impacts of squirrels on the thrushes; these could involve nest predation studies that measure impacts of red squirrel predation on Gray-cheeked Thrush recruitment. However, the near allopatry we documented between these species may make such research challenging. The effect of squirrel introduction on the broader bird community of Newfoundland is also unknown. It would be valuable for management efforts directed at this community to investigate whether any other species have experienced a decline concurrent with colonization by red squirrels, or if their distributions have been altered as a response to the arrival of squirrels to the island's forests. A meta-analysis of the population trends of other ground or low-nesting birds could help confirm whether Gray-cheeked Thrushes are adversely affected because they do not respond appropriately through anti-predator behaviour or merely because the locations of their nest sites render them more vulnerable. Finally, it is important to note that additional stressors may be acting simultaneously on the Newfoundland population of Gray-cheeked Thrushes. For example, Whitaker et al. (2018) present evidence suggesting that Newfoundland Gray-cheeked Thrushes winter in a region in northern South America near the Venezuela/Colombia border that has experienced large scale loss and degradation of potential thrush habitat. This highlights the importance of taking a full annual cycle approach to research and conservation of this and other species (Marra et al. 2015).

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