

**EVALUATING HOW STAND LEVEL FOREST DYNAMICS INFLUENCE
CARIBOU WINTER RANGE**

by

Erin Colleen Hall

BSc., University of Northern British Columbia, 1999

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL STUDIES

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

August 2023

© Erin Hall, 2023

Abstract

Forest ecosystems and the ecological services they provide are complex and dynamic. Disturbance and successional processes impact habitat for animals such as caribou (*Rangifer tarandus caribou* Gmelin 1788, Banfield 1961, 1974) and moose (*Alces alces* L.). The forested winter habitat of the Tweedsmuir-Entiako caribou herd has been significantly affected by recent disturbance. In order to evaluate the mid- and long-term consequences for habitat, we require an understanding of how habitat attributes change as stand structure changes over time.

I developed a framework to link a stand dynamics model (SORTIE-ND), via linker functions, to three ecosystem elements relevant to caribou populations: terrestrial forage lichen, moose forage, and vertical cover. I first used SORTIE-ND to model stand structure dynamics following mountain pine beetle (*Dendroctonus ponderosae* Hopkins) attack and clearcut harvesting. I developed linker functions and refined them with empirical data. These functions were applied to stand structure output from SORTIE-ND to project the response of habitat to the disturbance agents. I addressed three questions: 1. What is the influence of edaphic site on the provision of elements of caribou habitat over time? 2. What is the influence of stand type on the provision of elements of caribou habitat over time? 3. How do recovery trajectories of caribou habitat elements differ in response to disturbances such as mountain pine beetle and clearcut harvest?

I found that site and stand type interacted to influence the suitability of terrestrial lichen, moose forage and vertical cover. Poor productivity sites were most favourable for terrestrial forage lichen. Higher productivity stands and broadleaf stands provided the greatest suitability for moose shrubs. Both mountain pine beetle attack and clearcut harvest improved stand suitability for lichen and moose browse though for different sites and stand types.

Interestingly, I found that severe mountain pine beetle attack resulted in conditions that favoured forage lichen for longer than clearcuts. Clearcuts resulted in conditions that were more suitable than mountain pine beetle attack for winter forage for moose. When operating on landscapes with caribou winter habitat, forest managers should consider disturbance history, the distribution of sites and stand types, silviculture systems and the future desired state of ecosystem services. The SORTIE-ND modelling framework could be used to support the evaluation of alternative management decisions in caribou winter habitat including alternative silviculture strategies. This approach could also provide stand- and site-specific trajectories of the recovery of caribou habitat that could be applied to habitat supply models.

Table of Contents

Abstract	ii
Table of Contents	iv
List of Tables	vi
List of Figures	vii
Acknowledgements	x
Chapter 1	1
Introduction	1
1.1 Background	1
1.1.1 Forest Ecosystem Dynamics	1
1.1.2 Caribou Forested Winter Habitat	3
1.1.3 Effects of Mountain Pine Beetle and Timber Harvesting on Caribou Winter Habitat	8
1.2 Thesis Objectives and Structure	10
Chapter Two	13
Developing Linker Functions to Enable Projection of Elements of Caribou Winter Habitat	13
2.1 Introduction	13
2.2 Methods	17
2.2.1 Study Area and Caribou Habitat Context	17
2.2.2 SORTIE-ND	20
2.2.3 Linker Functions	21
2.2.4 Model Description	22
2.2.5 Field Data Collection	29
2.2.6 Linker Function Fitting and Calibration	35
2.3 Results	36
2.3.1 Lichen	36
2.3.2 Moose Shrubs	39
2.3.3 Moose Cover	43
2.4 Discussion	43
Chapter Three	50
Modelling the Effects of Disturbance on Caribou Winter Habitat	50
3.1 Introduction	50
3.2 Methods	54
3.2.1 Study Area and Caribou Habitat Context	54

3.2.2 Stand Modelling	55
3.3 Results	60
3.3.1 Component Linker Functions	60
3.3.2 Terrestrial Lichen Dynamics	64
3.3.3 Moose Shrub Dynamics	66
3.3.4 Vertical Cover Dynamics	68
3.4 Discussion	70
3.5 Conclusions	78
Chapter Four	79
Conclusions	79
4.1 Main Findings and Management Implications	80
4.2 Contributions	82
4.3 Next Steps and Future Considerations	83
4.4 Concluding Remarks	86
Literature Cited	87
Personal Communication	114
Appendix 1	115
Appendix 2	119
Appendix 3	122
Appendix 4	124
Appendix 5	125
Appendix 6	137
Appendix 7	145

List of Tables

Table 1. Structure and evaluation of linker functions developed to project the relative value of a forest stand to support forage lichens.	36
Table 2. Structure and evaluation of linker functions developed to project the relative value of a forest stand to support forage shrubs used by moose.	37
Table 3. Parameter values for linker functions developed to project the relative value of a forest stand to support forage lichen in west-central BC	39
Table 4. Parameter values for linker functions developed to project the relative value of a forest stand to support forage shrubs used by moose in west-central BC	41
Table 5. Structure of stands used to initiate SORTIE-ND model scenarios for mature stands across gradients of edaphic site and stand type.	57
Table 6. Stand establishment characteristics for sub-boreal clearcut scenarios modelled with SORTIE-ND including planting densities (in stems/ha) and natural regeneration ('seed').	58

List of Figures

Figure 1. The range of the Tweedsmuir-Entiako caribou population (red outline) located in west-central British Columbia, Canada.	5
Figure 2. Distribution of empirical plots (black triangles) established within the Sub-Boreal Spruce moist cold Babine variant (SBSmc2) (purple) during the summer of 2019 in west-central British Columbia, Canada.	18
Figure 3. Linker function components that represent how the suitability of a stand to support forage lichen varies as a function of stand state	38
Figure 4. Observed lichen (a) and moose shrub (b) suitability estimated from empirical plots (n = 76) vs. predicted suitability derived from developed linker functions.	40
Figure 5. Linker function components that represent how the suitability of a stand to support moose shrubs for forage varies as a function of stand state	41
Figure 6. Distribution of species of moose shrubs across soil moisture and nutrient gradients.	42
Figure 7. The linker function that represents the effect of conifer basal area (trees taller than 10 m) on the suitability of a stand to provide vertical cover in winter.	43
Figure 8. Output of the component linker functions for forage lichen on subxeric sites.	61
Figure 9. Output of the component linker functions for moose browse on subhygric sites.	62
Figure 10. The projected response of lichen suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours).	65
Figure 11. The projected response of moose shrub suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours).	67
Figure 12. The projected response of suitability to provide vertical cover over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours).	69
Figure 13. Comparison of the linker functions for lichen parameterized with the calibrated parameters (blue) versus parameterized with the maximum likelihood estimates (black).	122
Figure 14. Comparison of the linker functions for moose shrubs used for forage parameterized with the calibrated parameters (blue) versus parameterized with the maximum likelihood estimates (black).	123
Figure 15. Distribution of the abundance of forage lichen, moose shrubs, aspen (0.5 - 3 m in height), subalpine fir (0.5 - 3 m in height), and conifer basal area in the empirical dataset (n = 76).	124

Figure 16. Output of the component linker functions for forage lichen in three different stand types (colours) on subxeric sites.	125
Figure 17. Output of the component linker functions for forage lichen in four different stand types (colours) on submesic sites.	126
Figure 18. Output of the component linker functions for forage lichen in four different stand types (colours) on mesic sites.	127
Figure 19. Output of the component linker functions for forage lichen in four different stand types (colours) on subhygric sites.	128
Figure 20. Output of the component linker functions for moose browse in three different stand types (colours) on subxeric sites.	129
Figure 21. Output of the component linker functions for moose browse in four different stand types (colours) on submesic sites.	131
Figure 22. Output of the component linker functions for moose browse in four different stand types (colours) on mesic sites.	133
Figure 23. Output of the component linker functions for moose browse in four different stand types (colours) on subhygric sites.	135
Figure 24. The projected response of lichen suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours).	137
Figure 25. The projected response of moose shrub suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours).	138
Figure 26. The projected response of moose browse suitability (includes aspen and subalpine fir 0.5 – 3 m in height and moose shrubs) over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours).	139
Figure 27. The projected response of the suitability of a stand to provide vertical cover over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours).	140
Figure 28. The projected response of lichen suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (colours) and four stand types (rows).	141
Figure 29. The projected response of moose shrub suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (colours) and four stand types (rows).	142
Figure 30. The projected response of moose browse suitability (includes aspen and subalpine fir 0.5 – 3 m in height and moose shrubs) over time in undisturbed mature forest (1st	

column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (colours) and four stand types (rows). 143

Figure 31. The projected response of the suitability of a stand to provide vertical cover over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (colours) and four stand types (rows). 144

Figure 32. Comparison of the variability in lichen suitability for four stand types (colours) on four edaphic sites (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep. 145

Figure 33. Comparison of the variability in lichen suitability between four edaphic sites (colours) for four stand types (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep. 146

Figure 34. Comparison of the variability in moose shrub suitability for four stand types (colours) on four edaphic sites (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep. 147

Figure 35. Comparison of the variability in moose shrub suitability between four edaphic sites (colours) for four stand types (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep. 148

Figure 36. Comparison of the variability in suitability of a stand to provide vertical cover for four stand types (colours) on four edaphic sites (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep. 149

Figure 37. Comparison of the variability in suitability of a stand to provide vertical cover between four edaphic sites (colours) for four stand types (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep. 150

Acknowledgements

There are many people who have been involved and encouraged me along this journey, all of whom enriched my experience and the final product. I sincerely thank each and every one of you.

To my supervisory committee, Ché Elkin, Dr. Chris Johnson, and Erica Lilles, thank you for your support throughout this project. I sincerely appreciate all that I've learned from each of you as well as your time, patience, mentoring and encouragement. Additionally, Ché, thank you for your enthusiastic support and many contributions that turned an idea and vision for this project into a reality.

I am very appreciative of the funding I received from the Province of British Columbia's Caribou Recovery Program and the Bulkley Valley Research Centre. Further support from Jocelyn Campbell, Anne-Marie Roberts, and the British Columbia Ministry of Forests was key to initiating and carrying out this project. The Cheslatta Carrier Nation generously provided me with barge access to my research sites on the south side of Ootsa Reservoir.

So many people have contributed to this project. Working with Dave Coates and Allen Banner studying stand dynamics and ecosystem recovery played a large role in inspiring this project and provided a strong base to build upon. I've appreciated the camaraderie, support, and perspectives provided by members of the Mixed Wood Ecology lab and our informal Vertebrate Ecology lab group. Weekend sessions with fellow MSc students in Smithers were invaluable to completing this project and made working on the weekends much more enjoyable – thank you Nadia Nowak for instigating and Emily Mason and Bryce O'Connor for continuing to join me. I appreciate the knowledgeable and thoughtful insight that Deb Cichowski and Karine Pigeon provided in their reviews of my thesis. I have enjoyed the

many insightful discussions I've had with numerous people throughout this project including: Alana Clason, Anne-Marie Roberts, Dave Coates, Sybille Haeussler, Benita Kaytor, Genevieve Perkins, Jodi Axelson, John Hagen, Dave Wilford, Charlie Canham, Paula Bartemucci, Roy Rea, Darwyn Coxson, Shannon Crowley, and Dexter Hodder. I appreciated and enjoyed time spent with Paula Bartemucci honing my lichen and moss identification skills. Thank you all for readily agreeing to take the time out of your busy schedules to participate in these discussions and provide valuable perspective, suggestions and insight.

I have great memories from the many weeks of field work across the breadth of the SBSmc2. Many thanks are due to my field assistants Bronwyn Hobson and Jonathan VanElslander as well as several others who filled in over the summer: Erin Holtzman, Marie-Lou LeFrançois, Brandy Hughes, Joanna Lee and Jeremy Roscoe. Ben Steele, Lauren Runge, Alex Ritz, and Erin Holtzman volunteered to assist with data entry – their contributions sped analysis along considerably.

Finally, I am forever grateful to my partner in life, Jeremy Roscoe, for his unwavering support throughout my MSc.

Chapter 1

Introduction

1.1 Background

1.1.1 Forest Ecosystem Dynamics

Ecosystems are dynamic and change over time, driven by shifting environmental conditions, abiotic and biotic disturbances, competition dynamics, successional processes, and the interplay between these factors. As ecosystems change, the type and provisioning level of ecosystem services are expected to shift. For example, biodiversity and habitat quality are spatially and temporally dynamic ecosystem services that reflect changes in ecosystem structure and disturbance history (Carroll and Bliss 1982, Halpern et al. 2012, Lilles et al. 2018, Greuel et al. 2021).

Vegetation dynamics often underpin terrestrial ecosystem dynamics. At the landscape level this is reflected in the distribution and dynamics of vegetation biomes (grasslands, savanna, forests etc.). At a finer scale, such as a forest stand, vegetation dynamics also drive changes in the provisioning of ecosystem services through time. For example, the vegetation community at the stand level determines the amount of forage available to ungulates and, by extension, the habitat quality of the stand (Crête and Courtois 1997, Keim et al. 2017). Some ecosystem components, such as lichen communities used by caribou (*Rangifer tarandus* Lin.), may require decades or centuries to develop (Maikawa and Kershaw 1976, Boudreault et al. 2009). Others, such as shrub communities favoured by moose (*Alces alces* L.) develop more rapidly following disturbance (Eastman 1977, Julianus et al. 2019).

Forest management, implemented through different silviculture systems, influences forest composition and structure, the successional trajectory of stands, and the associated provision

of ecosystem services (Marzluff et al. 2002, Maleki et al. 2021). Trees play a pivotal role in forested ecosystems, modifying ecosystems through influencing the availability and distribution of resources such as light and nutrients and therefore driving understory vegetation dynamics (Bartemucci et al. 2006, Haughian and Burton 2015). As a result, forest management activities directly influence the spatial and temporal provisioning of a broad variety of ecosystem services in forested systems (Marzluff et al. 2002, Mönkkönen et al. 2014, Lilles et al. 2018). To manage for these multiple ecosystem services, we need to understand the temporal dynamics of forests and ecosystem services, and how recovery trajectories of these services are affected by management activities and natural disturbance (Marzluff et al. 2002). Improving our understanding of how stand structure and stand dynamics influence forest-based ecosystems services will improve our ability to robustly manage for a range of economic, ecological, and social values (Mönkkönen et al. 2014).

In recent years there has been considerable improvement in the methods for modelling the dynamics of some ecosystem services. Many of these methods use existing models of forest dynamics that have a fifty-year history of development (Bugmann and Seidl 2022). These models enable the projection of stand dynamics including stand structure and tree species composition over time (Bugmann 2001, Bugmann and Seidl 2022). However, most models do not explicitly and dynamically project other ecosystem services provided by the forest. Recently, modellers and ecologists have begun to link ecosystem services to forest dynamics models via models called linker functions (Elkin et al. 2013, Cordonnier et al. 2014, Mönkkönen et al. 2014, Lafond et al. 2017). Linker functions enable the projection of ecosystem service dynamics from stand structure output. Thus, linker functions extend our ability to dynamically model not only stand structure attributes but also ecosystem services such as habitat, carbon, and biodiversity (Elkin et al. 2013, Cordonnier et al. 2014, Mönkkönen et al. 2014, Lafond et al. 2017).

The overarching aim of this thesis is to improve our understanding of how forest structure and composition affect key habitat elements for caribou, an ungulate of conservation concern, and how these habitat elements recover following mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) outbreaks and clearcut harvesting. In the following section I provide an overview of the forest habitat elements that are important for caribou winter habitat. I then describe the agents of habitat disturbance evaluated in this thesis and their impact on forest structure, and by extension caribou habitat. I conclude Chapter 1 by describing the thesis chapters and how they relate to the thesis objectives.

1.1.2 Caribou Forested Winter Habitat

Caribou are a species of conservation concern with an uncertain future in Canada (Festa-Bianchet et al. 2011, Johnson et al. 2015). As of 2011, most caribou populations in Canada were listed under the *Species at Risk Act* as either Endangered, Threatened or Special Concern. Predation and, for some populations, overharvest are proximate causes of decline (Festa-Bianchet et al. 2011). However, habitat change is the primary cause of decline for many populations of caribou (Festa-Bianchet et al. 2011). Activities such as forestry and oil and gas exploration and development create early seral forests that provide habitat for the apparent competitors of caribou, namely moose and deer (*Odocoileus* spp.). These apparent competitors support larger and more abundant populations of wolves (*Canis lupus* L.) and bears (*Ursus* spp.) that ultimately lead to unsustainable predation for caribou (Wittmer et al. 2007, Festa-Bianchet et al. 2011).

Although only one species of caribou is recognized throughout its global distribution, caribou exhibit a wide range of migratory and movement behaviours in addition to morphological and genetic variability (COSEWIC 2011, Festa-Bianchet et al. 2011). In North America, four extant subspecies were described by Banfield: woodland (*Rangifer tarandus caribou* Gmelin

1788, Banfield 1961, 1974), Grant's caribou (*R. t. granti* Allen, 1902), barren-ground caribou (*R. t. groenlandicus* L. 1767), and Peary caribou (*R. t. pearyi* Allen, 1902) (COSEWIC 2011). Due to challenges with this classification and availability of improved information, COSEWIC proposed twelve Designatable Units to classify caribou populations within Canada (COSEWIC 2011). These Designatable Units were developed using available information regarding caribou phylogenetics; genetic diversity and structure; morphology; movements, behaviour and life history strategies; and distribution (COSEWIC 2011). Designatable Units are intended to recognize discrete and evolutionarily significant populations of species in Canada that are considered irreplaceable (COSEWIC 2009, 2011).

The Tweedsmuir-Entiako caribou herd (TEC) is the focus of this project. These caribou are classified as the northern mountain ecotype of woodland caribou and are included in the Northern Mountain Designatable Unit (COSEWIC 2002, 2011, 2014). The herd's home range is located in west-central British Columbia (BC), east of the Coast Mountains, and southwest of Prince George (Figure 1).

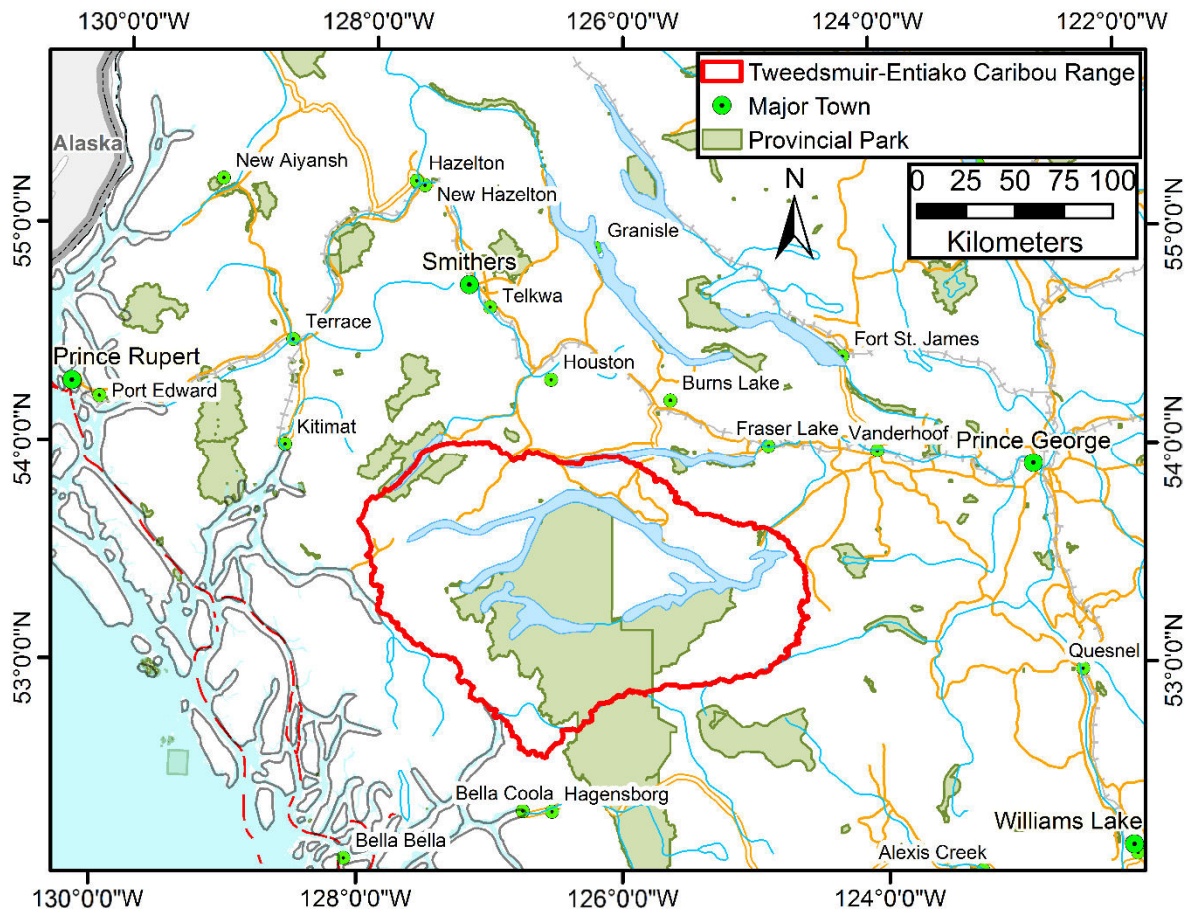


Figure 1. The range of the Tweedsmuir-Entiako caribou population (red outline) located in west-central British Columbia, Canada.

As with many northern mountain caribou, TEC migrate annually in spring and fall. From December to the onset of spring migration in early May, the majority of winter is spent in the east in low-elevation lodgepole pine (*Pinus contorta* var. *latifolia* Douglas ex Loudon) forests in the Entiako Park area south of Tetachuk Lake. However, during some years, caribou may also move to alpine and subalpine areas in the Fawnie Mountains or reside in the Cheslaslie River area (northwest of Entiako Park and the core of the winter range) (Cichowski 1993, Steventon 1996). In late winter the caribou congregate near the Entiako River where they inhabit mature lodgepole pine and mature mixed pine-interior spruce (*Picea glauca* (Moench) Voss) forests on mesic sites. By early May the caribou cross Tetachuk Lake and migrate west to the mountains in the northern portion of Tweedsmuir Park and mountains further to

the west and northwest. By late November almost all of the caribou return to the winter range in the Entiako Park area (Cichowski 1989, 1993).

The TEC herd, and specifically its forested winter habitat, was selected as the focus of this study. Forested winter habitat was selected for two reasons. First, the herd is in decline, blue-listed (designated as threatened by the Province of British Columbia), listed as Threatened under the federal *Species at Risk Act* (COSEWIC 2014), and habitat management in the herd's range is a provincial priority. Second, the herd's forested winter habitat has been subject to significant levels of recent disturbance from wildfire, mountain pine beetle and timber harvest. For simplicity, I will refer to forested winter habitat as winter habitat for the remainder of the thesis. Winter habitat is important because forage availability, diversity and quality are most limited in winter. In summer, the diet of northern mountain caribou reflects that of a generalist herbivore consuming deciduous shrubs, forbs, lichens, and mushrooms (Denryter et al. 2017). In the winter, caribou transition to a specialized diet consisting primarily of lichen (Cichowski 1993, Johnson et al. 2000). However, forage comprises only one component of habitat. Habitat is defined as “the resources and conditions present in an area that produce occupancy, which may include survival and reproduction by a given organism” (Hall et al. 1997 p. 175).

TEC winter range is characteristic of northern mountain caribou and reflects prevailing topography, vegetation, and weather of their range (COSEWIC 2011, 2014). Winter ranges of northern mountain caribou are generally gentle with rolling mountains interspersed with lower elevation plateaus (COSEWIC 2011). Winters are colder and the snow pack generally lower than conditions typical of neighbouring ranges of central and southern mountain caribou to the east and southeast (COSEWIC 2011). In winter, northern mountain caribou feed primarily on terrestrial lichens found either in low-elevation mature conifer forests

(lodgepole pine and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.)) or on high windswept alpine slopes (COSEWIC 2011). Arboreal lichens are also consumed during winter especially where they are more abundant such as in mixed stands of pine and spruce and along the fringes of wetlands. These lichen are often sourced later in the winter when snow pack is deeper or less amenable to cratering (Cichowski 1993, 1993, Johnson et al. 2001, 2003). In addition to the availability of lichen, an important characteristic of caribou winter habitat is the canopy condition that influences the availability of terrestrial lichen. A conifer canopy intercepts snow reducing the depth of the snowpack; it may also protect the snow from developing as thick a crust as may form in open conditions (Cichowski 2010, Seip and Jones 2010, Kivinen et al. 2010).

In addition to stand types that provide caribou forage, another important attribute of northern mountain caribou habitat relates to their primary defense strategy. Similar to all woodland caribou, northern mountain caribou avoid predation through the use of habitats with a relatively low density of deer and moose and their shared predators including wolves and bears (Rettie and Messier 2000, Wittmer et al. 2007, Venier et al. 2014). Landscapes with habitat that supports abundant prey species have the potential to support larger wolf populations; this heightens mortality risk for caribou. This relationship, where the population of one species indirectly results in the decline of another prey species via a common predator, is termed apparent competition (Holt 1977, Wittmer et al. 2007, Anderson et al. 2018). Therefore, an important metric of caribou habitat is the presence and quality of moose habitat. Elements of moose habitat include forage, vertical and security cover, and abundance of predators (Peek 2007).

In this study, I focus on caribou habitat and stand dynamics at the stand scale. Oliver and Larson (1990 p. 1) define a stand as “a spatially continuous group of trees and associated

vegetation having similar structures and growing under similar soil and climatic conditions”. Habitat elements that can be assessed at a stand scale include abundance of individual forage species or basal area of a particular tree species. In contrast, landscape-scale elements of habitat include patterns of disturbances or networks of roads and linear features. Studies of caribou habitat are generally situated at the landscape scale (Johnson et al. 2002, DeCesare et al. 2012, Stockdale et al. 2019, Leblond et al. 2022). However, stand-scale studies and process-based modelling of stand and habitat dynamics can inform our understanding of landscape-scale patterns (Holt et al. 1995, Leblond et al. 2022). In addition, process-based models at the stand-scale allow us to explore the implications of different severities of disturbance or forest management decisions such as the application of alternative silviculture systems (Maleki et al. 2021).

1.1.3 Effects of Mountain Pine Beetle and Timber Harvesting on Caribou Winter Habitat

There are a number of interacting reasons that habitat disturbance, either natural or industrial, is reported as the ultimate cause of caribou population decline. In the previous section I outlined two important aspects of winter habitat for northern mountain caribou: forage availability and co-occurrence of moose habitat. Disturbance affects these as well as other elements of caribou habitat (Festa-Bianchet et al. 2011). Severe disturbances that remove old forest result in reduced lichen abundance (Cichowski et al. 2022). The resulting younger stand types provide a greater abundance of winter forage for moose and deer and thereby increase predation risk via apparent competition (Holt 1977, Wittmer et al. 2007, Festa-Bianchet et al. 2011, Barber et al. 2018). Development of roads and linear corridors also increases predation risk by providing wolves with access to caribou habitat and increased hunting efficiency (Whittington et al. 2011, Dickie et al. 2017, Mumma et al. 2018).

Over the last two decades disturbance within TEC winter habitat has been significant with several large wildfires and the largest MPB epidemic documented in Canadian history (Dhar et al. 2016, Cichowski and Haeussler 2020, Province of British Columbia 2023). Extensive salvage harvest of standing dead trees has occurred following the wildfire and MPB events.

MPB attack affects winter habitat through killing pine trees and thus altering the structure and species composition of the overstory. The degree to which MPB attack affects the provision of caribou habitat will depend upon the intensity of the attack and the proportion of pine trees killed (Nobert et al. 2020, Cichowski et al. 2022). Where pine are killed, microclimate and light levels change gradually over several years as the dead trees slowly lose needles (needle loss occurs for up to five years following attack) and then fall (Cichowski and Haeussler 2020). Monitoring plots within the TEC winter range have documented that tree fall occurs gradually. Few trees fell within the first ten years following MPB attack, but after an additional five years, 26% of MPB attacked trees had fallen and fall rates had increased (Cichowski and Haeussler 2020).

The most immediate ecological impact of MPB attack is that, with the death of pine trees, the availability of water and nutrients increases for other plants. A study in the TEC winter range found a significant increase in kinnikinnick cover (*Arctostaphylos uva-ursi* (L.) Spreng.) for the first several years following MPB attack (Cichowski and Haeussler 2020). A similar response in dwarf *Vaccinium* species was observed in central BC following MPB attack (Seip and Jones 2010). In contrast, abundance of terrestrial lichen declined significantly. After about ten years, these trends reversed on the poorest productivity sites; kinnikinnick abundance declined and lichen decline stopped (in the Tweedsmuir-Entiako lichen monitoring plots, Cichowski and Haeussler 2020). When considering these dynamics it is

important to keep in mind that lichen are slow growing and poor competitors in comparison to other ground vegetation and mosses (Rowe 1984).

Timber harvest can have significantly different effects on caribou winter habitat, depending on the silviculture system and the timing of harvest. The effects of silviculture systems could be considered along an intensity gradient, from low intensity single-tree selection to gradually higher intensity group selection, shelterwoods, clearcuts with dispersed retention or reserves, to high-intensity clearcuts. Clearcuts completely remove the mature trees and associated vegetation structure that caribou often select (Joly et al. 2003, Fortin et al. 2008). Further, caribou avoid young and immature cutblocks (Fisher and Wilkinson 2005, Metsaranta and Mallory 2007, Courtois et al. 2008, Courbin et al. 2009). Partial harvest systems provide the option to extract revenue from timber yet also retain some stand structure. Although there is extensive information regarding caribou interactions with clearcuts, there is limited information regarding caribou interactions with partial harvest systems (Fisher and Wilkinson 2005, Courtois et al. 2007, Waterhouse et al. 2011). Some partial harvest systems are being tested and evaluated to assess the degree to which they retain elements of caribou habitat (Waterhouse et al. 2011, Nadeau Fortin et al. 2016). Harvesting methods also play a role in the degree to which winter habitat is affected. Harvesting on a thick snowpack can minimize the physical disturbance to terrestrial lichen associated with the machinery necessary to cut and remove trees (Webb 1998, Coxson and Marsh 2001). Harvest methods that limit the distribution of logging debris can also minimize the direct impacts to lichen (Kivinen et al. 2010, Cichowski et al. 2022)

1.2 Thesis Objectives and Structure

In this thesis I evaluated how elements of caribou winter habitat changed through time in response to stand dynamics following disturbance events. This study addresses the need for a

greater understanding of the recovery and successional dynamics of winter habitat for northern mountain caribou. Researchers have developed the capability to model the dynamics of stand structure from a tree perspective. However, we lack the corresponding ability to model and project how habitat elements within forests respond and change as the stands that they are embedded within regenerate, mature, and respond to disturbance over time. It is important to be able to project the influence of disturbance events and proposed treatments on both present and future habitat values to manage for caribou habitat and prioritize treatments that favour the recovery of winter habitat (Holt et al. 1995, Mäkelä et al. 2012).

In Chapter 2, I develop a framework that uses the output of the stand dynamics model SORTIE-ND (Coates et al. 2003) to project the temporal dynamics of caribou habitat. To develop the framework, I developed linker functions based on literature review and interviews with subject experts. I then conducted a field study across a broad range of stand types and collected data representative of the occurrence and abundance of caribou habitat and associated site and stand structure. I used the empirical data to calibrate and evaluate the linker functions.

In Chapter 3, I used the framework developed in Chapter 2 to assess the effect of disturbance on the trajectory of forest stands and caribou habitat. I used SORTIE-ND to model mountain pine beetle attack and clearcut harvest. I used the resulting model projections to compare the temporal recovery of caribou winter habitat in disturbed stands to undisturbed mature stands. Based on those comparisons, I examined three specific questions:

1. What is the influence of edaphic site on the provision of elements of caribou habitat over time?
2. What is the influence of stand type on the provision of elements of caribou habitat over time?

3. How do recovery trajectories of caribou habitat elements differ in response to disturbances such as mountain pine beetle and clearcut harvest?

In Chapter 4, I synthesize the results of the thesis and discuss future work and management implications.

Chapter Two

Developing Linker Functions to Enable Projection of Elements of Caribou Winter Habitat

2.1 Introduction

“The complexity of a forest ecosystem makes difficult any attempt to synthesize knowledge about forest dynamics or to perceive the implications of information and assumptions regarding forest growth.” (Botkin et al. 1972a p. 849)

Forest ecosystems are complex and dynamic with interactions across spatial and temporal scales (Botkin et al. 1972a, Filotas et al. 2014). Many processes influence ecosystem dynamics including disturbance, competition dynamics, and seasonal change in resource availability (Angelstam and Kuuluvainen 2004, Filotas et al. 2014). Models are useful for testing our understanding of complex ecosystem dynamics and for providing a framework within which to set existing knowledge (Botkin et al. 1972b, Filotas et al. 2014). Models also enable us to visualize and project the effects of ecosystem dynamics and management actions on ecosystem elements of interest (Mönkkönen et al. 2014, Leblond et al. 2022). These elements may include indices of economic output, carbon sequestration or habitat for species of conservation concern (Marzluff et al. 2002, Spies et al. 2007, Mönkkönen et al. 2014).

Caribou are a species of conservation concern in Canada and habitat management is a priority in many jurisdictions (COSEWIC 2014, Leblond et al. 2014). As presented in Chapter 1, the ultimate cause of decline is habitat disturbance (Festa-Bianchet et al. 2011). Timber harvesting, wildfire, and insect outbreaks can change the quality or result in the loss of habitat for caribou across Canada. As introduced in Chapter 1, winter habitat is an important component of caribou habitat and is sensitive to disturbance. Two components of the winter

habitat for northern mountain caribou that can be assessed at the stand scale are terrestrial lichen for winter forage and moose habitat that indirectly leads to greater rates of predation for caribou. Moose habitat at the stand scale consists of forage as well as thermal and security cover (Peek 2007).

Although there has been much research focused on understanding stand conditions that provide high-value caribou habitat, the response of these habitat types to the dynamics of the stands that they are embedded within is not well understood (Cichowski 1993, Johnson et al. 2000, Cichowski and Haeussler 2020, Nobert et al. 2020). Dynamic, stand-scale models of caribou habitat would support our understanding of the longer-term implications of disturbance on caribou habitat. Those models could be used to identify current forest types and management actions that best support development of high-value habitat in the mid- to long-term. Trade-offs exist between management strategies that retain high-value habitat in the short-term versus those that promote habitat supply in the long-term (Coxson 2015, Nobert et al. 2020). Models could be used to support strategic application of management approaches to balance the short-term and long-term provision of habitat on the landscape.

Habitat models are available for informing management of ungulate habitat. Species distribution models have a long history of use and inform how landscape- and stand-scale ecological conditions influence the space use of animals (Metsaranta et al. 2003, Johnson et al. 2004, Leblond et al. 2014, Whitman et al. 2017). Some recent studies have used models of vegetation dynamics to forecast habitat dynamics into the future (Barber et al. 2018, Leblond et al. 2022). The effect of disturbance depends upon the severity of the disturbance. Some events are severe and stand-replacing, such as a high-intensity wildfire or clearcutting. However, other disturbances affect only portions of a stand resulting in complex stand structures (e.g., partial-cut silviculture methods, light to moderate severity fire, and MPB

attack). Variability in disturbance types and the resulting stand structure can lead to different seral stand types (species composition, density, size of trees, etc.) on similar edaphic sites (Meidinger and Pojar 1991, Banner et al. 1993, Bergeron 2000). Incorporating the ability to model the dynamics of habitat in response to complex changes in stand structure would add further value to habitat models. This is especially relevant for habitat elements that develop over relatively long time frames or that are sensitive to stand structure, such as terrestrial lichen communities (Holt et al. 1995).

There are a number of forest dynamics models that represent the stand- and landscape-scale processes related to the tree components of forest stands (Bugmann 2001, Bugmann and Seidl 2022). SORTIE-ND is one such model that has been developed for use in northwest BC including forests that provide habitat for the TEC. SORTIE-ND is an individual-tree, spatially explicit model of forest dynamics (Coates et al. 2003, Astrup et al. 2008a). SORTIE-ND has been developed to model complex stand dynamics including multi-layered and multi-species stands and partial harvest silviculture systems (Canham et al. 2004, Coates et al. 2009, Maleki et al. 2021) (Appendix 1).

To manage for the sustainable provision of wildlife habitat over time, the ability to project future dynamics of habitat elements and their response to disturbance is important (Holt et al. 1995). In Europe, recent studies have developed frameworks that enable researchers to extend the results of stand dynamics models to project stand-level ecosystem services (Bugmann et al. 2017, Lafond et al. 2017, Cristal et al. 2019). Several of these studies have labelled the functions used to project ecosystem services as “linker functions”. Bugmann et al. (2017 p. 8) define linker functions as: “algorithms that provide an unbiased and accurate quantification of ecosystem service provision from forest simulation model outputs”. Linker functions have been used to relate broad suites of ecosystem services such as vegetation

biodiversity and deadwood to stand dynamics resulting from forest management (Lafond et al. 2015, 2017, Bugmann et al. 2017, Blattert et al. 2017). Less common are the development of linker functions that relate species-specific habitat elements to stand structure dynamics; however, some have been developed for species such as the flying squirrel, the Eurasian tree creeper, and numerous woodpeckers and grouse species (Mönkkönen et al. 2014, Bugmann et al. 2017).

SORTIE-ND, as a spatially explicit individual-tree model, is well-suited to applying linker functions to model ecosystem services. Although output from SORTIE-ND is limited to variables that represent tree, light, and forest floor substrate (Pacala et al. 1996, Coates et al. 2003), linker functions can relate those outputs to ecosystem services such as wildlife habitat. SORTIE-ND can be used to model the response of stand structure to disturbances that result in complex stand structure such as natural disturbances (windthrow patches or species-specific pests such as mountain pine beetle), partial harvest silviculture systems and a variety of silviculture treatments (e.g., thinning or broadleaf tree removal). Applying linker functions allows researchers and forest managers to address questions regarding habitat dynamics following disturbance events or management activities.

Linker functions extend forest dynamics models to ecosystem services by representing relationships between stand structure and ecosystem elements (Elkin et al. 2013, Mönkkönen et al. 2014, Bugmann et al. 2017). The overstory tree canopy plays an important role in determining the structure and composition of the understory (Coxson and Marsh 2001, Sulyma and Coxson 2001, Bartemucci et al. 2006, Haughian and Burton 2015). Thus, habitat elements within forested stands are intrinsically linked to overstory dynamics. Developing linker functions that represent these relationships enables modelling not only tree dynamics but the corresponding dynamics of habitat as it responds to changes in the overstory. Most

studies develop linker functions from existing literature and expert knowledge (e.g., Elkin et al. 2013, Mönkkönen et al. 2014, Bugmann et al. 2017, Cristal et al. 2019). However, Lafond et al. (2015, 2017) provided instances where linker functions were derived from forest inventory data.

I used literature and informal interviews with experts to develop linker functions that represented the foraging habitat of TEC caribou and their apparent competitors, moose. I then conducted a field study and used empirical data to fit and calibrate the linker functions. These functions could be applied to a number of modelling platforms, but I developed them for use with SORTIE-ND as it was the stand dynamics model best suited to modelling the complex stand dynamics of the region.

The objectives of this chapter were to describe the method I used to develop linker functions premised on empirical data. When applied to the output from SORTIE-ND, these linker functions can be used to model the winter habitat of northern mountain caribou over space and time at the scale of the forest stand. These linker functions can support research or conservation planning designed to understand and maintain the habitat for northern mountain caribou, a species of high conservation priority.

2.2 Methods

2.2.1 Study Area and Caribou Habitat Context

The study area is located in west-central BC, Canada. The area is classified as the Sub-Boreal Spruce moist cold Babine variant (SBSmc2) (Figure 2) and characterized as a montane zone with a continental climate (Meidinger and Pojar 1991, Banner et al. 1993).

Mature upland coniferous forests are dominated by hybrid spruce (*Picea glauca* x *engelmannii*) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) with lodgepole pine and

trembling aspen (*Populus tremuloides* Michx.) as common seral species (lodgepole pine is also common in drier mature stands) (Meidinger and Pojar 1991). This area was selected because it comprises a portion of TEC winter range that is subject to timber harvesting. Wildlife managers are interested in developing timber management strategies that support the provision of winter habitat for caribou.

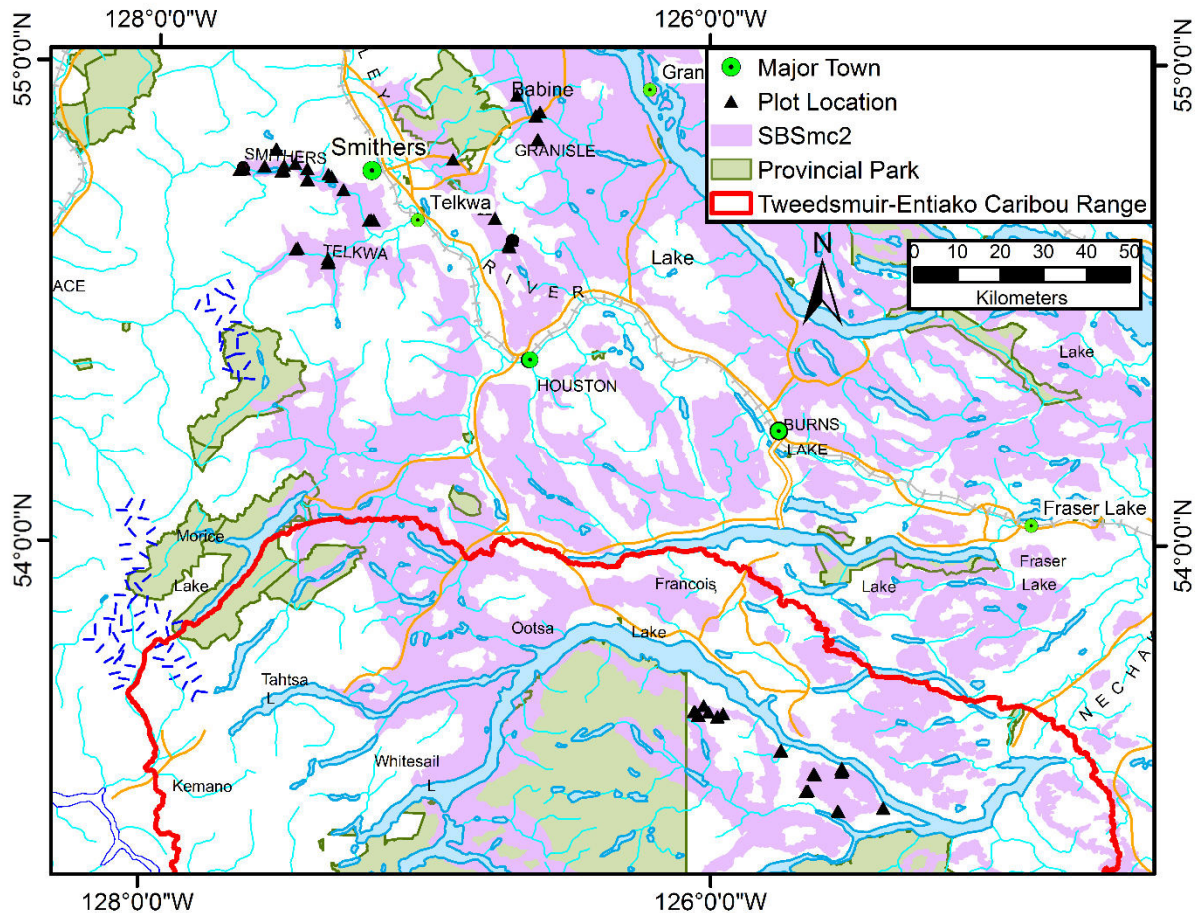


Figure 2. Distribution of empirical plots (black triangles) established within the Sub-Boreal Spruce moist cold Babine variant (SBSmc2) (purple) during the summer of 2019 in west-central British Columbia, Canada.

TEC winter habitat consists predominantly of mature (greater than 80 years of age) pine forests on poor productivity sites (Cichowski 1989, 1993). These forests support the primary winter forage of Tweedsmuir-Entiako caribou: terrestrial lichens in the genus *Cladonia* (P.

Browne) (the *Cladina* morphotype (*Cladonia* subgenus *Cladina*) and the *Cladonia* morphotype (squamulose species in *Cladonia* subgenus *Cladonia*)), *Cetraria* (Ach)., *Flavocetraria* (Kärnefelt & Thell), and *Stereocaulon* (Hoffm.) (Cichowski 1989, Cichowski and Haeussler 2013, Denryter et al. 2017). I will refer to this group of terrestrial lichen as forage lichen or simply lichen for the remainder of the thesis. This is the response variable for the first linker function.

There have been few studies of the structural attributes of pine stands within the TEC range that support abundant forage lichens. A study by Lance and Mills (1996) assessed the structure of stands used by the TEC in the Chelaslie migration corridor (this area is occasionally also used as winter habitat (Steventon 1996)). These stands were noted as having similar habitat characteristics to the winter habitat described by Cichowski (Lance and Mills 1996). The heavily used stands in the Chelaslie corridor had less than 1600 stems/ha of trees greater than 12.5 cm diameter at breast height (dbh) and stand density was rarely greater than 2000 stems/ha (Lance and Mills 1996).

High-quality caribou habitat should have abundant forage, but also relatively little risk of predation due to poor-quality moose habitat (Rettie and Messier 2000, Wittmer et al. 2007, Venier et al. 2014; see apparent competition discussion in Chapter 1). This is consistent with the known distribution of TEC as they avoid habitats that coincide with vegetation communities that are used by moose. That includes more productive site types and mixed broadleaf stands, cutblocks between 11 and 35 years of age, and spruce-dominated stands (Cichowski 2015, DeMars and Serrouya 2020).

Peek (2007) stated that forage is the most important component of habitat for moose. Although there are regional differences, the primary winter browse species for moose in northern B.C. are trembling aspen, birch (*Betula* spp.), subalpine fir, willow (*Salix* spp.), red-

osier dogwood (*Cornus stolonifera* Michx.), saskatoon (*Amelanchier alnifolia* (Nutt.) Nutt. Ex M. Roem.), highbush-cranberry (*Viburnum edule* (Michx.) Raf.), and mountain ashes (*Sorbus scopulina* (Greene) and *S. sitchensis* (M. Roem.)) (Eastman 1974, Goulet 1985, Westworth et al. 1989, Rea and Booth 2011). The suite of shrubs suitable as moose browse will hereafter be referred to as moose shrubs. The majority of these moose shrubs are associated with mesic to rich sites and younger stands (Eastman 1977, Beaudry et al. 1999).

Canopy cover, primarily from conifer trees, is also recognized as an important component of moose winter habitat (Mysterud and Østbye 1999, Peek 2007). Canopy cover provides thermal cover and snow interception that enables moose to conserve energy throughout the winter months (Eastman 1977). Throughout this paper, the cover provided by a conifer canopy is referred to as vertical cover. Moose shrub and vertical cover are response variables for the second and third linker functions developed in this study.

2.2.2 SORTIE-ND

I used SORTIE-ND to simulate within-stand dynamics. SORTIE-ND was initially developed from a small-scale disturbance model of transitional oak-northern hardwood forests in the northeastern United States (Pacala et al. 1996). In 1995, research scientists at the British Columbia Ministry of Forests in northwest BC began collaborating with the developers of SORTIE and initiated a SORTIE research program to model the dynamics of two local forest types (Canham et al. 2004, Astrup et al. 2008a). As a result, SORTIE-ND has now been parameterized for sub-boreal spruce (SBS) and northern temperate interior cedar-hemlock forests (ICHmc2) (Meidinger and Pojar 1991, Banner et al. 1993, Canham et al. 2004).

SORTIE-ND simulates changes in tree populations at the stand scale. The model uses a combination of empirical and mechanistic behaviours. Empirical behaviours (sub-models) were developed from field experiments that measured fine-scale and short-term interactions

among individual trees, to project forest dynamics (Canham et al. 2004, Coates and Hall 2005, Maleki et al. 2020). The model structure uses field experiments and testing of alternate hypotheses to best parameterize the demographic processes and tree growth relationships found in the model (Kobe and Coates 1997, Wright et al. 1998, 2000, Canham et al. 1999, 2004, LePage et al. 2000, Coates and Hall 2005, Coates et al. 2013).

SORTIE-ND is a spatially explicit, individual-tree model. The model tracks not only individual tree size, regeneration, growth and mortality information but also the spatial distribution of the trees and the simulated light environment in a grid across the entire stand (Canham et al. 2004). A snag sub-model represents the dynamics of dead trees (Bose et al. 2015). Appendix 1 provides an in-depth description of SORTIE-ND following the protocol presented by Grimm et al. (2006, 2010). I selected SORTIE-ND for this study because it is a neighborhood dynamics (i.e. stand) model that has been parameterized to represent interactions between all major tree species in the study area, and allows growth and regeneration dynamics following mountain pine beetle attack and partial cutting silviculture systems to be simulated.

2.2.3 Linker Functions

I developed functions that represented how stand structural attributes influenced target habitat elements (see Mönkkönen et al. (2014) and Cordonnier et al. (2013) for the development of a comparable framework). I used a four-step process to develop the linker functions. First, mathematical functions were chosen for forage lichen, moose shrub cover, and vertical conifer cover based on a literature review and discussions with regional experts (see Appendix 2). The predictor variables included: understory light, time since disturbance, edaphic site condition, competing low vegetation, humus depth, conifer basal area and broadleaf basal area. Second, these linker functions informed a field sampling effort where

corresponding stand structure, edaphic site condition, and vegetation community data were collected. Third, the empirical data were used to fit the linker functions. Fourth, the functions were calibrated and the predictor variables were limited to only those that could be output from the stand dynamics model SORTIE-ND.

The linker functions were designed to output a “suitability index” that represented the suitability of a stand to provide vertical cover or support the occurrence and growth of forage lichen or moose shrubs. This is not equivalent to the conventional habitat suitability index (HSI) developed by the United States Fish and Wildlife Service (1981) for the quantification of wildlife habitat (Roloff and Kernohan 1999, Pecchi et al. 2019). My linker functions did not directly model species abundance, cover or biomass nor did they evaluate habitat at the scale represented by most HSI models (Roloff and Kernohan 1999, Pecchi et al. 2019). My linker functions were also not full indices of habitat availability because the suite of predictor variables was limited to those that can be derived from SORTIE-ND output. Also, I was not able to test the relevance of all potential stand-scale variables (e.g., stand initiating disturbance intensity). The linker functions provided a proxy measure of whether a certain stand had the potential to support the occurrence and growth of lichen or moose shrubs, or provide vertical cover. As a short form, throughout this thesis I refer to this potential for a stand to support or provide a habitat element as simply “suitability” (e.g., lichen suitability or suitability for lichen). Appendix 2 describes the linker functions following the protocol presented by Grimm et al. (2006, 2010).

2.2.4 Model Description

2.2.4.1. Lichen

The suitability of a forest stand to support terrestrial forage lichen was represented as the product of time (Equation 2) since the area was disturbed, light availability in the understory (Equation 3), abundance of broadleaf trees (Equation 4), and the stand’s edaphic conditions

(Equation 5). Equation 1 illustrates how these four variables were combined multiplicatively to define the full linker function for lichen suitability. Although competing low vegetation and humus were identified as potential predictor variables, these are not presented here because they were not selected for the final set of linker functions and are not simulated by SORTIE-ND.

$$Lichen\ suitability = Time * Light * Broadleaf * Edaphic \quad (1)$$

Forage lichen requires time to establish following a stand replacing disturbance that removes or severely disturbs the forest floor. Other lichen may establish more quickly following disturbance but this linker function represents only those lichen species selected by caribou as forage lichen (Maikawa and Kershaw 1976). Previous studies have found that the cover and biomass of lichen is much less following disturbance but increases as lichens re-colonize the site (Maikawa and Kershaw 1976, Johnson 1981, Rowe 1984, Coxson and Marsh 2001). Although there are regional and ecosystem differences, studies have shown that, in general, approximately 30–50 years are required before species of forage lichen establish in quantities similar to pre-disturbance levels (Maikawa and Kershaw 1976, Johnson 1981, Carroll and Bliss 1982, Rowe 1984, Coxson and Marsh 2001). I represented this post-disturbance recovery period using a Weibull function that assumed that suitability for forage lichens was initially low and increased to an asymptote of 1 by approximately year 50 (Equation 2, Figure 3a).

$$Time = 1 - e^{-z * tdisturbance} \quad (2)$$

where *tdisturbance* represented time since stand replacing disturbance

Lichen are symbiotic organisms that consist of fungi and associated photobionts (cyanobacteria or algae) (Brodo et al. 2001, Spribille 2018). Although lichen may be present in stands with low light levels, a minimum amount of light is required to support

photosynthesis. Numerous studies have found that abundance of terrestrial lichen is positively associated with higher light levels typically found under open conifer canopies (Carroll and Bliss 1982, Sulyma and Coxson 2001, Haughian and Burton 2015, Lewis et al. 2019).

I used a logistic function to represent the positive relationship between light (GLI) and site suitability for lichen (Equation 3, Figure 3b). The inflexion point in the function represented the significant increase in lichen suitability, evident in the empirical data, at light levels between 25 to 40% (Figure 3b). Lichen suitability approached full suitability above 50% of full light.

$$Light = d + \frac{a}{1 + e^{(b - c * gli)}} \quad (3)$$

Terrestrial lichen is generally limited in abundance in broadleaf stands (Longton 1992, Crites and Dale 1998, Russell and Johnson 2019). The abundant and repeated litterfall of deciduous broadleaf trees and vascular plants limits the abundance of slow growing lichen (Canter et al. 1991, Cornelissen et al. 2001). However, terrestrial lichen can be found in low abundance in some stands with a broadleaf component (Figure 3c) (Johnson 1981). The negative logistic function provided flexibility in the rate at which lichen suitability declined in response to increasing broadleaf abundance.

$$Broadleaf = 1 - \frac{1}{1 + e^{(b1 - b2 * BAdecid)}} \quad (4)$$

where *BAdecid* represented the average basal area per hectare of all broadleaf stems

Terrestrial forage lichens grow slowly and are poor competitors in comparison to other ground vegetation and moss (Johnson 1981, Rowe 1984). These lichen survive and persist in conditions unfavourable for other vegetation (Rowe 1984, Haughian and Burton 2015). Primary determinants of vegetation abundance are soil nutrient level and water holding

capacity (Maikawa and Kershaw 1976, Meidinger and Pojar 1991, Banner et al. 1993, Coxson and Marsh 2001, Sulyma and Coxson 2001). In British Columbia, relative soil moisture regime (SMR) and relative soil nutrient regime (SNR) are indices for soil water holding capacity and nutrient availability (respectively) that are commonly used to describe edaphic site characteristics (Meidinger and Pojar 1991). These indices correlate well with field measurements of moisture and nutrient availability (Kranabetter et al. 2007, Kranabetter and Simard 2008). SMR and SNR are highly correlated in the study region and were therefore combined into one edaphic variable (Equation 5).

I used a negative logistic equation to represent the relationship between lichen suitability and edaphic condition (Equation 5, Figure 3d). Suitability is greatest on low productivity edaphic sites (low moisture or nutrients) and declines as site productivity increases. The inflexion point provided flexibility to reflect how steeply suitability declines as edaphic site productivity increases.

$$Edaphic = 1 - \frac{a4}{1 + e^{(b4 - c4 * smnr)}} \quad (5)$$

where $smnr = \frac{\frac{snr}{5} + \frac{smr}{6}}{2}$

2.2.4.2. Moose

Browse for moose during winter consists of both shrubs and low trees (Eastman 1974, Goulet 1985, Westworth et al. 1989, Rea and Booth 2011). Browse availability from trees can be derived directly from SORTIE-ND (individual tree data). However, linker functions were still required to project the relative suitability of the tree component within the stand (on a scale of 0 to 1). Linker functions were also developed to project the suitability of the stand to support understory shrubs browsed by moose. The moose shrub (Equation 7) linker function was combined with the aspen (Equation 11) and subalpine fir (Equation 12) linker functions to project the overall suitability of the stand to provide winter browse for moose (Equation 6).

$$\text{Moose browse suitability} = \frac{\text{Moose Shrub} + \text{Aspen} + \text{Subalpine Fir}}{3} \quad (6)$$

i. Moose Shrubs

The suitability of a forest stand to support shrub species used by moose for winter browse (Equation 7) was represented as a function of time since disturbance (Equation 8), conifer basal area (Equation 9) and edaphic site condition (Equation 10) (Figure 5).

$$\text{Moose shrub suitability} = \text{TimeM} * \text{Conifer Basal Area} * \text{EdaphicM} \quad (7)$$

As with lichen, shrubs require time to recover or establish following stand replacing disturbances. Abundance of moose forage has been shown to peak approximately 25 years post-disturbance (Julianus et al. 2019); a lognormal function enabled a peak in suitability (Equation 8, Figure 5a) (Canham et al. 2004).

$$\text{TimeM} = e^{-0.5 * \left(\frac{\log\left(\frac{\text{tdisturbance}}{Xo}\right)}{xb} \right)^2} \quad (8)$$

where *tdisturbance* represented time since disturbance

Conifer trees outgrow moose shrubs in height and size and over time limit the light, water and nutrients available for shrubs in the understory. I used a negative logistic function to represent the competitive effect of conifers on moose shrubs, with conifer basal area representing conifer abundance (Equation 9, Figure 5b). The shape of this function reflected the decline in suitability for moose shrubs as conifer basal area increases.

$$\text{Conifer Basal Area} = 1 - \frac{aaa}{1 + e^{(bbb - ccc * \text{conBA})}} \quad (9)$$

where *conBA* represents total basal area of conifers greater than 12.5 cm dbh

Understory plants require moisture and nutrients to grow. Following bark beetle outbreaks, competition from overstory trees is rapidly reduced resulting in an increase in available soil

moisture and nutrients. A corresponding increase in understory vegetation abundance has been documented (Pec et al. 2015, Cichowski and Haeussler 2020). Therefore, I hypothesized that in general, as site productivity increases, the biomass of understory vegetation will increase. I used a simple linear function to represent the positive relationship between edaphic condition and suitability to support moose shrubs (Equation 10, Figure 5c).

$$EdaphicM = \frac{\frac{snr}{5} + \frac{smr}{6}}{2} \quad (10)$$

ii. *Aspen*

Young aspen trees often comprise a component of moose winter diet (Eastman 1977, Rea 2014). Aspen is available as browse until fresh shoots are out of reach of moose (Cumming 1987, Timmermann and McNicol 1988). Vegetation between 50 cm and 3 m in height is considered accessible to moose in the winter (Peek et al. 1976, Cumming 1987, Timmermann and McNicol 1988). I used a linear function to reflect the increase in suitability as stem density of young aspen increases (Equation 11, Figure 5d). I set a threshold, above which, additional stems did not provide a further increase in browse suitability.

$$Aspen = \min\left(\frac{at}{maxat}, 1\right) \quad (11)$$

where *at* represented the density of aspen 0.5 - 3 m in height and *maxat* represented the density threshold for aspen

iii. *Subalpine fir*

Advanced regeneration of subalpine fir constitutes a significant component of moose diet in some areas and some winters (Eastman 1977, Rea 2014). For example, Hodder et al. (2013) found that approximately 45% of moose diets consisted of subalpine fir during a deep-snow winter. I used a linear function to reflect the increase in browse suitability with increased availability of subalpine fir stems (Equation 12, Figure 5e). Similar to aspen, I applied a

maximum density threshold and only trees 0.5 - 3 m in height contributed to browse suitability.

$$Subalpine\ fir = \min\left(\frac{bl}{maxbl}, 1\right) \quad (12)$$

where *bl* represented the density of subalpine fir 0.5 - 3 m in height and *maxbl* represented the density threshold for subalpine fir

iv. *Vertical cover*

Canopy cover has been shown to provide significant value for moose winter habitat through snow interception and thermal protection (Peck et al. 1976, Eastman 1977). I selected a positive linear function to represent the increase in suitability with increased conifer presence. Conifers greater than 10 m in height are considered to provide suitable vertical cover (Allen et al. 1987, Timmermann and McNicol 1988). Because the function was linear, a maximum threshold was required. In discussions with local experts, fifty years of age was regarded as the approximate age at which stands in the region provided sufficient cover for moose (Crowley, Hodder, Johnson, pers. comm. 2020). This was supported by results from Norway that found moose increased selection of stands greater than 40 years of age in winter (Bjørneraas et al. 2011). Local growth and yield curves (Goudie 1984) were used to determine that, at age 50, hybrid spruce and lodgepole pine stands achieved a basal area of 30 m²/ha. Therefore the maximum threshold for vertical cover was set at a conifer basal area of 30 m²/ha.

$$Cover = \min\left(\frac{con}{maxcon}, 1\right) \quad (13)$$

where *con* represented basal area of conifers greater than 10 m in height and *maxcon* represented the threshold for conifer basal area

2.2.5 Field Data Collection

I established plots and collected data across the SBSmc2 subzone (Figure 2). Due to logistical constraints, I did not restrict sampling to solely within the winter habitat of the TEC. This improved the dataset as I was able to sample mature stands with live pine trees that were located in the western portion of the SBSmc2. There was lower incidence of MPB attack in this area. In addition, the larger sample area contained unlogged, mature stands across a broader range of edaphic site types.

I used a purposeful sampling approach to acquire a balanced dataset across three gradients of site and stand conditions. Purposeful sampling was employed because it provides an efficient means to acquire a balanced data set that includes rare stand types and ecosystems (Lilles and Astrup 2012). This site selection method was employed by other studies in the region that used the same analysis methods (Lilles and Astrup 2012, Coates et al. 2013, 2018).

Gradients of stand age, trees species composition, and edaphic condition were selected to guide sampling with the intent to acquire a representation of the full range of stand and site variables.

I developed maps that stratified the study area according to: (1) stand age (four age classes: 0–40, 41–80, 81–140, > 140 years of age), (2) tree species composition (aspen leading stands, pine leading stands, spruce leading stands, subalpine fir leading stands), and, where available, (3) edaphic condition (from poor and subxeric to rich and subhygric). I used the Province of BC's Vegetation Resource Inventory mapping (British Columbia Data Catalogue n.d.) and available ecosystem mapping to develop these maps and identify potential sample sites. To develop a sample plan, I identified stands that were mapped as containing rare combinations of stand conditions missing from my sample set (e.g., dry sites, aspen stands, mature spruce stands on mesic or productive sites). Other suitable stands, encountered in the vicinity, would

be opportunistically sampled. I limited sampling to stands that were within approximately 2000 m of a road or a reasonable walking distance.

I sampled stands if they were uniform in stand structure, uniform in edaphic condition (soil moisture and nutrient regime), and at least 50 m from a disturbance edge. To be considered uniform in stand structure, the stand needed to have a similar species composition and similar canopy structure throughout (e.g., either uniformly dense or uniformly open). This was to control for a relatively uniform light level within the plot. Once a stand was determined to be suitable, plot center was established by moving 10 paces along a randomly selected azimuth.

Each sample site consisted of two nested plots. Large plots were 7.98 m in radius (200 m²) and were used to describe the site, measure large trees (all live and dead trees > 12.5 cm dbh), perform a vegetation cover assessment, and survey for signs of moose browsing and pellet piles. I also assessed the percent cover of ground cover in the large plots (low growing vegetation, terrestrial cryptogams, litter, wood, and rock). Within a smaller 3.99-m radius plot (50 m²), I measured trees less than 12.5 cm dbh.

Site description

I followed the Province of British Columbia's "Field Manual for Describing Terrestrial Ecosystems" (hereafter referred to as the Field Manual) to record sample site information and describe the ecological conditions at each sampled site (2010). Site information included: GPS location, elevation, slope, aspect, mesoslope position, surface shape, and stand structural stage. For naturally regenerated stands, I determined stand age by taking a tree core from one of the dominant canopy trees (at 1.3 m height, corrected for the time to grow to 1.3 m using height-age site index curves (Thrower et al. 1994)). For plantations, I used the age of the planted trees recorded in the Province of BC's silviculture database. In mountain pine beetle attacked stands, I estimated the time since mountain pine beetle attack by noting the years

since release when counting the age of a tree. I cross-referenced this estimate by counting the number of years of release exhibited in the growth whorls of understory advance regeneration. I dug a soil pit in each plot to a minimum depth of 30 cm or until a restricting soil layer was reached. I recorded the following soil information as per the Field Manual: depth of humus layer (including litter, fermented, and humic organic horizons (LFH)), humus form identification (mor, mormoder, moder or mull), seepage depth, rooting depth, root restricting layer, A and B horizon identification, A horizon depth, dominant soil texture (of the rooting zone), and percentage of coarse fragments (in the rooting zone) (Province of British Columbia 2010). I used the soil and site description information to determine the soil moisture regime and soil nutrient regime of each site. Vegetation was used to cross-reference the site determination and site series (Banner et al. 1993).

I took hemispherical photos at five locations within the plot: one at plot center and one in each ordinal direction, 3.99 m from plot center. The photos were taken 1.3 m above the ground with a Nikon Coolpix 5000 digital camera and Nikon FC-E8 fisheye lens converter. I analysed the images using Gap Light Analyzer software (GLA 2.0) to obtain the gap light index (GLI), a measure of the percentage of full sunlight (sum of direct and diffuse light) that a point receives throughout the growing season (Frazer et al. 1999). GLA models the seasonal and daily solar radiation transmitted through the canopy (Canham 1988, Wright et al. 1998). I used the mean GLI of the five photos to provide a metric of light available in the understory of the stand.

Ground Cover

I assessed lichen cover and other classes of ground cover in each of the four quadrants of the 7.98-m plot. I used an ocular method to estimate the percent cover of 12 classes of ground cover: forage lichen, non-forage lichen (all other species of lichen), feathermoss (*Pleurozium schreberi*, *Ptilium cristaecristensis*, *Hylocomium splendens*), non-feathermoss moss, dwarf

shrubs, grass, herbs, conifer litter (woody debris < 5 cm in diameter), deciduous litter, wood (> 5 cm in diameter), rock, and bare ground (Province of British Columbia 2010). Lichen cover was recorded by species and was subsequently averaged across all quadrants to provide the estimate of percent cover by species for the plot.

I used percent cover of forage lichen as a surrogate for forage lichen biomass. Bergerud (1971) and Thomas et al. (1996) demonstrated a strong correlation between lichen cover and biomass and recommend the use of cover where efficient measurement is required. Johnson et al. (2000) noted that caribou browsing would reduce lichen biomass; browsing pressure could be inconsistent and percent cover was considered to be less sensitive to bias. Also, lichen cover is measured much more quickly than volume. That efficiency was important considering that I collected an extensive amount of data within in each plot. Lichen cover was normalized to produce a relative index of cover that ranged from 0 to 1.

Vegetation and Tree Mensuration

I recorded vegetation cover for each species located in the 7.98-m radius plot. I assessed vegetation by layer: tree (A), shrub (B), herb (C), and moss/lichen/seedling layer (D) (Province of British Columbia 2010). I assessed cover of tree species by sub-layer with cover of each species (any woody species > 10 m in height) differentiated into cover of the sub-layer: dominant trees (A1), main canopy trees (A2), sub-canopy trees (A3). I differentiated the cover of shrub species (woody plants including trees and shrubs) into a tall shrub layer (2–10 m in height) and a low shrub layer (< 2 m in height except low-growing woody or trailing plants that are usually < 15 cm in height) (Province of British Columbia 2010). I evaluated the cover of each species of terrestrial moss, lichen, liverwort, and tree seedling < 2 years old (D layer). I followed the methods presented in the Field Manual for a full vegetation plot with the only differences being the plot size and shape. Unknown species were collected for later identification.

I measured the diameter (dbh) of all standing trees ≥ 12.5 cm dbh in the 7.98-m radius plot. In addition to dbh, I recorded tree species, live/dead status, canopy position (dominant, co-dominant, intermediate or suppressed) and cause of death (if possible). I tallied the number of fallen trees killed by mountain pine beetle and estimated the dbh of each fallen tree. I measured the height of a tree that represented the average canopy height of the stand.

I assessed smaller trees in the 3.99-m radius plot. I measured the diameters of trees with 7.5–12.4 cm dbh. I tallied trees < 7.5 cm dbh by the following size classes: 0–10 cm in height, 10–30 cm in height, 30–130 cm in height, 0–2.4 cm dbh, 2.5–4.9 cm dbh, and 5–7.4 cm dbh. I recorded tree species and live/dead status for trees of all size classes.

Browse on Moose Shrubs

I recorded the species and percent cover of each shrub and shrub-sized tree within the 7.98-m plot. For the purposes of quantifying available moose browse, I collected further data on individuals that had branches available for browse (< 3 m height). For these individuals, I recorded percent cover and modal height (measured to the nearest 10 cm). I also assessed the trees and shrubs for signs of moose browse. Moose and deer browse were difficult to distinguish. The areas sampled were not considered high-quality winter habitat for deer therefore browsing was attributed to moose. Signs of moose browse was differentiated from rabbit browse because moose browsing results in a torn, ragged edge; rabbit browsing leaves a sharp edge at a 45° angle.

I adapted the “Procedures for Environmental Monitoring in Range and Wildlife Habitat Management Version 5.0” method to assess the degree of browse (Habitat Monitoring Committee 1996). For each species, I estimated the percent of each plant browsed instead of assigning an ordinal browse class. I also assessed the hedging on any species that was browsed. I used the utilization form classes outlined in the B.C. Ministry of Environment

manual “Describing Ecosystems in the Field” (Luttmerding et al. 1990). I condensed the six-code system into two simple codes: code 1 indicated little or no hedging and code 2 indicated moderate to severe hedging. The number of piles of moose pellets in each plot was also recorded.

I used the moose browse data in combination with regional literature sources (Eastman 1974, Goulet 1985, Westworth et al. 1989, Baker 1990, Rea and Booth 2011) to determine which plant species should be considered moose forage in the study area. The majority of browse in our field plots occurred on species that were previously documented as winter browse: trembling aspen, subalpine fir, willow, red-osier dogwood, saskatoon, highbush-cranberry, and mountain ash. However, additional species were also browsed in some field plots. I compared the amount that each species was browsed to the abundance of the species in the plots. Red elderberry (*Sambucus racemosa* L.) and Douglas maple (*Acer glabrum* Torr.) occurred in low abundance but moderate to heavy browse was evident when the shrubs were present; therefore, I included these species as moose shrubs. Black cottonwood (*Populus balsamifera* ssp. *Trichocarpa* (T. & G.) was also browsed when present but was not included because it is a tree. Twinberry (*Lonicera involucrata* (Richardson) Banks ex Spreng.), prickly rose (*Rosa acicularis* Lindl.), and thimbleberry (*Rubus parviflorus* Nutt.) were only occasionally browsed when the species were present. Hedging was not evident, therefore, I did not include these species as moose shrubs.

I derived the moose shrub variable from the total cover of all moose shrub species in a plot. Total cover was normalized across all plots to provide an index of cover between 0 and 1 for each plot.

2.2.6 Linker Function Fitting and Calibration

I used the empirical data (76 sample points) to fit and calibrate the lichen and moose shrub linker functions. During calibration, predictor variables were limited to only those available as SORTIE-ND output.

First, I used likelihood methods presented in Canham and Uriarte (2006) to parameterize and select the most parsimonious models. The likelihood method follows a 4-step process: “(1) model specification, (2) parameter estimation using maximum likelihood methods, (3) model comparison, and (4) model evaluation” (Canham and Uriarte 2006 p. 64). I compared a nested suite of models to determine the degree of support for including each of the hypothesized predictor variables (Table 1 and Table 2; see Lilles and Astrup (2012) for a similar application of the likelihood method)). I used the Cran R ‘likelihood’ package (v1.7, (Murphy 2015)) in R (version 4.0; R Core Team 2021) for parameterization and model comparison. This package uses simulated annealing to produce maximum likelihood estimates for each parameter in each model and calculates support intervals for parameter estimates (Edwards 1992, Goffe et al. 1994). Parameters within each model were estimated simultaneously (Canham and Uriarte 2006, Murphy 2015). The likelihood estimation used in this package requires a probability model; here I used a gaussian distribution for the probability density function. In this package R^2 is calculated as the sum of squared expected divided by the sum of squared total (Murphy 2015). Akaike information criterion corrected for small sample size (AIC_c) was used to assess model fit and evaluate the suitability of functional forms (Burnham and Anderson 2002).

After parameterizing the functions and selecting the model with the most support from the data, I evaluated the best fit parameters and model forms. For some functions, calibration was required. Due to the small sample size, there was the potential that the likelihood method

Table 1. Structure and evaluation of linker functions developed to project the relative value of a forest stand to support forage lichens. Linker functions were developed using data collected in sub-boreal forests of west-central British Columbia during the summer of 2019. Goodness of fit and parsimony of each model was assessed using ΔAIC_c and R^2 .

Model	Variables	Number of parameters	AIC _c	ΔAIC_c	R^2
Null		1	13929.3	13380.5	0
Light	light	4	605.7	56.9	0.17
Time	time	3	616.9	68.1	0
Broadleaf	BAdecid ¹	3	613.5	64.7	0.05
SMR ²	smr	4	578.2	29.4	0.42
SNR ³	snr	4	574.8	26.0	0.44
SMNR ⁴	smnr	4	574	25.2	0.45
Full Model (C.Veg ⁵)	time * light * decid * veg.effect	8	582.7	33.9	0.46
Full Model (SMNR)	time * light * decid * smnr	8	562.4	13.6	0.58
Full Model + Humus	time * light * decid * smnr * humus	9	548.8	0	0.66

¹ BAdecid = basal area of broadleaf trees (m²/ha) ² SMR = relative soil moisture regime; ³ SNR = relative soil nutrient regime; ⁴ SMNR = (SMR + SNR) / 2; ⁵ C.Veg = competing low vegetation.

overfit the data. Some best fit statistical models produced inappropriate values that did not enable suitability on sites where the empirical data showed habitat elements did occur. For these situations I calibrated the linker function to ensure a minimum level of suitability was possible (Table 3, Table 4, Appendix 3).

Metrics of the tree species that are browsed by moose (i.e., aspen and subalpine fir stem density) and conifer cover (BA) are directly output by SORTIE-ND models, and therefore did not require calibration.

2.3 Results

2.3.1 Lichen

In my field plots, the maximum cover of terrestrial forage lichen was 61% (mean cover was 5.3%, median cover was 0.04%) (Figure 15 in Appendix 4). I used 61% to define the

Table 2. Structure and evaluation of linker functions developed to project the relative value of a forest stand to support forage shrubs used by moose. Linker functions were developed using data collected in sub-boreal forests of west-central British Columbia during the summer of 2019. Goodness of fit and parsimony of each model was assessed using ΔAIC_c and R^2 .

Model	Variables	Number of parameters	AIC_c	ΔAIC_c	R^2
Null		1	479.9	162	0
SMR ¹	smr	2	324.8	6.9	0.11
SNR ²	snr	2	332	14.1	0.02
Light	light	3	334.7	16.8	0.01
Time	time	4	325.5	7.6	0.15
Conifer BA ³	conBA	4	328.3	10.4	0.12
SMR, SNR, Light	SNR * SMR * Light	3	324.8	6.9	0.13
SMNR ⁴ , Light	SMNR * light	3	325.6	7.7	0.12
SMNR, Light, Time	smnr * time * light	5	321	3.1	0.22
SMNR, Light, Time, Conifer BA	smnr * time * conBA * light	7	320.4	2.5	0.27
SMNR, Light, Time, Conifer BA 12.5 ⁵	smnr * time * conBA12.5 * light	7	320.3	2.4	0.28
SMNR, Light, Time, Conifer BA 17.5 ⁶	smnr * time * conBA17.5 * light	7	318.9	1	0.29
SMNR, Time, Conifer BA 12.5	smnr * time * conBA12.5	6	317.9	0	0.28

¹ SMR = relative soil moisture regime; ² SNR = relative soil nutrient regime; ³ BA = basal area (m²/ha) of all conifer trees; ⁴ SMNR = (SMR + SNR) / 2; ⁵ BA 12.5 = basal area of all conifer trees with diameter at breast height (dbh) $\geq$ 12.5 cm; ⁶ BA 17.5 = basal area of all conifer trees with dbh $\geq$ 17.5 cm

maximum Lichen Suitability Index of 1.0 (Figure 3). For lichen, the non-linear model with time, light, broadleaf basal area, edaphic site and humus was the model that best fit the data (Full Model + Humus, Table 1). However, humus data can not be derived from SORTIE-ND output so I selected the second-best model for the lichen suitability linker function (Full Model (SMNR)).

Lichen suitability approached maximum suitability within 50 years following a stand-replacing disturbance (Figure 3a). Lichen suitability, and observed lichen cover, increased with increasing light availability (Figure 3b). For the light component of the lichen linker function, I set the minimum suitability to 0.2 (Table 3, d = 0.2) because forage lichen

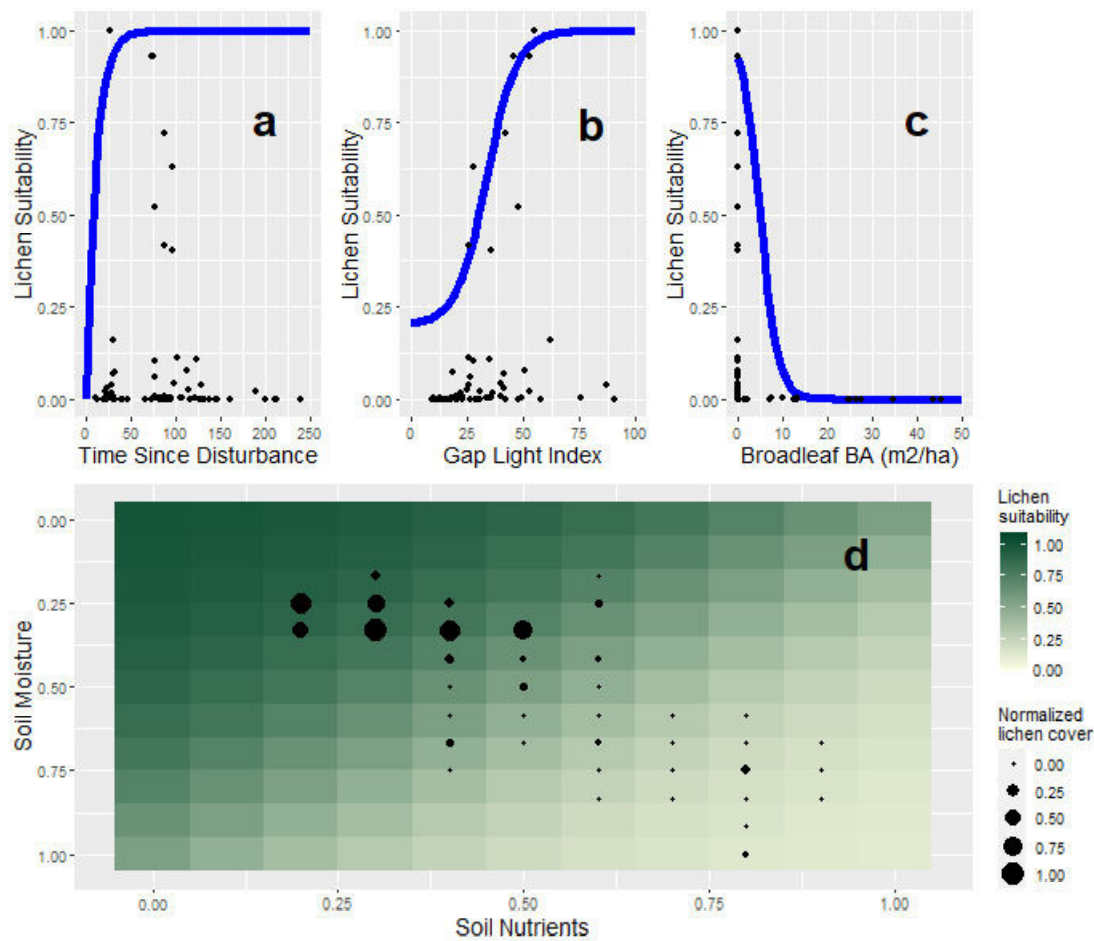


Figure 3. Linker function components that represent how the suitability of a stand to support forage lichen varies as a function of stand state: (a) years since stand replacing disturbance, (b) light level represented by Gap Light Index (GLI), (c) basal area of broadleaf trees in the stand and (d) soil nutrients and soil moisture (normalized gradients: SNR/5 and SMR/6 respectively). Linker functions are represented by the blue lines in (a) - (c) and by shading in (d). Empirical plot data ($n = 76$) collected during the summer of 2019 in sub-boreal forests of west-central British Columbia are represented by black dots.

occasionally occurred when understory light was very low (Figure 3b). The suitability of a stand to support lichen decreased as broadleaf tree basal area increased (Figure 3c). I calibrated the logistic function to enable stands with a small broadleaf component to support lichen suitability since lichen occurred in plots with up to a 10% broadleaf component. I set the inflection point at a low broadleaf basal area of 5 m²/ha (Figure 3c). Lichen suitability, and observed lichen cover, was greatest in dry stands with low soil nutrients (Figure 3d). The edaphic component of the lichen linker function was calibrated so that the poorest productivity edaphic sites in the empirical data (that had the greatest amount of lichen) had

Table 3. Parameter values for linker functions developed to project the relative value of a forest stand to support forage lichen in west-central BC: maximum likelihood estimates (with support intervals) and calibrated parameter values (where calibration occurred) are shown for each of the parameters.

Lichen Linker Function Parameter	Maximum Likelihood Estimate	Support Interval	Calibrated Parameter Value
z	0.09	0.04 – 5.00 (upper bound set to 5.0)	
a	1 (not estimated)	n/a	0.8
b	4.98	4.33 – 5.68	
c	0.15	0.14 – 0.18	
d	0 (not estimated)	n/a	0.2
b1	n/a ¹		2.5
b2	n/a ¹		0.5
a4	0 (not estimated)		0.9
b4	6.15	5.72 – 6.53	4
c4	17.70	16.63 – 18.87	8

¹ b1 and b2 did not have a maximum likelihood estimate because a Weibull model was initially included in the model set. It was not included in the final linker function because the Weibull form did not allow for lichen occurrence at low levels of overstory broadleaf abundance.

suitability approaching 1.0 (Figure 3d) (see also Haughian and Burton 2015). The minimum suitability of 0.1 ($a = 0.9$) was set to reflect the occasional sparse presence of lichen on some higher moisture sites (Figure 3d, (Ahti and Oksanen 1990)).

Compared to the empirical data, the lichen linker function predicted lichen suitability well for plots with > 0.2 suitability (Figure 4). The linker function over-predicted lichen suitability for many plots with low observed suitability (< 0.2). The root mean squared error was 0.2045.

2.3.2 Moose Shrubs

The maximum horizontal cover of moose browse in the empirical data was 10%; this was used to define the maximum Moose Shrub Suitability Index of 1 (mean cover was 1.5%, median cover was 0.8%) (Figure 15 in Appendix 4). I selected the model with the best fit to the data as the linker function for suitability for moose shrubs: time, conifer basal area and edaphic site (SMNR, Time, Conifer BA 12.5, Table 2).

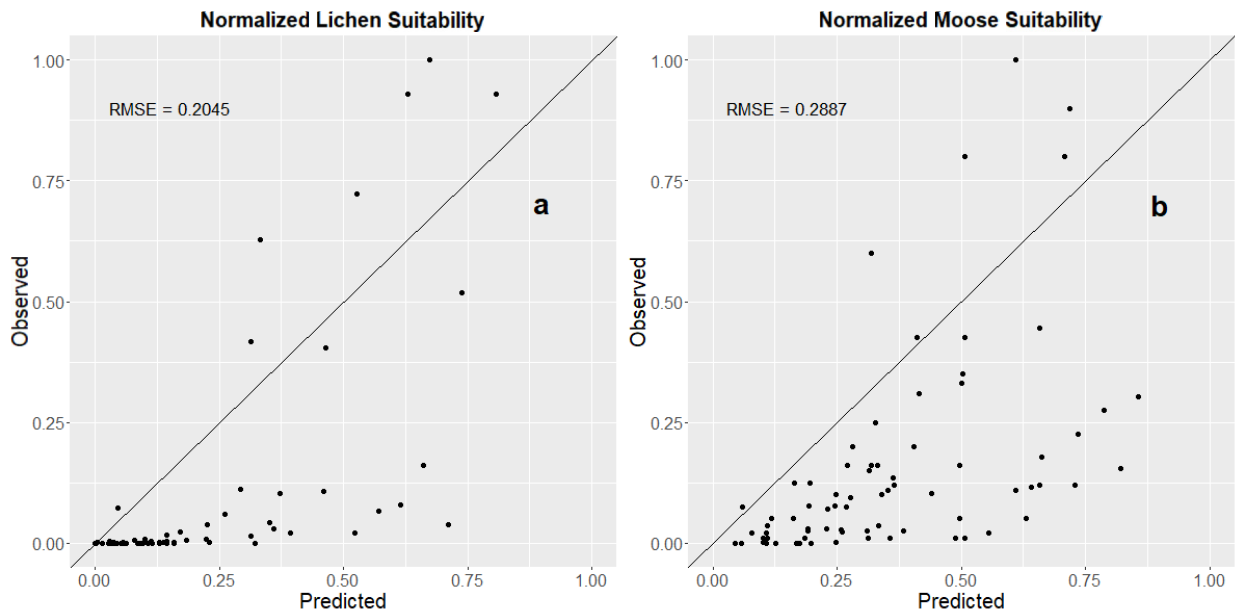


Figure 4. Observed lichen (a) and moose shrub (b) suitability estimated from empirical plots ($n = 76$) vs. predicted suitability derived from developed linker functions. Empirical data collected in sub-boreal stands in west-central British Columbia during the summer of 2019.

Abundance of moose shrubs was greatest in stands 20–30 years post-disturbance (Figure 5a), and subsequently decreased as stands aged. The potential for elevated moose shrub suitability was maintained until the basal area of large conifers (> 12.5 cm dbh) reached ~ 20 m^2/ha (Figure 5b); above this basal area, moose shrub cover declined. I set a lower threshold for moose suitability at 0.25 for stands with conifer basal areas greater than 40 m^2/ha (Table 4). This reflected the presence of moose shrubs in some stands with greater conifer basal area (Figure 5b). In contrast to the response of lichen cover to edaphic conditions, the occurrence of moose shrubs was greatest in stands with high soil moisture and nutrient levels (Figure 5c).

Shrubs eaten by moose grow across a broad range of edaphic sites (Figure 6). For example, willow (*Salix* spp.) was found across all edaphic sites whereas saskatoon was generally found on poorer productivity sites and red-osier dogwood on higher productivity sites.

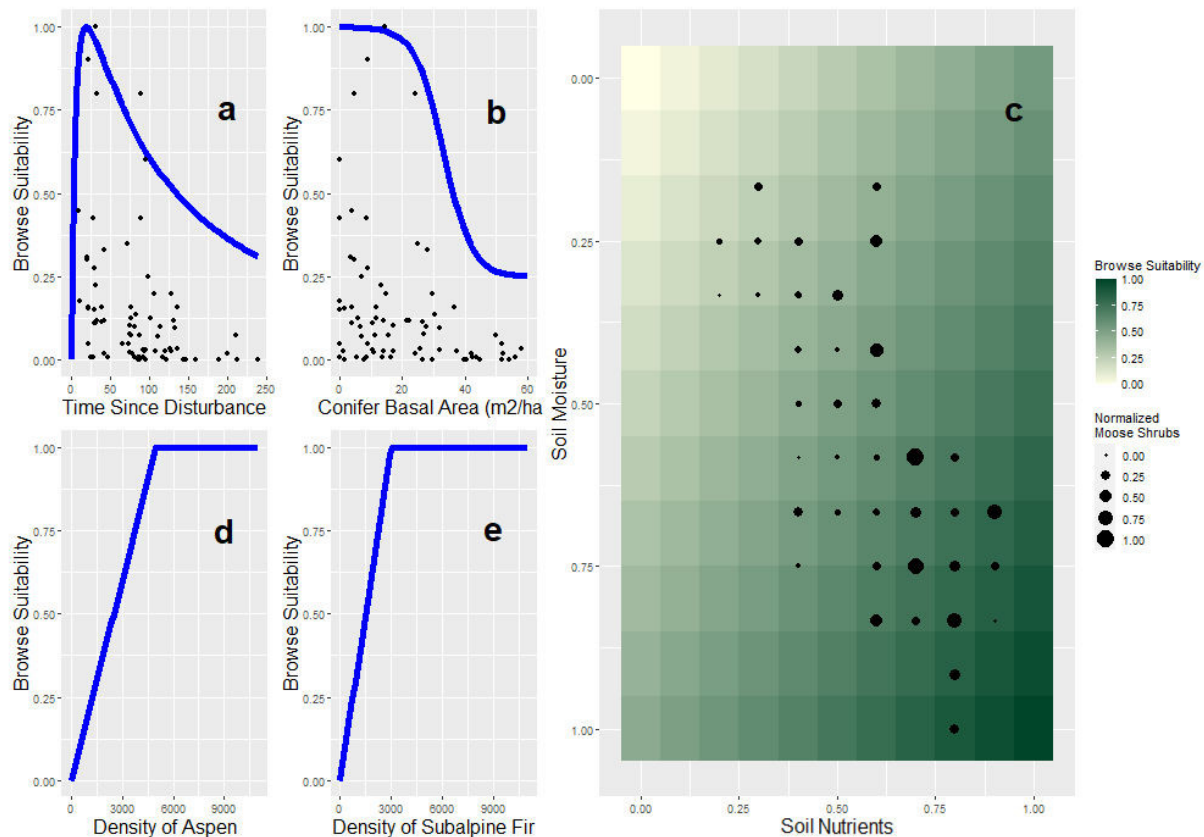


Figure 5. Linker function components that represent how the suitability of a stand to support moose shrubs for forage varies as a function of stand state: (a) years since stand replacing disturbance, (b) basal area of all conifers greater than 12.5 cm dbh, c) soil nutrients and soil moisture (normalized gradients: SNR/5 and SMR/6 respectively), and (d) and (e) density of aspen and subalpine fir trees (respectively) 0.5 - 3 m in height. Linker functions are represented by shading in (c) and blue lines in the other panes. Empirical plot data ($n = 76$) collected during the summer of 2019 in sub-boreal forests of west-central British Columbia are represented by the black dots.

Table 4. Parameter values for linker functions developed to project the relative value of a forest stand to support forage shrubs used by moose in west-central BC: maximum likelihood estimates (with support intervals) and calibrated parameter values (where calibration occurred) are shown for each of the parameters.

Moose Shrub Linker Function Parameter	Maximum Likelihood Estimate	Support Interval	Calibrated Parameter
Xo	19.58	10.77 – 40.88	
Xb	1.64	1.15 – 3.03	
aaa ¹	1 (not estimated)	n/a	0.75
bbb	7.28	5.61 – 9.95	
ccc	0.22	0.16 – 0.29	
maxat			5000
maxbl			3000
maxcon			30

¹ aaa did not have a maximum likelihood estimate because it was set to 1 during model fitting and therefore was not estimated (aaa = 1).

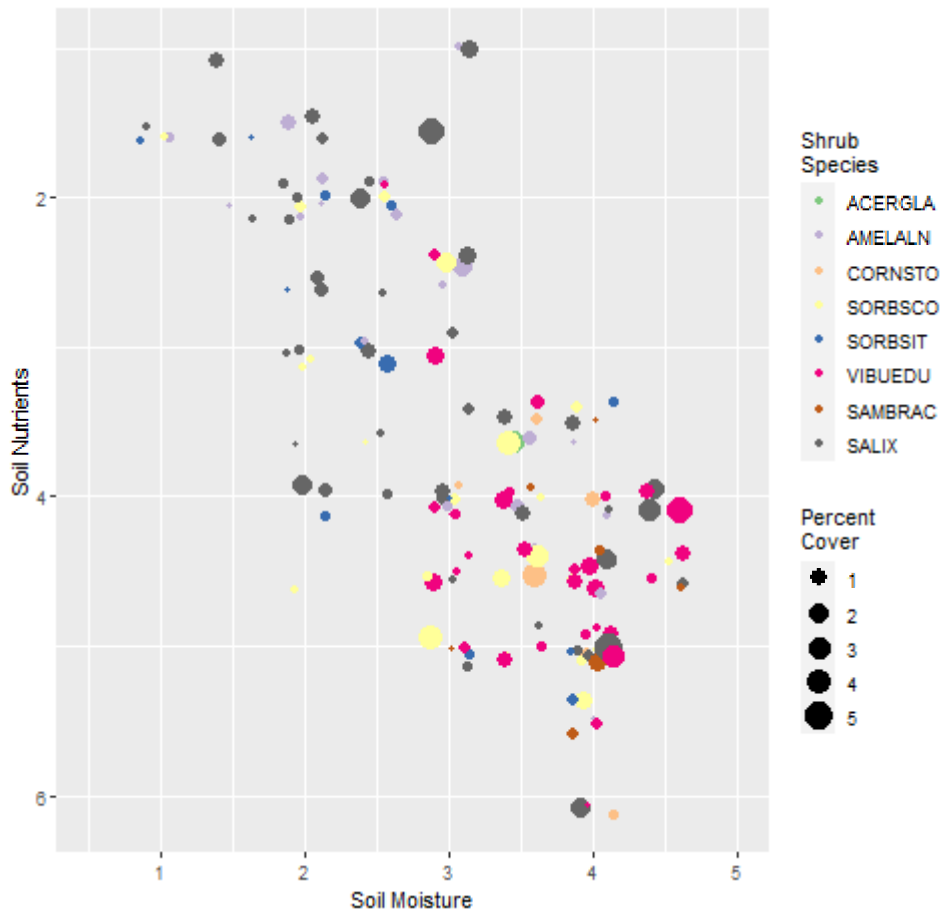


Figure 6. Distribution of species of moose shrubs across soil moisture and nutrient gradients. Data points are scaled in size to represent the percent cover of each observation in the empirical dataset ($n = 76$). Data points are displaced slightly to display individual points that would otherwise entirely overlap at the same moisture/nutrient junction. Species codes: ACERGLA – Douglas maple, AMELALN – saskatoon, CORNSTO – red-osier dogwood, SORBSCO – western mountain-ash, SORBSIT – Sitka mountain-ash, VIBUEDU – highbush-cranberry, SAMBRAC – red elderberry, SALIX – willow. Data collected during the summer of 2019 in sub-boreal forests of west-central British Columbia.

Density of aspen and subalpine fir between 50 cm and 3 m in height are direct outputs of the stand simulation model. The suitability of a stand to support moose browse increased with increasing abundance of these trees until an asymptote was reached at 5000 and 3000 stems/ha (Figure 5d and Figure 5e, respectively). The distribution of aspen and subalpine fir saplings varied significantly within the empirical data (Appendix 4).

Compared to the empirical data, the moose shrub linker function predicted shrub suitability better for plots with > 0.4 suitability than for plots with < 0.4 suitability (Figure 4). The linker

function over-predicted moose shrub suitability for many plots. The root mean squared error was 0.2887.

2.3.3 Moose Cover

Conifer trees provide vertical cover, contributing to the suitability of a stand as moose habitat. Vertical cover suitability increased as conifer basal area increased until an asymptote was reached at a conifer basal area of 30 m² (conifers > 12.5 cm dbh, Figure 7). Conifer basal area varied within the empirical dataset between 0 and 58 m²/ha (Appendix 4).

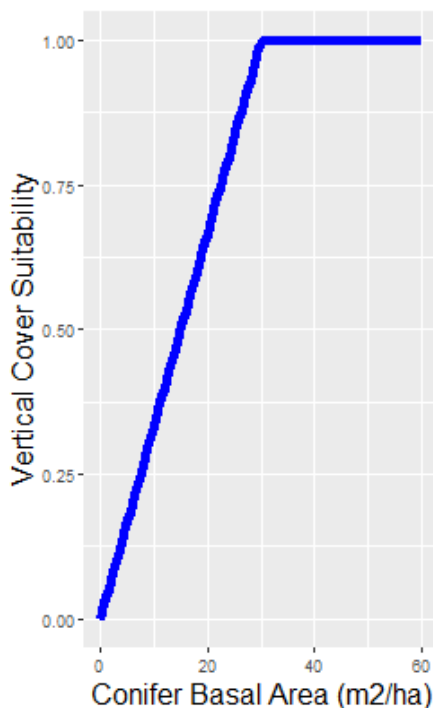


Figure 7. The linker function that represents the effect of conifer basal area (trees taller than 10 m) on the suitability of a stand to provide vertical cover in winter.

2.4 Discussion

Past studies have developed linker functions primarily through extensive literature review, related studies, and application of expert knowledge (Cordonnier et al. 2014, Mönkkönen et al. 2014, Blattert et al. 2017, Cristal et al. 2019). I built on that approach by also incorporating empirical data I collected during a focused field study. I used the empirical data

to improve the predictive ability of these linker functions for the target study area and local caribou population. The empirical data enabled me to select predictor variables that best explained patterns in the data and to evaluate the fit of the linker functions.

I used simulated annealing to test and simultaneously parameterize the linker functions. This resulted in linker functions that isolated the effect of each individual predictor variable on habitat suitability. For example, the linker function for time reflects solely the time required for lichen to re-establish on a site following stand-replacing disturbance. The function is not initially concave as is often observed in stands where forage lichen becomes established following fire, declines as conifer trees establish, and then increases again as stands mature (Thomas et al. 1996). However, when the conifer basal area linker function is combined with the time linker function, the expected concave pattern becomes evident for stands that follow this successional pattern. The separation of these two linker functions provided the flexibility to represent the pattern observed in other stand types that transition from lichen-dominated to moss-dominated understories due to increasing overstory density and biomass (Sulyma and Coxson 2001, Horstkotte and Moen 2019). Fitting these functions simultaneously enabled the linker functions to model this interaction of time and overstory structure.

At low suitability, predicted values exceed observed values because predicted values only reflect the influence of stand structure and edaphic site on lichen and moose shrub development (Figure 4). Other ecological variables also influence stand suitability and, if incorporated, would dampen the suitability of sites to support the elements. These variables include past disturbance type and severity, competing vegetation and bryophytes, and edaphic differences between moose shrub species. In addition, landscape and microsite scale factors are also known to influence the provision of caribou habitat (Sulyma and Coxson 2001, Wittmer et al. 2007, Haughian and Burton 2015). Although the suite of linker functions may

not represent a complete ecological model, the linker functions allow for comparisons of the relative effect of changes in stand structure on forage lichen and moose shrub suitability.

Disturbance type and severity are not reflected in the lichen and moose shrub linker functions though they play a significant role in the regeneration success of these communities (Viereck and Schandelmeier 1980, Cichowski et al. 2022). Disturbances such as wildfire, timber harvest and insect attack differ in terms of the degree of impact that they have on vegetation communities and the potential for persistence or regeneration for individual species.

Disturbances impact vegetation either directly through physical damage or indirectly through the provision of substrate suitable for regeneration or abundance of competing vegetation (most significant for lichen) (Viereck and Schandelmeier 1980, Haughian and Burton 2015, Lewis et al. 2019).

Linker functions did not directly reflect disturbance type and severity because historical disturbance data were not available. Even if available, expanding sampling to extend across disturbance type and severity gradients would not have been feasible. Balanced sampling of each disturbance type across gradients of intensity, would have required more resources and time than available for this study. In addition, modelling the effects of disturbance type and severity are not fully available in SORTIE-ND.

Humus depth is affected by past disturbance severity and type: low intensity surface fires, high intensity crown fire, and season of burn will influence the degree to which the fire burns the humus layer (Viereck and Schandelmeier 1980, MacCracken and Viereck 1990). Lichen is associated with microhabitats that have a shallow humus layers (Haughian and Burton 2015). The lichen model that included the depth of the forest floor (Table 1, model “Fullmodel + Humus”) had substantially more support from the data than the comparable model without humus thickness ($\Delta AIC_c = 13.6$). Humus depth could be considered a

surrogate metric that reflects intensity of historic stand-level disturbance. However, many other factors also influence humus depth including dominant tree species, soil type, humus form, and associated microbial activity, etc. Humus layer dynamics are not modelled in SORTIE-ND so it was not included in the final linker function set.

Understory vegetation influences lichen abundance through litter fall in addition to competition for light, space, and resources (Cornelissen et al. 2001). Increases in vegetation cover from dwarf shrub species such as kinnikinnick and dwarf *Vaccinium* species have been correlated with reductions in terrestrial lichen communities following mountain pine beetle attack (Seip and Jones 2010, Cichowski and Haeussler 2020). Understory vegetation other than tree regeneration is not currently modelled in SORTIE-ND. I tested a linker function that included a function representing the suitability of a site to support low-growing (e.g., dwarf shrubs) vegetation (see Table 1, model “Full Model (C.Veg)”). However, limiting the suite of linker functions to incorporating SMR and SNR directly had greater support in the data. Therefore, I selected the more parsimonious suite of linker functions that did not incorporate a linker function representing the presence of low-growing vegetation.

It was challenging to develop one index to represent the total amount of browse for moose. This required combining a diverse array of species into one response variable; the linker function needed to represent species that differed in edaphic niche and regeneration strategies (Figure 6, Beaudry et al. 1999). I did not have a large enough dataset to develop linker functions for the individual species that were browsed by moose. I also did not identify willow to the species-level due to differentiating features such as catkins being unavailable at the time of sampling. In general, however, greater diversity and abundance of moose shrubs was associated with higher productivity sites. Schrempp et al. (2019) also found higher abundance of moose shrubs on higher productivity sites.

I expected light to be an important predictor variable of moose shrub suitability. However, the likelihood analysis revealed that adding light to the linker function did not improve support for a model that already incorporated conifer basal area. It should be noted that incorporating conifer basal area rather than light results in a linker function that is not sensitive to the effect of edge on understory species. There is a gradation of light conditions between full light in the center of a large gap, partial light at the edge of gap adjacent to a forest edge, and low light under a full forest canopy (Chen et al. 1995). This gradual change in light and corresponding vegetation growth, is not reflected by simply incorporating conifer basal area in the immediate vicinity. The suitability for moose shrubs under a forest canopy, but in a location with higher light levels due to an adjacent gap, may be underestimated. Alternatively, suitability may be overestimated for a location in a gap that is directly adjacent to a forest canopy that provides shade. The presence and abundance of understory vegetation species are influenced by proximity to edge as well as the orientation of the site relative to the edge (i.e., south side vs. north side of a gap) (Canham 1988, Matlack 1994, Nelson and Halpern 2005).

Moose often select mixedwood and broadleaf stands in winter (Osko et al. 2004, Street et al. 2015, Mumma et al. 2021) and mixedwood and broadleaf stands can provide a greater quantity of moose forage (Crête and Courtois 1997). I did not explicitly include the broadleaf component of the stand in the linker function because I was unable to find evidence in the literature providing a direct mechanistic link between broadleaf tree presence and moose shrubs. Interestingly, the support for conifer basal area rather than light, does indirectly reflect the presence of the broadleaf component in a stand. A mixed stand with a broadleaf component would have a reduced conifer basal area in comparison to a comparable pure conifer stand with the same number of total stems.

Past studies of wildlife habitat often have focused on landscape-scale analyses and applications (Whitman et al. 2017, Stockdale et al. 2019, Stewart et al. 2020, Leblond et al. 2022). This modelling framework, projecting habitat dynamics using a stand dynamics model and linker functions, can be used to inform landscape-scale habitat models. Modelling of the forest cover component of caribou habitat has historically been static or dynamic at the landscape scale (e.g., resetting stand age and cover type due to wildfire or timber harvest or tracking change in stand age through time but not representing the corresponding changes in forest cover) (Johnson et al. 2015, Barber et al. 2018, Nagy-Reis et al. 2021, Leblond et al. 2022). Some disturbances affect only a portion of the stand or vary in terms of the intensity of disturbance (e.g., different intensities of mountain pine beetle attack or partial harvest). Employing process-based, individual-tree, stand dynamics models provides the ability to evaluate the effect of these complex disturbances on stand structure and, via linker functions, on habitat dynamics (Holt et al. 1995, Maleki et al. 2021). Scaling output from this modelling framework to the landscape scale could enable modelling of habitat dynamics customized to the dynamics of unique stands on the landscape (Barber et al. 2018, St-Laurent et al. 2022).

There are elements of caribou habitat that are beyond the scope of this study because they are best modelled at a landscape scale. For example, linear disturbances play a key role in predation risk (Dickie et al. 2017, DeMars and Boutin 2018, Mumma et al. 2018), but cannot be effectively modelled at the stand scale by SORTIE-ND. Roads have been shown to improve the hunting efficiency of wolves through improved access to caribou habitat and predation refugia as well as increasing the efficiency at which they hunt (Dickie et al. 2017, DeMars and Boutin 2018). The effect of linear features on habitat value could be modelled with a buffer along the linear corridor representing the zone of avoidance of these features (Johnson et al. 2015). However, at the scale at which stands are modelled in SORTIE-ND (a 300 x 300-m or 500 x 500-m polygon), applying a buffer of over 1 km is not feasible.

SORTIE-ND can be used to model the dynamics of stand revegetation along linear features such as roads or skid trails and to model the effect of higher light levels on the stand dynamics of the adjacent stands.

I developed a simple but robust modelling framework to relate stand structure to three key ecological elements of the winter habitat of northern mountain caribou: terrestrial forage lichen, moose shrubs, and vertical cover. I developed linker functions that can be used to relate the output from forest simulation models to habitat suitability. As with all models there are limitations, but these limitations should not shadow the contributions that these linker functions make for providing insight into the effects of operational forest management decisions on habitat for a species of conservation concern. Where disturbance events result in stands with complex structure, informing landscape-scale habitat models with habitat dynamics that are stand and site specific would further improve our understanding of the overall dynamics of habitat across landscapes and longer time scales.

Chapter Three

Modelling the Effects of Disturbance on Caribou Winter Habitat

3.1 Introduction

Abiotic and biotic disturbances can significantly change forest ecosystems and substantially alter the ecosystem services that forests provide (Buma 2015). The impact of disturbances on forest ecosystems will vary with the type of disturbance (Thom and Seidl 2016, Viljur et al. 2022), the severity and magnitude of the disturbance (Seidl et al. 2016), and the ecosystem services being evaluated (Thom and Seidl 2016, Sánchez et al. 2021). Disturbances will often immediately impact the provisioning of forest ecosystem services, but can also influence the recovery trajectory of the ecosystem and rate at which ecosystem services are regained (Seidl et al. 2016, Bartels et al. 2016, Sutherland et al. 2016, Bergeron et al. 2017). For example, a severe wildfire removes most vegetation from the landscape, significantly reduces the depth of forest floor, and adds a significant pulse of nutrients. One of the outcomes of that fire could be a reduction in habitat for wildlife that depend on older trees and associated forest structure. As a corollary, numerous wildlife species will benefit from the early successional plant communities that establish following the fire (Viereck and Schandelmeier 1980).

Managing for diverse ecosystem services is complex and interacting disturbances add further challenges (Schwenk et al. 2012, Mönkkönen et al. 2014, Bowd et al. 2021). For example, forest canopy removal is positive for some species but negative for others and the response can differ depending on the pattern and intensity of canopy removal (Halpern et al. 2012). In many regions, planning decisions are made for landscapes where not only timber harvest but also natural disturbance (e.g., wildfire, insect infestations) influences the provision of

ecosystem services. Interactions between disturbances, management actions, and successional forest dynamics add further complexity (Seidl et al. 2011, Elkin et al. 2013, Buma 2015). We need the ability to project the influence of both management decisions and natural disturbances to support the sustainable provision of these services (Seidl et al. 2011, Whitman et al. 2017).

Numerous factors play a role in the response of ecosystems to a particular disturbance. At a landscape scale, these include past disturbance history, current disturbance severity and intensity, and landscape structure (Racey et al. 1996, Angelstam and Kuuluvainen 2004). Type and intensity of disturbance influence the species composition and structure of the regenerating stands following disturbance. For example, shade tolerant species are more likely to survive or regenerate following a low intensity fire or MPB attack (Astrup et al. 2008b, Kielland and Brown 2015). At a stand scale, factors such as stand structure, species composition, and edaphic site conditions influence the response and recovery of the ecosystem and ecosystem services (Brulisauer et al. 1996, Clark et al. 2003, Lilles et al. 2018). Understanding how these factors interact and influence the response of ecosystem features is required to manage and maintain these features following disturbance.

Caribou is an ungulate species of conservation concern in Canada with habitat that has been affected by a variety of disturbance agents (COSEWIC 2014). Habitat change due to both anthropogenic factors and natural disturbance are considered ultimate factors in the decline of mountain caribou populations that reside throughout the interior of British Columbia, Canada (COSEWIC 2014). The forests of the central interior of BC have experienced the largest mountain pine beetle epidemic in Canadian history (Dhar et al. 2016) and numerous large wildfires (Cichowski and Haeussler 2020, Province of British Columbia 2023). Extensive timber salvage resulted in the removal of a large proportion of pine leading stands that serve

as winter habitat of caribou. Therefore, to ensure the sustainable provision of caribou winter habitat, managers need to understand the effects of disturbance and the recovery trajectories of critical habitat elements.

Forest managers require tools that support tactical and strategic land-use decisions for timber harvest within caribou habitat. Models allow us to project what we know across longer time frames and integrate the interactions of multiple factors. As such, models provide useful tools for exploring the impacts of disturbance on ecosystem services (Seidl et al. 2011). Dynamic forest models have a long history of development and use for improving our understanding of stand dynamics and projecting changes in tree populations and stand structure over time (Bugmann 2001, Bugmann and Seidl 2022). These models were developed to quantitatively represent stand dynamics and are typically focused on the demographics of individual trees or stands of trees (Bugmann and Seidl 2022). Less common are models that project the response of non-tree ecosystem elements to changes in stand structure (e.g., the response of specific ungulate habitat attributes such as terrestrial lichen to changes in stand structure due to differing disturbance events such as clearcutting, partial harvest or MPB attack). A tool that models habitat dynamics at the stand scale provides the ability to evaluate the effects of alternative management strategies over time.

SORTIE-ND is a complex stand dynamics model that can be used to project the response of stands to harvest or disturbance over a timeframe of hundreds of years. As introduced in Chapter 2, SORTIE-ND enables the modelling of mixed-species stands and stands with complex vertical structure including snags. Linker functions provide a link between stand models and ecosystem features that enables modelling ecosystem features that are responsive to changes in stand structure. By providing the linkage from stand structure to ecosystem features, stand dynamics models such as SORTIE-ND can be used to project not only stand

dynamics following disturbance but also the dynamics of ecosystem features, such as important habitat elements. Projecting the response of habitat elements over time can inform management decisions on a disturbed landscape.

Forests in the central interior are valued for timber production as well as providing habitat for wildlife such as caribou (Cichowski 1996). The ability of forests to grow trees and provide wildlife habitat is expected to depend on forest management decisions and the legacies of disturbances such as MPB and wildfire. In order to develop improved forest management strategies we need to improve our understanding of how forest composition and structure influences caribou habitat, and how stand dynamics will alter caribou habitat value through time. I applied linker functions to SORTIE-ND model output to evaluate the influences of different disturbance events on the dynamics of elements of caribou habitat. I examined three specific questions:

1. What is the influence of edaphic site on the provision of elements of caribou habitat over time?
2. What is the influence of stand type on the provision of elements of caribou habitat over time?
3. How do recovery trajectories of caribou and moose habitat elements differ in response to disturbances such as mountain pine beetle and clearcut harvest?

I evaluated these three questions by applying them to three important elements of caribou winter habitat: terrestrial forage lichen, moose shrubs, and vertical cover.

3.2 Methods

3.2.1 Study Area and Caribou Habitat Context

The focus of this study is the winter habitat of the Tweedsmuir-Entiako caribou herd (TEC). This herd of northern mountain caribou is in decline and is blue-listed or designated as threatened by the Province of British Columbia (BC) (COSEWIC 2014, Min. of Env. and Climate Change 2018). The herd's home range is located in west-central BC southwest of Prince George (Figure 1). The herd's winter habitat has been heavily affected by MPB, wildfire, and timber harvesting. Maintaining both healthy caribou herds and sustainable timber supplies are provincial and federal priorities.

The study area is defined by the Sub-Boreal Spruce moist cold Babine variant (SBSmc2), a biogeoclimatic subzone and variant described by the local biogeoclimatic ecosystem classification system (BEC) (Figure 1, Banner et al. 1993). Chapter 2 includes a description of the geography and forests that are characteristic of this subzone. Although the TEC winter habitat extends across several BEC subzones, the SBSmc2 was selected for this study because it comprises a portion of the winter habitat that is subject to industrial forest management and caribou winter habitat management.

Three elements of TEC winter habitat are the focus of this paper: terrestrial lichens favoured as caribou forage (henceforth referred to as forage lichen or lichen), shrubs favoured by moose for winter forage (moose shrubs), and vertical canopy cover. These elements are described in detail in the methods section of Chapter 2. Other stand-scale habitat elements are important for caribou during winter and throughout other seasons, however this study is focused solely on the three elements of forested winter habitat described above.

3.2.2 Stand Modelling

SORTIE-ND simulates changes in tree populations across small stands (generally less than nine hectares) over time. As a spatially explicit model, output includes not only individual tree size, regeneration, growth and mortality information but also the spatial distribution of the trees and the resulting light environment in a grid across the entire stand (Canham et al. 2004). A snag sub-model enables modeling of snag dynamics (Bose et al. 2015). SORTIE-ND was parameterized to model four edaphic sites of the SBSmc2 by applying growth relationships derived from previous studies (Lilles and Astrup 2012, Coates et al. 2013).

SORTIE-ND plots can be conceptualized as a torus (donut) where the trees on the apparent ‘edge’ of a plot are neighbours of trees on the opposite ‘edge’ of the plot. Therefore, trees on the western edge of the plot are modelled as growing next to the trees located on the eastern edge (at the same latitude); the same relationship holds for trees on the north and south edges of plots. Thus, 9ha clearcut plots model the interior condition of a stand with no forest edge.

I modelled four stand types crossed with four edaphic sites on a 9-ha plot. The stand types were categorized as: lodgepole pine dominant, mixed conifer and broadleaf (lodgepole pine, hybrid spruce, subalpine fir and trembling aspen), mixed conifer (lodgepole pine, hybrid spruce and subalpine fir), and hybrid spruce dominant. Throughout this paper, these stand types will be referenced as *pine*, *conifer/broadleaf*, *conifer mix*, and *spruce* (respectively) and individual tree species as spruce, pine, subalpine fir and aspen. The four edaphic sites are situated along a productivity gradient from a poor subxeric site to a rich subhygric site and referenced as: subxeric, submesic, mesic, and rich subhygric. All four stand types were modelled on submesic, mesic, and rich subhygric sites. Spruce-dominated stands aren’t found on subxeric sites and therefore were not modelled on this site.

Edaphic conditions at a given forest site can give rise to a range of stand conditions (i.e. species composition, age class distribution, DBH distribution) as a result of interactions between stand age, disturbance history and the forest's regeneration pathway (Meidinger and Pojar 1991, Banner et al. 1993, Coates et al. 1994). I evaluated the impact of stand type by simulating a range of forest compositions that naturally occur under a given edaphic condition. Initialization of each stand type was based on tree lists from the empirical plot data described in Chapter 2. I selected one field plot that was representative of each stand/edaphic site combination (Table 5). I used the following criteria to select stands: 1) the trees in the dominant canopy were between 75 and 125 years of age; 2) all stands within each site type had similar basal areas; 3) for *pine* and *spruce* stands, the pine or spruce component (respectively) comprised at least 60 percent of the total basal area; 4) for *conifer/broadleaf* stands, a significant component of aspen was required but the stand could not be dominated by aspen (I targeted 30–60% aspen by basal area); and 5) *conifer mix* stands had no broadleaf component and a relatively even representation (by basal area) of all three conifer species. Some stand/edaphic site combinations did not have suitable field plots so the tree list from a stand for a similar edaphic site was used (the tree list for the mesic *spruce* stand was used to initiate the tree composition of the submesic *spruce* stand, the submesic *conifer/broadleaf* tree list was used for mesic *conifer/broadleaf* stand, and the mesic *pine* tree list was used for the subhygric *pine* stand). Stands were initiated as pre-mountain pine beetle attack stands so all pine found in the field plots (live and dead from MPB attack) were initiated as live pine.

Three scenarios were modelled: no disturbance, mountain pine beetle attack (MPB), and clearcut harvest. All scenarios were simulated for 200 timesteps (years). The scenarios were initiated with the stand conditions described in the previous paragraph. For the MPB scenario I applied 100% mortality to all pine greater than 15 cm dbh and 50% mortality to all

Table 5. Structure of stands used to initiate SORTIE-ND model scenarios for mature stands across gradients of edaphic site and stand type. This stand structure data was drawn from data collected during the summer of 2019 in sub-boreal forests of west-central British Columbia, Canada.

Site Type	Site Series	Stand Type	Species composition (% basal area)	Basal Area (m ² /ha)	Conifer Basal Area (m ² /ha)	Broad-leaf Basal Area (m ² /ha)	Density (> 5 cm dbh)	Light (% GLI)	Age (yrs)
subxeric	02	<i>pine</i>	Pl 100	28.2	28.2	0	1000	42	88
subxeric	02	<i>conifer/broadleaf</i>	Pl 37 At 31 Bl 20 Sx 12	23.8	16.6	7.2	700	35	77
subxeric	02	<i>conifer mix</i>	Bl 44 Sx 32 Pl 24	13.2	13.2	0	750	48	77
submesic	01c	<i>pine</i>	Pl 79 Sx 18 Bl 3	28.0	28.0	0	800	26	76
submesic	02-01	<i>conifer/broadleaf</i>	At 60 Pl 30 Bl 10	22.4	8.7	13.7	750	33	95
submesic	01c	<i>conifer mix</i>	Bl 50 Pl 41 Sx 9	47.7	47.7	0	1800	22	88
submesic	01	<i>spruce</i>	Sx 61 Pl 33 Bl 6	38.1	38.1	0	3400	22	87
mesic	01	<i>pine</i>	Pl 98 Sx 2	37.9	37.9	0	1900	34	121
mesic	02-01	<i>conifer/broadleaf</i>	At 60 Pl 30 Bl 10	22.4	8.7	13.7	750	33	95
mesic	01	<i>conifer mix</i>	Bl 44 Pl 29 Sx 27	17.9	17.9	0	600	22	76
mesic	01	<i>spruce</i>	Sx 61 Pl 33 Bl 6	38.1	38.1	0	3400	22	87
subhygric	01	<i>pine</i>	Pl 98 Sx 2	37.9	37.9	0	1900	34	121
subhygric	05	<i>conifer/broadleaf</i>	Sx 69 At 31	43.3	30.5	12.8	650	15	84
subhygric	05-06	<i>conifer mix</i>	Bl 52 Sx 37 Pl 11	38.4	38.4	0	3750	10	108
subhygric	05	<i>spruce</i>	Sx 100	63.7	63.7	0	2700	15	92

trees between 10 and 15 cm dbh (SORTIE-ND randomly selected 50% of the trees in the 10 to 15 cm tree population). This differential level of attack across pine diameter classes mimicked the intensity of MPB attack observed during the recent MPB epidemic in BC (Safranyik 2004, Dhar et al. 2015). The MPB attacked trees became snags, thus, decay and

fall-down rates were simulated. All trees were removed in the clearcut scenario and the establishment of an even-aged plantation was simulated. Seedlings were planted at a density of 1800 stems/ha (average height of seedlings was 21 cm; see Table 6). Natural regeneration of all conifer species (seed rain) was simulated for all stand types in each timestep. Natural regeneration of aspen was included for the *conifer/broadleaf* stand type only.

I tested the amount of variation in output that resulted from stochastic elements within SORTIE-ND to determine if multiple simulations should be run for each stand/site/disturbance combination. Stochastic elements included the location of individual trees, the assignment of tree diameters (within a diameter class) to trees of each species, the probability of mortality, the spatial distribution of seed rain and the probability of seed establishment. To do this, I conducted 10 replicate runs of a clearcut harvest scenario for each stand type and edaphic site combination. The variance between the 10 replicated simulations was minor. Therefore, I determined one simulation for each treatment/edaphic site/stand type combination was sufficient because limited additional information on variability was gained from 10 simulations.

Table 6. Stand establishment characteristics for sub-boreal clearcut scenarios modelled with SORTIE-ND including planting densities (in stems/ha) and natural regeneration ('seed').

Stand type	Hybrid Spruce	Lodgepole Pine	Subalpine Fir	Trembling Aspen
<i>Pine</i>	seed	1800 + seed	seed	0
<i>Conifer/Broadleaf</i>	700 + seed	700 + seed	seed	400 + seed
<i>Conifer Mix</i>	400 + seed	1000 + seed	400 + seed	0
<i>Spruce</i>	1400 + seed	400 + seed	seed	0

Output from all simulations consisted of tree maps and light maps at each timestep. A tree map is a list of all trees (live and dead) in the simulated 9-ha stand with the following data for each tree: tree species, live/dead indicator, dbh, diameter at 10 cm height, height, and location (x and y coordinate). The light map provided the Gap Light Index (GLI, see Chapter 2 Methods for a description) estimated at 1.3 m height for each 1×1-m grid cell in the simulated stand.

The calibrated linker functions presented in Chapter 2 were applied to the SORTIE-ND output to project the dynamics of the three habitat elements. The linker functions related stand metrics (light, basal areas of conifer and broadleaf trees, densities of aspen and subalpine fir saplings, edaphic site condition, and time since disturbance) to the suitability of a site to support terrestrial lichen, moose shrub communities, and vertical cover. Each timestep of SORTIE-ND output was rasterized into 10 x 10-m rasters using the raster package (v3.4-13; (Hijmans 2021) in R (v. 4.1.2; R Core Team 2021). All seven stand metrics were calculated for each raster. The linker functions were used to calculate the suitability indices for each raster using the applicable stand metric value. The median suitability index of the stand and the 5th and 95th quantiles were reported. The 5th and 95th quantiles provide a measure of the variability of the data around the median for data that may not be normally distributed.

The terrestrial lichen and moose shrub linker functions were comprised of component linker functions. Each component linker function represented the influence of one stand variable on the suitability of the stand to support the habitat element. The component linker functions were combined multiplicatively to project the relative suitability for terrestrial lichen and moose shrubs across the plot (scaled from 0 to 1) (Equation 1 and 7). The vertical cover

linker function was a single function projecting relative canopy cover based on conifer basal area (Equation 13).

The linker functions projected a relative measure of suitability of a stand. They did not project the expected abundance of each habitat element in a stand. Other factors are known to influence the abundance of terrestrial lichen and moose shrubs (e.g., disturbance history, abundance of competing vegetation). Because I developed the linker functions with the specific intent of applying them to output from the stand model SORTIE-ND, the predictor variables were constrained to those available from SORTIE-ND. The linker functions were not predictive, ecological models of abundance of terrestrial lichen or moose shrubs.

3.3 Results

3.3.1 Component Linker Functions

Applying the component linker functions to SORTIE-ND output allowed me to parse out the effects and interactions of individual stand characteristics on lichen and moose shrub suitability over time. Lichen dynamics were best illustrated by focusing on subxeric sites (Figure 8, Appendix 5) and moose habitat dynamics were best illustrated on the subhygric sites (Figure 9, Appendix 5).

The full lichen linker function was comprised of four component functions representing the combined effects of stand-level determinants on the suitability of a stand to support terrestrial lichen: edaphic site, time since stand-replacing disturbance, understory light, and overstory broadleaf abundance. Edaphic effect was static and did not change over time (Figure 8). Time since stand-replacing disturbance also appeared static for mature and MPB-attacked stands, reflecting the length of time since a severe stand-replacing disturbance (Figure 8). Applied to the clearcut scenario, the time since disturbance linker function reflected the

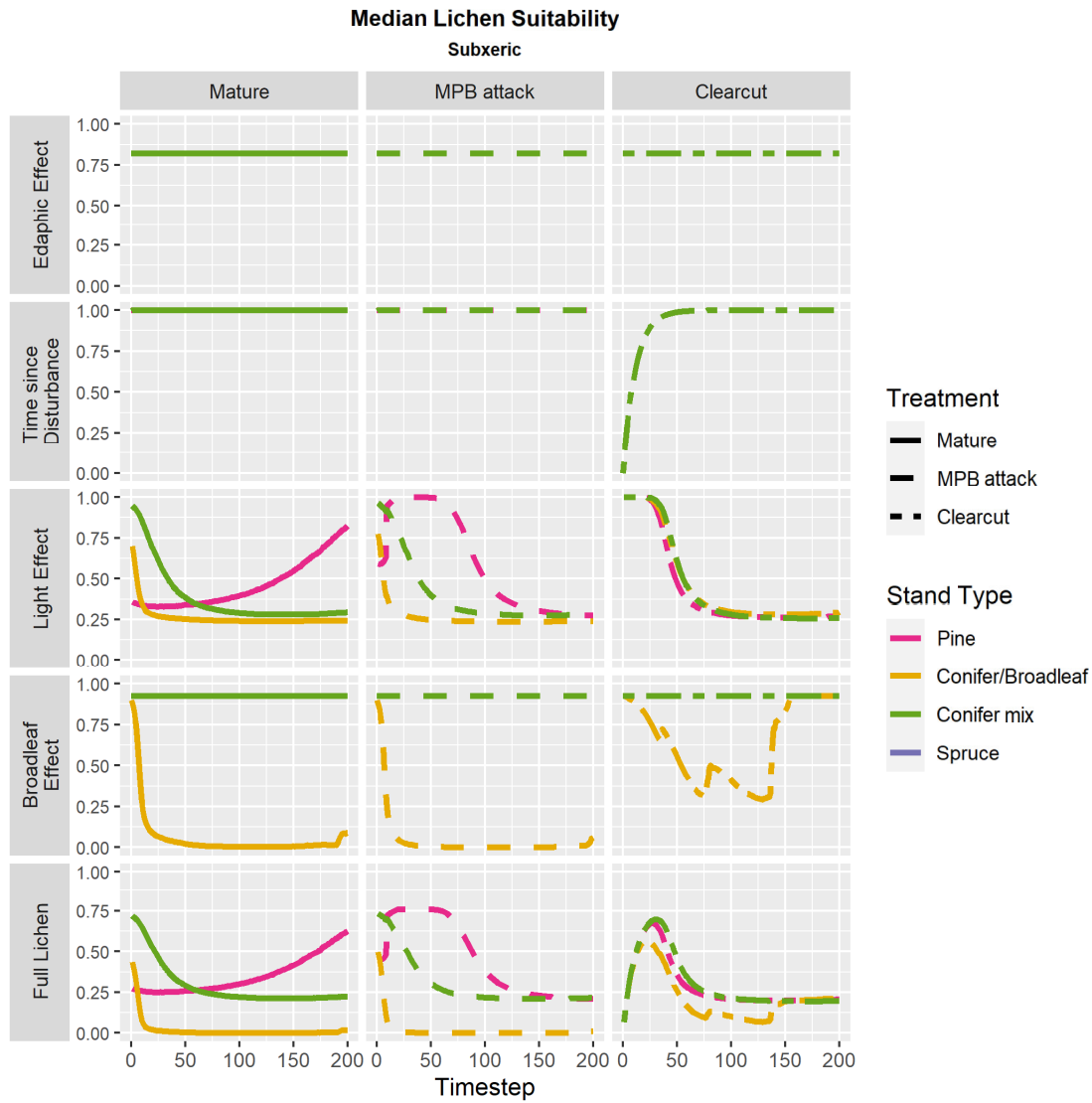


Figure 8. Output of the component linker functions for forage lichen on subxeric sites. The top four rows present the output of the component linker functions, with the full suitability index for forage lichen shown in row five. Coloured lines represent different stand types. Where only the *conifer mix* stand suitability appears on the figure, the other stand types have the same suitability (e.g., the broadleaf effect for the mature pine-dominated stand is the same as the *conifer mix* stand).

physical damage to lichen communities from timber harvest and the time required for lichen communities to re-populate and regenerate on the site. The light effect was dynamic reflecting changes in stand structure including relative tree species abundance and growth. The light effect decreased with increasing canopy closure for *conifer mix* and *conifer/broadleaf* stands. The *pine* stand exhibited an increase in light effect over time in response to tree mortality due to senescence. The broadleaf effect suggested that once broadleaf species were well-established in a mature or MPB attacked stand, the stands were

unsuitable for lichen. Following clearcutting, the suitability for lichen was reduced during mid-succession for stands with a low-density broadleaf component. Considering the combination of all these variables, the best subxeric stands for lichen (> 0.35 suitability) were mature *conifer mix* stands before the slow growing trees matured further, *pine* stands experiencing mortality due to senescence, and clearcut stands of all types 20–45 years old.

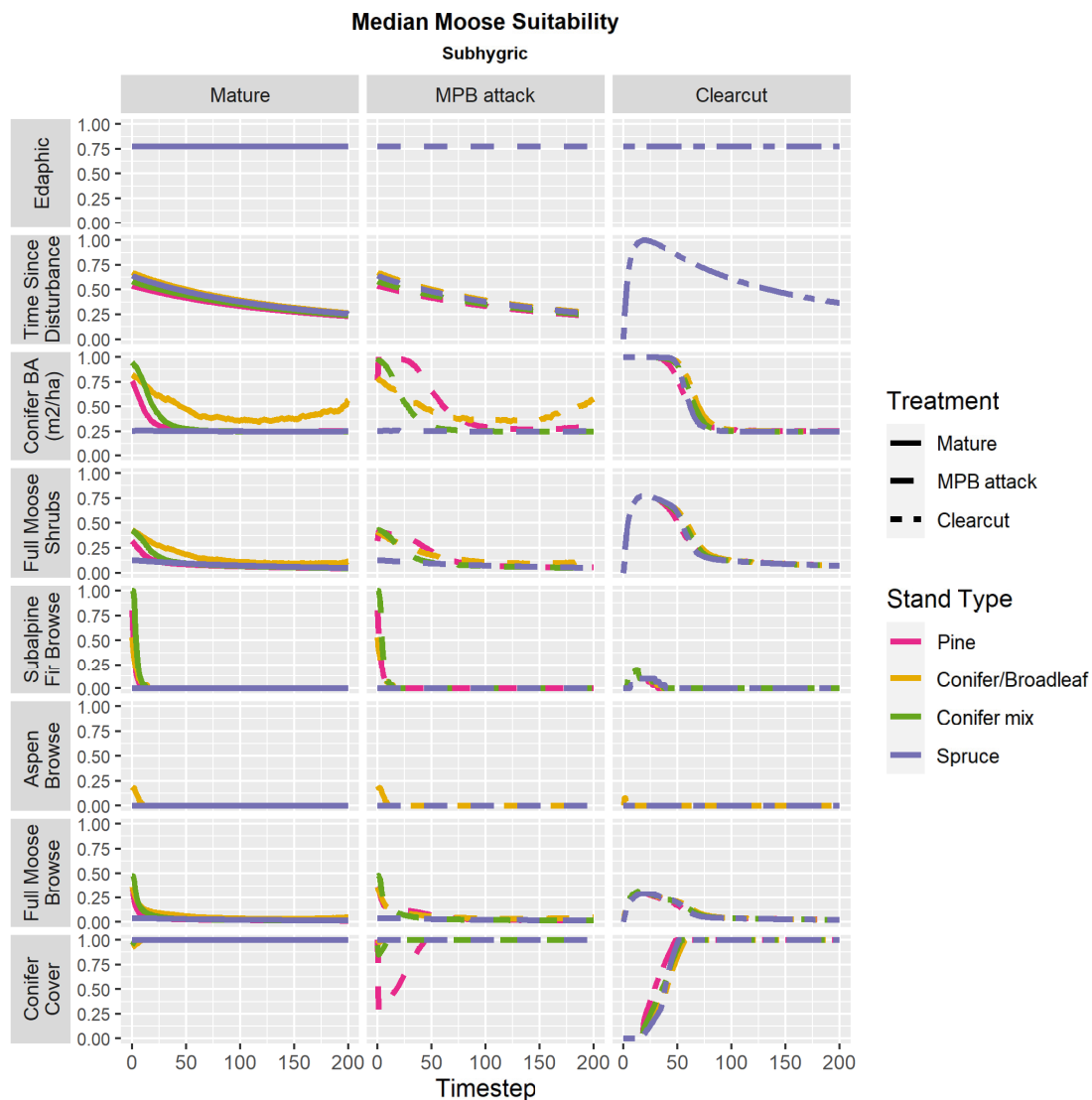


Figure 9. Output of the component linker functions for moose browse on subhygric sites. The top three rows present the output of the component linker functions for moose shrubs, with the full suitability index for moose shrubs shown in row four. The suitability of a stand for subalpine fir and aspen browse are presented in rows five and six and the total moose browse suitability of a stand in row seven. The bottom row illustrates the suitability of a stand to provide vertical cover. Coloured lines represent different stand types. Where only the *spruce* stand suitability appears on the figure, the other stand types have the same suitability (e.g., vertical cover, bottom row).

The full moose shrub linker function was comprised of three component functions (top 4 panels of Figure 9). Similarly to terrestrial lichen, the edaphic effect was static over time. The time since severe disturbance curve showed a slow decline in the suitability of mature and MPB stands to support early-seral moose shrubs as they aged whereas clearcuts reached high suitability by year 20 as shrubs regenerated following harvest. The competitive effect of conifer basal area meant that mature stands declined in suitability as their basal area increased, MPB attacked *pine* stands had high suitability for about 50 years after attack (until their basal area recovered), and clearcut stands had high suitability that started to decline around 50 years. Overall for moose shrubs, the combined effects of the component functions suggested that the best subhygric stands were 5 to 50-year-old clearcuts (suitability > 0.35).

The full moose browse response combined moose shrub, aspen sapling and subalpine fir sapling suitabilities (Figure 9: 4th to 7th panels). Aspen and subalpine fir browse was above zero only at the very beginning of the scenario for mature and MPB stands and immediately following clearcutting. Disturbance resulted in good conditions for natural regeneration and release of advanced regeneration. However, the regenerating trees quickly grew beyond a height where they provided forage opportunities for moose. The suitability function for full moose browse showed very little difference between treatments, stand type or site over a 200-year timeframe because the shrub response was weakened by averaging it with the weak responses of fir and aspen. Therefore, the full moose browse suitability function will not be further evaluated in this thesis (figures are available in Appendix 6).

The vertical cover linker function reflected the dynamics of conifer basal area (Figure 9). Thus, mature stands provided full suitability for cover. MPB attacked *pine* stands exhibited a reduction in vertical cover until the basal area recovered after 50 years. Clearcut stands, on

these high productivity sites, also required approximately 50 years to develop suitable vertical cover for moose.

For the remainder of the results section I will evaluate the dynamics of habitat suitability by focussing on the response of the full lichen, full moose shrub, and vertical cover linker functions.

3.3.2 Terrestrial Lichen Dynamics

Effect of Site: Poorer productivity sites provided much greater lichen suitability than richer and wetter stands (Figure 10). However, an interaction between stand type and site was evident where *conifer/broadleaf* stands exhibited poorer suitability regardless of edaphic site. Improvements in lichen suitability following both MPB and clearcutting were greater and extended for longer as stands moved along the gradient from higher to lower productivity sites (subhygric to subxeric).

Effect of Stand Type: Differences in lichen suitability related to stand type became evident as site productivity declined (Figure 10). The greatest difference was on subxeric sites, however on submesic sites, differentiation between stand types was also evident. In general, subxeric and submesic *pine* stands provided the highest suitability for lichen. However the subxeric *pine* stand initially had lower suitability than the *conifer/broadleaf* and *conifer mix* stands. This reflected the greater conifer basal area of the subxeric *pine* stand compared to the other stand types. Following mountain pine beetle, *pine* stands provided greater suitability for lichen because the larger proportion of pine in the overstory (compared to other stand types with less pine) resulted in a greater proportion of the overstory being killed. The resulting increase in understory light was beneficial for lichen. There was limited effect of stand type following clearcutting for stands managed primarily for timber production. These stands were initiated with a relatively high density of conifers and only 400 stems per hectare

of aspen. Following clearcutting, all stand types initially increased in lichen suitability but the pulse was short lived. Although *conifer/broadleaf* clearcuts (with relatively low aspen density) initially also provide improved lichen conditions, in the mid-term (50 to 125 years) suitability is reduced in comparison to other stand types.

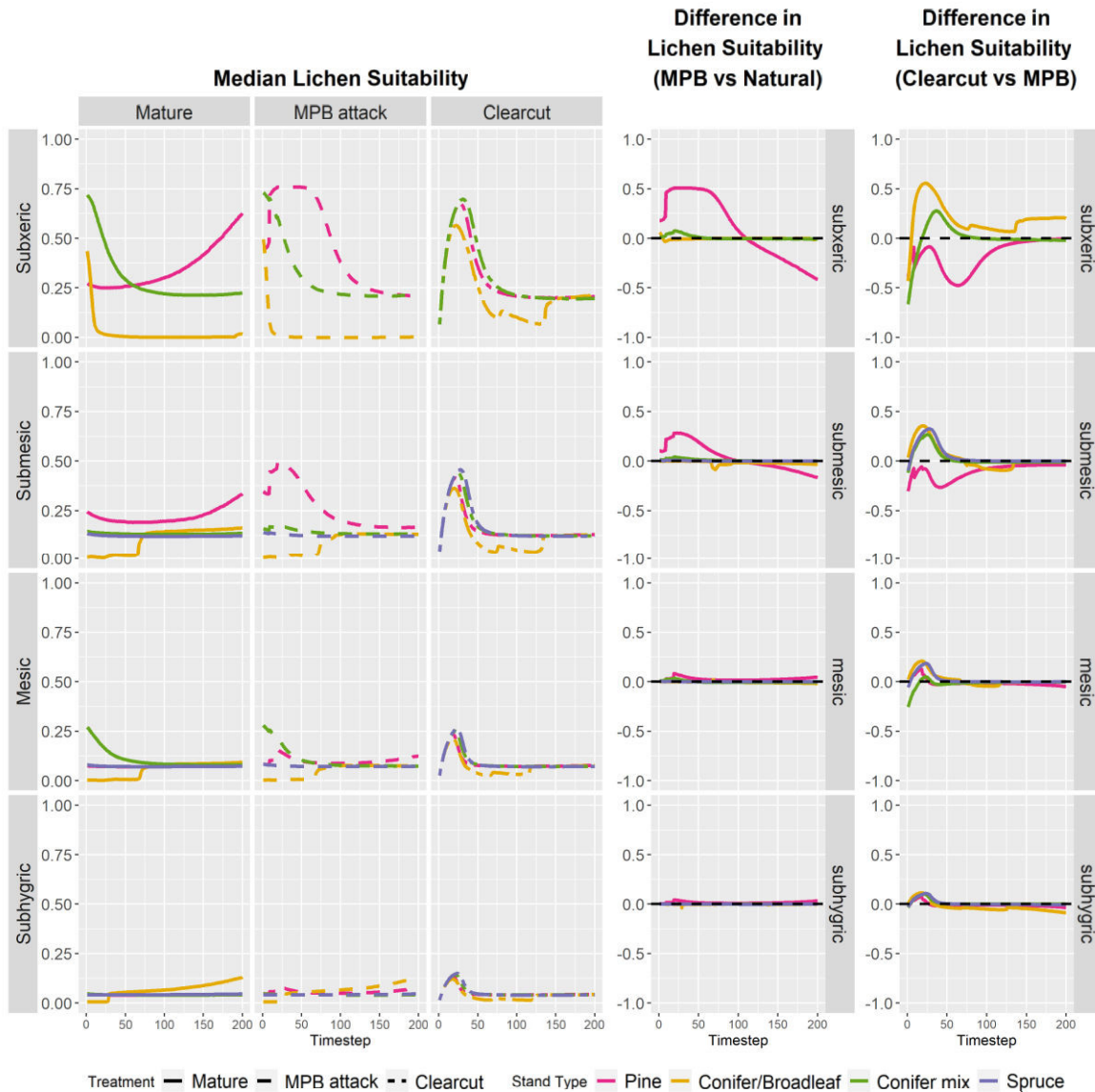


Figure 10. The projected response of lichen suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours). The 4th column illustrates the difference in lichen suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

Effect of Disturbance: MPB and clearcutting improved lichen suitability in certain stand types (Figure 8 and Figure 10) due to the reduction of the live overstory. However, MPB only improved suitability significantly in *pine* stands (compared to mature stands) because the proportion of susceptible host (pine) was limited in the other stand types; thus, the effect of MPB was also limited in comparison to mature stands. Interestingly, terrestrial lichen suitability was greater for drier MPB affected *pine* stands than clearcuts (subxeric and submesic sites) and suitability extended for a longer time frame following MPB attack. Clearcutting, through complete canopy removal, elevated the suitability of all stand types to support lichen in the short term, though only until canopy closure occurred (Figure 10).

Within-stand variability in lichen suitability differed across site, stand, and disturbance types (Appendix 7). The greatest variability was evident in subxeric and submesic *pine* stands (mature and MPB-attacked) and submesic *conifer/broadleaf* stands. In general, variability within clearcuts and *spruce* stands was low (except clearcut *conifer/broadleaf* stands) however, a pulse in variability did occur between 25 and 50 years following disturbance in conjunction with crown closure.

3.3.3 Moose Shrub Dynamics

Effect of Site: Across all disturbance scenarios, moose shrub habitat was least suitable on the poorer sites, regardless of stand type (Figure 11, Appendix 6, Figure 29). Following clearcutting, moose shrub suitability declines as site productivity declines. Time interacted with site effect following disturbance: as site productivity increased, the period of time that clearcuts and MPB stands supported greater suitability for moose shrubs declined (though subhygric and mesic stands were similar). In general, for mature stands (timesteps 0 to 50 which equated to approximately 80- to 130-year-old stands), subxeric and subhygric sites exhibited poorer moose shrub suitability than submesic and mesic sites.

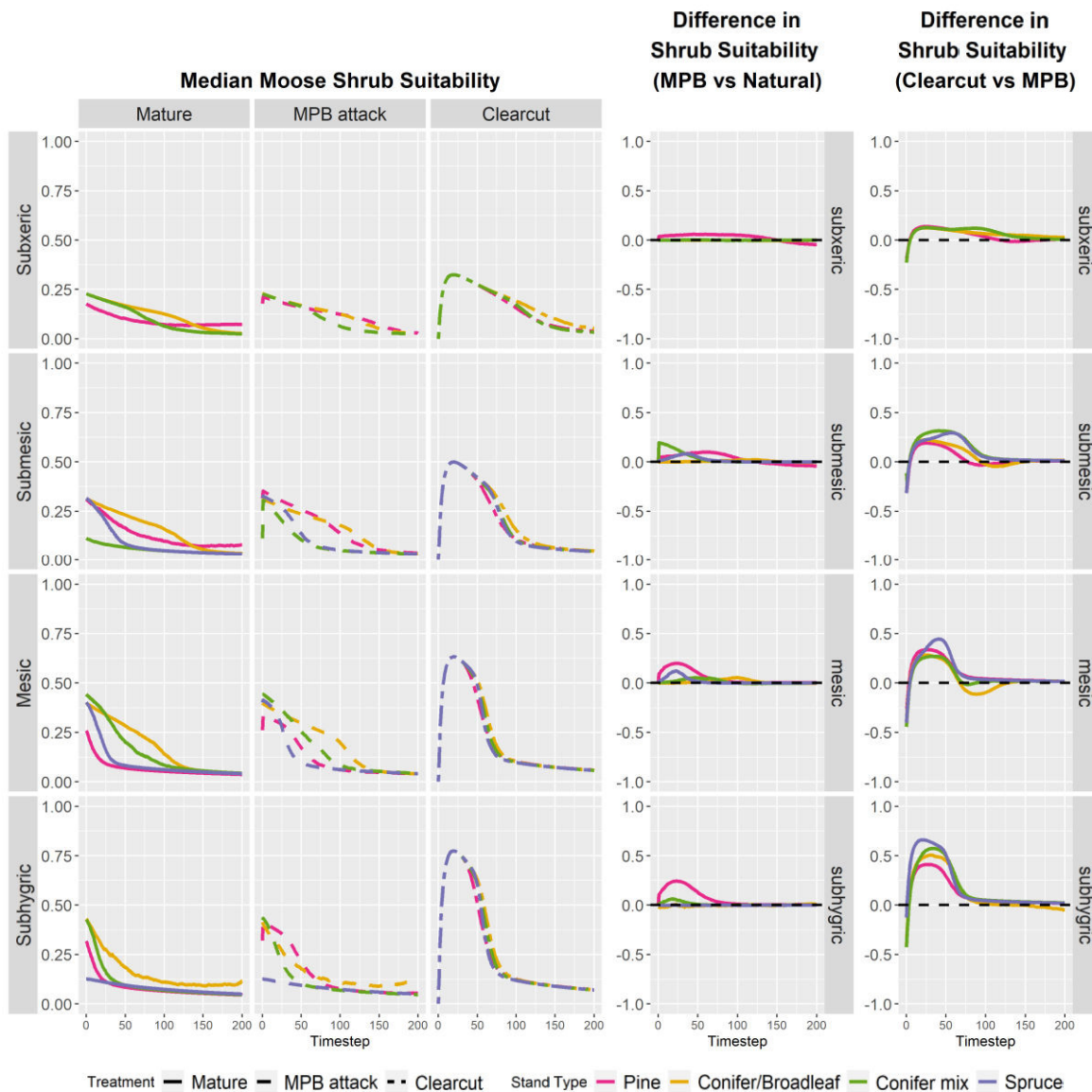


Figure 11. The projected response of moose shrub suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours). The 4th column illustrates the difference in moose shrub suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

Effect of Stand Type: All mature conifer stand types without a broadleaf component provided lower suitability for moose shrubs than mature *conifer/broadleaf* stands (Figure 11). Although all mature stand types exhibited a decline in moose shrub suitability over time, *conifer/broadleaf* stands retained elevated suitability for longer than the other stand types. For the first 75 years following MPB attack, *pine* stands provided equivalent or higher moose shrub suitability than *conifer/broadleaf* stands (except on mesic sites). MPB attacked *pine*

stands provided elevated moose shrub suitability in comparison to other MPB attacked conifer stands on all sites except *mixed conifer* stands on mesic sites. In mature stands there was not a consistent differentiation in suitability between the conifer stand types (e.g., mature *mixed conifer* stands provided the poorest suitability on submesic sites but greater suitability on mesic, subxeric, and subhygric sites).

Effect of Disturbance: Disturbance (MPB and clearcutting) increased moose shrub suitability; the complete removal of overstory canopy from clearcutting resulted in a greater relative effect compared to MPB (Figure 11). MPB attack had the greatest influence on moose shrubs in *pine* stands due to the larger proportion of pine in the stands.

There were no strong trends in within-stand variability for moose shrubs in mature and MPB-affected stands (Appendix 7). However, for clearcut sites within-stand variability decreased as sites decreased in productivity. For the first 100 years, the greatest within-stand variability for moose shrubs was evident in mature and MPB-attacked *conifer/broadleaf* stands on subhygric sites.

3.3.4 Vertical Cover Dynamics

Effect of Site: Following disturbance, stands on poorer sites developed vertical conifer cover more slowly (Figure 12). This reflected the slower growth of trees on those poor productivity sites. There was an interaction with stand type where, on higher productivity sites, there was little differentiation between stand type. However, as site productivity declined, the influence of stand type on the recovery trajectory of vertical cover grew stronger. On the poorest sites, *conifer/broadleaf* stands developed vertical cover most slowly.

Effect of Stand Type: Across most stand types and sites, vertical cover suitability was least for *conifer/broadleaf* stands (Figure 12). However, variability was also greatest for this stand type, so portions of these stands did have the potential to provide greater cover in addition to

less cover in other areas (Appendix 7). On the richest sites, although *conifer/broadleaf* stands provided full cover suitability (median at 1.0), there remains very high variability within the stand such that portions still provided low cover. *Spruce* stands consistently provided the highest cover of all stand types and the least within-stand variability.

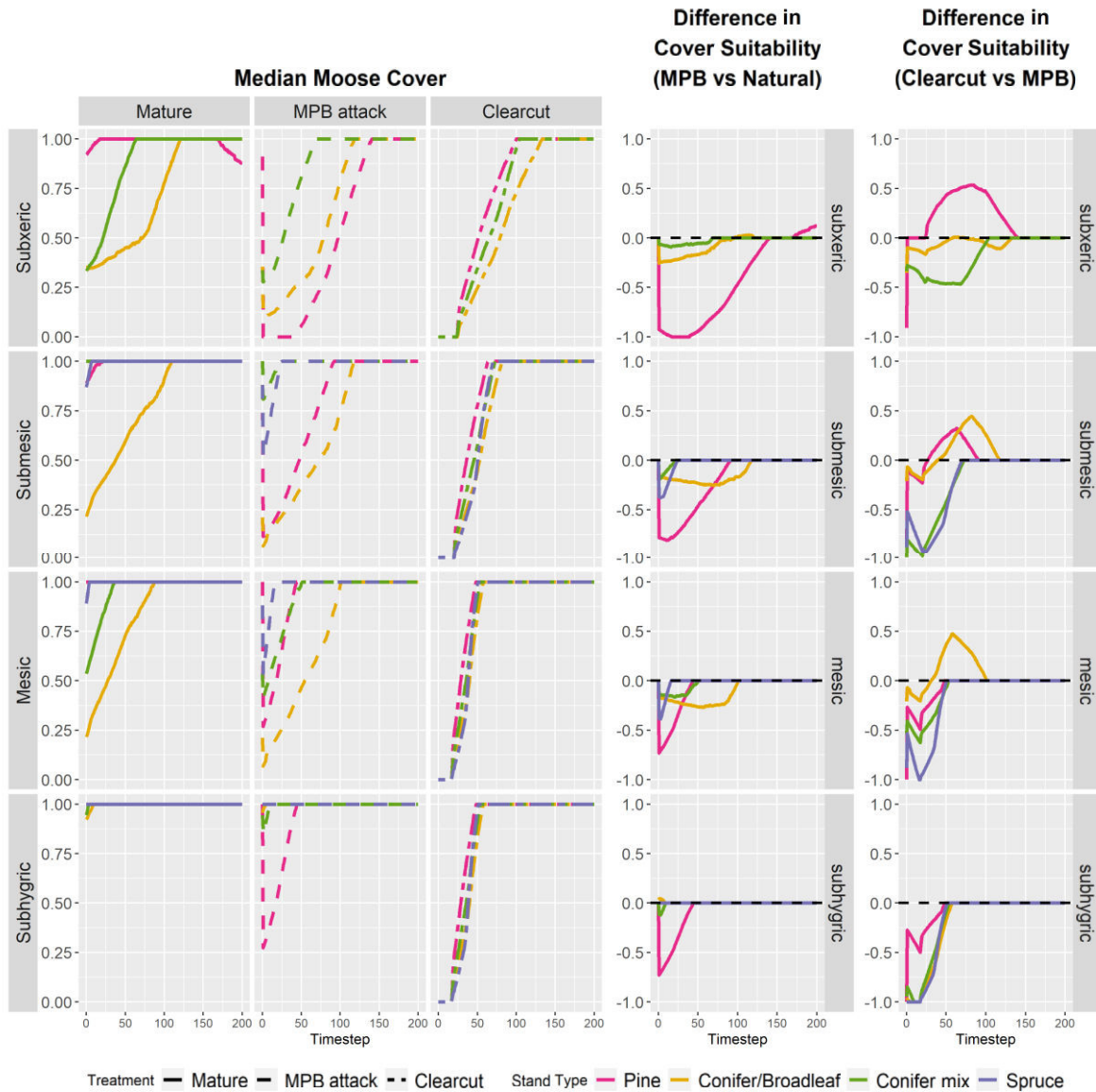


Figure 12. The projected response of suitability to provide vertical cover over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours). The 4th column illustrates the difference in suitability to provide vertical cover between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

Effect of Disturbance: Not surprisingly, both forms of disturbance reduced vertical cover.

MPB had an effect proportional to the amount of pine in the stand. Therefore, *pine* stands

had the greatest reduction in cover following MPB attack. *Conifer/broadleaf* stands exhibited a reduction in vertical conifer cover following MPB attack that extended for a longer period of time than the other stand types (except on xeric sites where *pine* stands had a longer period of time with reduced cover). Clearcutting reduced cover below MPB-attacked cover values for a brief period following MPB attack before planted stands regained cover value. However, in some poorer productivity stand types (drier *pine* (subxeric and submesic) and submesic and mesic *conifer/broadleaf* stands), MPB-attacked stands sustained reduced cover for longer than similar clearcut stands (for 25 to 125 years following disturbance).

3.4 Discussion

Model results show that forest disturbances differ in their effects on habitat elements and their recovery trajectories. Results also show that site and stand structure provide important context when evaluating the recovery of habitat elements. Managers should incorporate site, stand structure, and disturbance type when determining the best approach to managing for the recovery of habitat elements following disturbance events. On a mountain pine beetle affected landscape where recovery of caribou winter habitat is a priority, these model results indicate that certain forest management decisions, such as reserving MPB attacked subxeric stands from harvest, will promote the provision and recovery of caribou winter habitat more effectively than others.

Model results indicated that low productivity MPB attacked *pine* stands provided the greatest lichen suitability post-disturbance and suitability remained elevated for the longest period of time. MPB attacked stands were also less suitable for moose shrubs than clearcuts. In addition, low-productivity MPB attacked *pine* stands were projected to be slower to provide vertical cover when compared to clearcut stands. Comparing the effects of MPB versus clearcutting on all these habitat elements suggests that leaving low productivity MPB

attacked *pine* stands to recover naturally has greater value for caribou winter habitat than clearcutting the stands.

Our understanding of lichen ecology supports the finding that MPB attacked stands on subxeric sites have the potential to support suitable conditions for terrestrial lichen.

Terrestrial lichens are well adapted to dry poor sites as they are not dependent on soil to provide moisture and nutrients (Rowe 1984). Therefore, lichen have a competitive advantage on low productivity sites where resources aren't available for competing vegetation (Rowe 1984, Payette and Delwaide 2018). MPB disturbance does not physically damage lichen whereas lichen may be damaged by machinery or smothered by debris that falls to the ground during tree harvest and processing (Coxson and Marsh 2001, Waterhouse et al. 2011). In MPB attacked stands, the shade and competition from surviving trees and germination substrate limitations suppress natural regeneration (Astrup et al. 2008b) so stands may not achieve crown closure as quickly as fast-growing plantations following clearcutting.

Although these considerations indicate that poor productivity MPB attacked stands should provide suitable conditions to support terrestrial lichen, long-term studies monitoring the effect of MPB on lichen have found lichen declined in the first 10 years following MPB attack (Cichowski and Haeussler 2020, Nobert et al. 2020). This decline was associated with a positive response of understory vegetation following MPB attack (Cichowski and Haeussler 2020). After 10 years, the lichen decline stopped and abundance appeared to stabilize on subxeric sites but not submesic or mesic sites (Cichowski and Haeussler 2020). The discrepancy between the model projection and these empirical results indicate that the linker functions may not represent this competitive effect. More time is required to determine if the initial reduced lichen suitability is sustained or if, following a lag, suitability increases as projected over the 50–100-year time frame.

Studies monitoring lichen abundance following MPB attack have recommended protecting poor productivity stands from harvest to minimize the impact of the MPB on low-elevation caribou winter habitat (Seip and Jones 2010, Nobert et al. 2020, Cichowski et al. 2022). These studies found that, although lichen declines post-MPB attack, lichen abundance remains greater than in corresponding clearcuts (Nobert et al. 2020, Cichowski et al. 2022). These studies determined that clearcuts created conditions suitable for lichen recovery and expansion, however, the recovery trajectory was slow and uncertain. Cichowski and Haeussler (2020) found that forage lichen communities in clearcut stands had peaked and were declining 16–17 years post-harvest. They attributed the decline in lichen to growth of regenerating conifers; a similar finding to Lewis et al. (2019). Interestingly, numerous studies have found that although lichen is positively correlated with greater understory light levels in mature stands, as the percent of trees attacked by mountain pine beetle increases, there is a greater corresponding decline in terrestrial lichen abundance (Cichowski and Haeussler 2020, Nobert et al. 2020, Cichowski et al. 2022). This could also be attributed to competitive interactions with understory vascular plant and bryophyte communities. Despite reduced abundance of forage lichen in stands, caribou continued to forage in these stands for up to six years post-MPB attack (Cichowski 2010, Seip and Jones 2010).

These results could inform harvest practices: where harvest is planned within caribou winter habitat, employing harvest patterns that mimic mountain pine beetle conditions could promote the maintenance of caribou habitat (e.g., uniform partial harvest). Model results showed that stand thinning due to MPB caused tree mortality suppressed moose shrubs and provided conditions more suitable for forage lichen than those in a clearcut or closed canopy mature forest. Numerous studies have found higher forage lichen abundance associated with more open stand conditions and thus recommend stand thinning (citing reduced basal area and/or higher light levels) (Horstkotte and Moen 2019, Nobert et al. 2020). Thinning is also

recommended to maintain conditions that benefit lichen and reduce the environmental conditions that favour bryophytes in maturing stands (Coxson 2015, Vitt et al. 2019, Horstkotte and Moen 2019). However, thinning too heavily risks creating conditions suitable for vascular plants that compete with lichen and produce litter that suppresses lichen (Cornelissen et al. 2001, Coxson 2015, Cichowski and Haeussler 2020). Where harvest occurs, methods should be employed that minimize mechanical disturbance of the lichen (e.g., employ winter harvest or dedicated use of skid trails) and that limit the spread of debris over lichen (Coxson 2015, Horstkotte and Moen 2019, Cichowski et al. 2022). A stand thinning study in Alberta found that lichen cover remained either stable or slightly increased and moss cover significantly declined 19 years following treatment (Vitt et al. 2019). Although lichen abundance didn't increase with thinning in that study area, it didn't decrease as has occurred following clearcutting and mountain pine beetle (Webb 1998, Cichowski and Haeussler 2020, Cichowski et al. 2022). When considering partial harvest, the potential for increasing the density and network of active roads and the associated mortality risk must be taken into consideration (Dickie et al. 2017, Mumma et al. 2018).

Model results indicated that clearcutting should be avoided on mesic and high productivity sites within caribou winter habitat. Simulated clearcutting resulted in heightened moose shrub suitability on these sites in comparison to mature and MPB attacked stands. Although clearcutting on submesic sites was not projected to increase moose shrub suitability to as great an extent, it was projected to increase suitability above MPB attacked and mature stand levels and remained greater for a longer duration than on more productive sites. Although more productive sites are generally not suitable for terrestrial lichen, these results suggest that predation risk for caribou increases where subxeric lichen sites are located adjacent to sites with greater moose shrub suitability.

Numerous studies have found that clearcuts enhance moose forage and that moose select cutblocks over other habitat types (Carleton and MacLellan 1994, Fisher and Wilkinson 2005, Mumma et al. 2021). Clearcuts on mesic and higher productivity sites were projected to provide greater suitability for moose shrubs. This is supported by the work of Chen et al. (2004) where understory woody species was positively associated with site index.

Understory shrub species on most productive sites included preferred moose shrubs: *Cornus stolonifera* and *Viburnum edule* (Chen et al. 2004). Submesic clearcuts were projected to sustain moose shrub suitability above that found in MPB stands for longer than on richer sites due to the lower productivity of the sites. Growth of conifer trees is slower on these sites therefore more time elapses before crown closure limits light in the understory shrub layer.

On poorer productivity sites (subxeric and submesic), clearcuts were projected to provide conditions suitable for terrestrial lichen within 25 years; however, these conditions weren't sustained beyond 50 years (Figure 10). This mimics the common pattern of succession following wildfire where lichen communities initially establish but then diminish as tree crown closure occurs (Maikawa and Kershaw 1976, Coxson and Marsh 2001, Lewis et al. 2019). Where harvest methods protect the lichen community (e.g., winter harvest with a deep snow pack), lichen cover can be sustained or recover quickly (Coxson and Marsh 2001, Seip and Jones 2010). Although total lichen cover may be relatively high following harvest or fire, the *Cladonia* morphotypes often dominate the initial lichen community (Coxson and Marsh 2001). Within 40 to 60 years the lichen community transitions to *Cladina* morphotypes, providing greater forage biomass for caribou (Coxson and Marsh 2001).

Although lichen may be abundant, the characteristics of the snowpack in clearcuts can render terrestrial lichen inaccessible or limit detectability (Johnson et al. 2001); without a mature canopy to intercept snow, the snowpack is deeper and a hard crust may form (Kivinen et al. 2010). Caribou have been found to stop foraging on terrestrial lichen when the snow pack

exceeds a threshold height or hardness (Johnson et al. 2001, Seip and Jones 2010). Seip and Jones (2010) found that post-MPB attack, the dead snags continued to provide an ameliorative effect such that snowpack conditions did not limit cratering.

Model results suggest that where timber harvest is planned, broadleaf tree regeneration should be minimized to maximize caribou winter habitat. *Conifer/broadleaf* stand types support greater forage for moose in the form of both regenerating broadleaf saplings and greater moose shrub communities (Eastman 1977, Rea 2014). In addition, stands with significant broadleaf components are associated with greater moose forage (Eastman 1977, Crête and Courtois 1997, Rea 2014). Also, lichens were projected to be least abundant under *conifer/broadleaf* stands regardless of site or disturbance. Other studies have found a decreased likelihood of lichen presence under these stand types (Russell and Johnson 2019, Hillman and Nielsen 2020). Numerous studies provide evidence that deciduous litter, in addition to shade from vascular plants, suppresses lichen communities (Canter et al. 1991, Cornelissen et al. 2001). Studies of habitat selection have found that caribou avoid mixedwood and broadleaf stands (Metsaranta et al. 2003, Metsaranta and Mallory 2007, Fortin et al. 2008).

Interestingly, the mature subxeric *conifer mix* was projected to support greater lichen suitability than the pine stand type. This was due to the lower initial basal area of the stand; there was very little pine regeneration and reduced regeneration success and growth of subalpine fir and spruce on this very poor productivity site. As these trees grow and natural ingress occurs, tree cover will increase and lichen suitability will decline (Horstkotte and Moen 2019). However, in the short term, there was greater light and space available to support lichen than in a pine stand on a similar site where pine is best adapted to subxeric conditions.

Limitations and Qualifications

I modelled three habitat elements considered significant for caribou winter habitat however, other elements do play a role. Deadfall in stands limits caribou movement and hinders caribou's ability to crater for lichen (Metsaranta et al. 2003). Also, dead trees cover and eliminate lichen (Cichowski and Haeussler 2020). Horizontal cover affects the ability of caribou to see and escape from predators (Metsaranta et al. 2003). Dense young regenerating stands weren't used by caribou in southeast Manitoba despite available lichen; Schaeffer and Pruitt (1991) suggest this was due to the density of the trees limiting visibility. As discussed previously, the degree of vertical cover provided by a stand influences the snowpack characteristics and thus accessibility and detectability of terrestrial lichen. Although these additional factors influence the suitability of a stand for caribou winter habitat, I was not able to develop linker functions for these factors or model them with SORTIE-ND.

Planning of forest management activities should consider the provision of caribou habitat at a landscape scale. My work has focused on how stand level conditions influence key determinants of caribou and moose habitat. These findings can be used to inform both stand level management decisions, as well as landscape level planning. By combining the output of my work into a spatially explicit representation of a real forest landscape mosaic the landscape implications of forest disturbances and management decisions on caribou population dynamics could be better projected (Holt et al. 1995). For example, in Labrador SORTIE was linked to two other models, LANDIS-II (landscape scale disturbance and succession model) and Patchworks (spatial modelling tool for harvest planning) using SELES (a tool that links models) (Sturtevant et al. 2007). This interactive model system was developed to support sustainable management of a landbase with multiple resource values. SORTIE provided the succession trajectories and yield curves for complex stand types that

were needed to model alternative silviculture treatments throughout the landscape (Sturtevant et al. 2007). Scaling up to the landscape scale with LANDIS-II enabled modelling the interaction of alternative forest management options with natural disturbance across the region (Sturtevant et al. 2007).

Consideration of the density and location of roads and the size, distribution, and adjacency of stand types is important for caribou population management and requires a landscape scale approach. Roads provide wolves with efficient pathways to travel and access to areas that previously acted as refugia from predation. Both of those outcomes can increase predation or risk-related displacement (Whittington et al. 2011, Dickie et al. 2017, DeMars and Boutin 2018, Mumma et al. 2018).

Minimizing fragmentation and maintaining large areas of older forest are important landscape-scale management strategies for caribou (Racey et al. 1991). Longer rotations and maintaining MPB attacked stands can sustain arboreal lichen that provide forage when snow conditions limit availability of terrestrial lichen (Johnson et al. 2001, Seip and Jones 2010, Kivinen et al. 2010). Minimizing fragmentation is important for maintaining a landscape where caribou may forage more efficiently and also minimizes the co-occurrence of good lichen foraging sites adjacent to stands with moose forage (Kivinen et al. 2010). Among the first documented occurrences of caribou foraging in cutblocks, Racey et al. (1996) suggested the caribou used the young cutblocks, in part due to the close proximity to an adjacent extensive peatland complex that was undisturbed and had high early winter habitat value (Racey et al. 1991). Minimizing the provision of moose habitat should also be considered at the landscape scale to minimize the effects of apparent competition. The landscape primarily used by TEC for winter habitat is characterized as low-lying, flat to gently rolling terrain; subseric pine stands with abundant forage lichen often occur in close proximity to sites with

high potential for moose shrubs when disturbed (mesic and subhygric stands) (Cichowski 1993, Cichowski and Haeussler 2020). Therefore, planned management activities on a landscape should consider proximity to high-value caribou habitat, density and location of roads, and the distribution of moose habitat following disturbance.

3.5 Conclusions

I applied a framework that uses linker functions to quantitatively relate habitat elements to stand dynamics. That modelling framework allowed me to evaluate the post-disturbance recovery dynamics of caribou winter habitat. I projected the effects of mountain pine beetle attack and clearcut harvest on four different stand types across four different sites. My results suggest that managers must consider site, stand type, and disturbance type and history when planning forest harvest that will sustain winter range for caribou and reduce habitat for moose. In general, disturbance improves conditions for either lichen or moose shrubs depending on the site and disturbance type: MPB sustains greater terrestrial lichen suitability than clearcuts on dry, poor sites and there is little improvement in moose shrub suitability. Moose shrubs are enhanced on richer sites and following clearcut harvest. This framework can be used to inform landscape-scale habitat modelling of the supply of caribou winter habitat in areas subject to multiple disturbances of differing intensities.

Chapter Four

Conclusions

Forest ecosystems are dynamic, complex systems with many components interacting on different scales (Messier et al. 2013). Disturbances influence forest structure and composition, while also influencing the trajectory of succession. Forest ecosystems provide habitats for many species. Species also interact with forest ecosystems at a diversity of scales. Some organisms, such as lichen, interact with a stand at a small, local scale, others, such as northern mountain caribou, migrate over one hundred kilometres across broad landscapes and diverse forest ecosystems (Cichowski 1989, Haughian and Burton 2015). Each species relies on different components of the ecosystem. We are becoming increasingly aware of the importance of sustaining the diversity of components and processes within ecosystems to support resilient and robust systems (Messier et al. 2015).

Extensive forest management has far reaching impacts and affects a multitude of ecosystem components and services provided by forested communities (Mönkkönen et al. 2014, Suzuki and Parker 2016). Although forest management acknowledges the importance of the many ecosystem services, it is challenging to manage explicitly for ecosystem services beyond economic values (Schwenk et al. 2012). We have process-based models that represent the dynamics of trees within forest ecosystems, however, models of other ecosystem services such as wildlife habitat often operate at the landscape-scale and don't reflect stand-scale dynamics (Holt et al. 1995, Marzluff et al. 2002).

The objective of this study was to build upon an existing stand dynamics model to enable modelling habitat elements at the stand scale. I developed and applied a modelling framework to explore the habitat dynamics of a species of conservation concern, northern

mountain caribou. This chapter presents a synthesis of my findings, the contributions of this study, and future considerations.

4.1 Main Findings and Management Implications

Linking habitat elements to a stand dynamics model has allowed me to explore the implications of disturbance, stand structure, and edaphic site on habitat. Model results indicate that stand type and edaphic site must be taken into consideration when considering habitat suitability, whether in response to disturbance events or, in the absence of disturbance, in the context of ongoing stand structural development. For northern mountain caribou, these results can inform management decisions to support the provision of forested winter habitat over mid- to long-term timeframes. The results highlight sites and stand types where certain management actions would best support the provision of winter habitat.

Conifer stands on the poorest productivity sites provided the highest quality winter habitat for caribou of all the mature stands and sites. These stand types were the most suitable for terrestrial forage lichen and the least suitable for elements of moose habitat (moose shrubs and vertical cover). Maintaining these stands as mature stands should be prioritized to maintain existing caribou winter forage and limit predation risk. Pine stands on subxeric sites are projected to increase in suitability to support lichen as they mature (these stands were initiated at approximately 80 years of age). This is especially important for herds such as the TEC with heavily disturbed winter habitats. This is reflected in most planning for caribou habitat and recent calls for protection of critical caribou habitat (McNay et al. 2008, Festa-Bianchet et al. 2011, Environment Canada 2014, Johnson et al. 2015).

Disturbance on the poorest productivity pine stands was projected to generate the most suitable lichen habitat for caribou (for 50–75 years post-disturbance). For these same sites,

moose shrub suitability remained low and vertical cover was slow to recover from disturbance. These results suggested that leaving MPB attacked stands to recover naturally would maintain greater forage opportunities for caribou than clearcutting and limit the creation of higher value moose habitat. Recent studies evaluating the response of terrestrial lichen to MPB attack also recommend reserving poor productivity MPB attacked stands from harvest in order to support declining caribou populations (Cichowski and Haeussler 2020, Nobert et al. 2020, Cichowski et al. 2022). Although these studies have documented an initial decline in forage lichen following MPB attack, unharvested MPB-attacked stands still support more lichen than clearcuts (on comparable sites) for up to 14 years post-MPB attack (Cichowski et al. 2022). The decline post-MPB may also be short lived on the poorest productivity sites, as lichen did not decline between 10 and 16 years post-MPB (Cichowski and Haeussler 2020).

Stands with a substantial component of broadleaves are not beneficial for caribou winter habitat. These stands are projected to have very low suitability for lichen regardless of site. In addition, these stands negatively influence caribou habitat by supporting the growth of shrubs and trees that serve as moose forage. Numerous habitat selection studies have found that caribou select against mixed and broadleaf stand types (Cichowski 1989, Metsaranta and Mallory 2007, Fortin et al. 2008). Therefore, when managing for high-value caribou winter habitat, minimizing the occurrence of broadleaf trees on the landscape is desirable. This can be accomplished either through promoting and maintaining mature and old stands (Maleki et al. 2020) or minimizing the regeneration of broadleaf trees in regenerating stands.

Clearcut harvest of mesic and subhygric stand types are also projected to negatively affect caribou winter habitat. Clearcutting these sites can result in an increase of moose shrubs for up to 70 years. Although clearcutting reduces the availability of vertical cover for moose,

cover is reduced for a limited period of time in most stands. Caribou have been found to select against young stand types and harvested cutblocks (Cichowski 1989, Rettie and Messier 2000, Courtois et al. 2008). Thus, my research supports other work and management strategies that suggest limiting clearcut harvest especially in areas that promote habitat for apparent competitors of caribou, including moose and deer (Serrouya et al. 2011, Johnson et al. 2015, St-Laurent et al. 2022, Leblond et al. 2022).

4.2 Contributions

This thesis was initiated in part by my desire to explore the ability to use an existing stand dynamics model to evaluate the effects of stand management decisions on habitat elements beyond the tree components of forest ecosystems. The framework that has resulted contributes to caribou habitat management by providing resource managers with a means to evaluate the effects of management decisions on caribou winter habitat and could be used to support habitat supply modelling.

This work developed a new framework for modelling the influence of a variety of forest disturbances and silviculture approaches on ecosystem services. Developing the framework involved identifying key habitat elements, creating linker functions, and then collecting empirical data that were used to fit and calibrate linker functions. This framework allows one to evaluate the provision of ecosystem services following a variety of disturbances and alternative silviculture systems. Although I only evaluated the results of three treatments (no treatment, clearcutting and severe MPB attack), SORTIE-ND is very flexible and a variety of silviculture treatments and disturbances of varying intensities and spatial patterns can be modelled. For example, the effects of spruce budworm, partial harvest with gap cuts, partial harvest with individual tree removal, thinning treatments, and shelterwoods can be modelled (Ameztegui et al. 2017, Cristal et al. 2019, Maleki et al. 2020, 2021). This is an important

step towards evaluating the effects of forest management decisions on not only the tree component of the ecosystem but also other ecosystem services. This framework may be most useful for ecosystem elements that require longer time frames to develop such as terrestrial forage lichens (Holt et al. 1995).

This approach could also be scaled up to landscape-scale models of ecosystem services such as habitat supply. This could be highly valuable on a landscape heavily affected by a variety of disturbances such the TEC winter range. Enabling the dynamic (and site- and stand-specific) projection of the recovery of winter habitat elements allows the evaluation of the effects of alternate stand management decisions.

4.3 Next Steps and Future Considerations

Ecological models are powerful, useful, and provide a framework to test our understanding of ecological systems and explore the implications of perturbations to those systems (Filotas et al. 2014). Implicit in testing our understanding, is the recognition that we will discover areas that require further study. In addition, as models are applied and ecological problems are explored, additional potential uses become evident. Here I explore future considerations for extending the application of this framework to the TEC winter range as well as identify areas that would benefit from further study.

A valuable future step would be developing an optimization framework for evaluating alternative management strategies to address the sustained provision of caribou winter habitat for the TEC. Linking dynamic habitat modelling to caribou habitat supply models would be the first step. Optimization could be used to determine the type and distribution of treatments that ensured continual provision of winter habitat. In conjunction with evaluating habitat supply, the provision of additional ecosystem services such as timber value and carbon

sequestration could be simultaneously evaluated (Mönkkönen et al. 2014, Triviño et al. 2017, Lafond et al. 2017). Optimization requires assigning weights to each ecosystem service or habitat element; this can be challenging as weights significantly influence the selection of optimal outcomes (Schwenk et al. 2012, Lafond et al. 2017). Results of optimization studies indicate that the application of a diversity of silvicultural approaches can supply a broad range of ecosystem services and resolve conflicts between competing objectives (Schwenk et al. 2012, Mönkkönen et al. 2014, Triviño et al. 2017).

Another logical extension of this project is to evaluate the effect of partial harvesting on caribou habitat. SORTIE-ND is ideally suited to exploring partial harvest scenarios as it was designed to model the complex dynamics of stands with diverse mixtures of species and tree size classes. Partial harvest strategies have been suggested as a means to maintain lichen in mature stands where displacement of lichens by moss is a concern (Coxson 2015, Stevenson and Coxson 2015, Haughian and Burton 2015, Horstkotte and Moen 2019). Partial harvest strategies could also reduce the emergence of moose shrubs that follow clearcut harvest (Eastman 1974, Carleton and MacLellan 1994, Mumma et al. 2021). The results for MPB attacked pine stands suggest that it would be informative to explore partial cutting scenarios that mimic stand structure following MPB attack such as uniform partial cutting (e.g., enhanced forage lichen suitability and limited moose shrub response compared to clearcut harvest and mature forests).

Validation of the linker functions would add value to this study and lend support to model projections. Although I did not validate the linker functions in this thesis, the results from Chapter 3 are consistent with theoretical expectations and thus provide confidence that the linker functions adequately project lichen, moose, and cover suitability. Validation by withholding a portion of the dataset was not possible due to the small sample size.

It would be desirable to expand the dataset to provide greater insight into several ecological relationships. The existing empirical data illustrate that humus depth was a strong predictor variable for lichen suitability and I hypothesize that this could be related to disturbance history. Further data collection across disturbance types and severities could inform both the lichen and moose shrub linker functions. As discussed in Chapter 2, modelling all moose shrubs as one ecological unit is also problematic. Adding to the dataset to provide enough data to differentiate between some groups of moose shrubs could enable refinement of the moose shrub linker functions and improve projections of shrub suitability. Further work to investigate the interactions between terrestrial lichen, moss, and low growing vegetation (especially ericaceous shrubs) is important. Numerous studies have found lichen abundance correlated with changes in low vegetation or moss abundance (Canters et al. 1991, Pharo and Vitt 2000, Horstkotte and Moen 2019, Cichowski and Haeussler 2020). Developing a linker function that reflects the relationship between these groups of vegetation may improve modelling of low-intensity disturbances. Insights from indigenous knowledge were not included in this study but could enrich and inform our understanding and modelling of stand and habitat dynamics. This study, and the TEC herd range, falls within the traditional territories of several nations who could provide valuable perspective and knowledge of habitat and wildlife dynamics.

Climate change is an important factor when considering mid- to long-term modelling (Barber et al. 2018, Leblond et al. 2022). Further work is necessary to determine how best to consider the potential effects of climate change for these elements of winter habitat. The scale at which climate change is best modeled will need to be explored (e.g., the interaction between habitat elements and site, at the stand scale, or via disturbance dynamics at the landscape scale). The effects of climate change can be implemented in SORTIE-ND via tree growth and mortality parameters (Morán-Ordóñez et al. 2020, Moran et al. 2021).

Several recent studies have modelled the influence of climate change on the distribution of caribou habitat (Barber et al. 2018, Leblond et al. 2022, Neilson et al. 2022). Barber et al. (2018) reported significant shifts in upland habitat types as a result of the influence of climate change on dominant vegetation cover and wildfire. The other two studies found that habitat change via harvesting or wildfire played a greater role in affecting habitat suitability than climate induced changes to caribou habitat suitability itself (Leblond et al. 2022, Neilson et al. 2022). Although we need to be mindful that the drivers of ecosystem dynamics will shift as climate changes, the learnings in this study are important for projecting how systems will change in the future and what that means for caribou habitat.

4.4 Concluding Remarks

Here I have demonstrated that process-based forest models can be used to describe how forest structure changes and how these changes can then be extrapolated to other important ecosystem components such as habitat. Modelling the effects of disturbance on caribou winter habitat revealed that stand type, edaphic site, and disturbance type all influenced the suitability of forested habitat. This modelling approach can be used to evaluate silviculture decisions and habitat management options. Results can inform decisions regarding management of critical winter habitat for caribou at the stand scale and inform landscape-scale habitat supply modelling. This approach, though focused on caribou winter, can also be applied to questions of moose habitat where managing for moose is a priority.

Literature Cited

- Ahti, T., and J. Oksanen. 1990. Epigeic lichen communities of taiga and tundra regions. *Vegetatio* 86:39–70.
- Allen, A. W., P. A. Jordan, and J. W. Terrell. 1987. Habitat suitability index models: moose, Lake Superior region. Biol. Rep., U.S. Fish Wildl. Serv. 47 pp.
- Ameztegui, A., A. Cabon, M. De Cáceres, and L. Coll. 2017. Managing stand density to enhance the adaptability of Scots pine stands to climate change: A modelling approach. *Ecological Modelling* 356:141–150.
- Anderson, M., B. N. McLellan, and R. Serrouya. 2018. Moose response to high-elevation forestry: Implications for apparent competition with endangered caribou. *The Journal of Wildlife Management* 82:299–309.
- Angelstam, P., and T. Kuuluvainen. 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures - a European perspective. *Ecological Bulletins*:117–136.
- Astrup, R., K. D. Coates, and E. Hall. 2008a. Finding the appropriate level of complexity for a simulation model: an example with a forest growth model. *Forest Ecology and Management* 256:1659–1665.
- Astrup, R., K. D. Coates, and E. Hall. 2008b. Recruitment limitation in forests: lessons from an unprecedented mountain pine beetle epidemic. *Forest Ecology and Management* 256:1743–1750.
- Baker, B. G. 1990. Winter habitat selection and use by moose in the West-Chilcotin region of British Columbia. M.Sc. Thesis, University of British Columbia, Vancouver, B.C.
- Banner, A., W. MacKenzie, S. Haeussler, S. Thomson, J. Pojar, and R. Trowbridge. 1993. A field guide to site identification and interpretation for the Prince Rupert Forest Region. Province of British Columbia, Victoria, B.C.

- Barber, Q. E., M.-A. Parisien, E. Whitman, D. Stralberg, C. J. Johnson, M.-H. St-Laurent, E. R. DeLancey, D. T. Price, D. Arseneault, X. Wang, and M. D. Flannigan. 2018. Potential impacts of climate change on the habitat of boreal woodland caribou. *Ecosphere* 9:e02472.
- Bartels, S. F., H. Y. H. Chen, M. A. Wulder, and J. C. White. 2016. Trends in post-disturbance recovery rates of Canada's forests following wildfire and harvest. *Forest Ecology and Management* 361:194–207.
- Bartemucci, P., C. Messier, and C. D. Canham. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. *Canadian Journal of Forest Research* 36:2065–2079.
- Beaudry, L., R. Coupé, C. Delong, and J. Pojar. 1999. Plant indicator guide for northern British Columbia: Boreal, sub-boreal, and subalpine biogeoclimatic zones. Forestry Division Services Branch. Province of B.C., Victoria, B.C.
- Bergeron, J. A. C., J. Pinzon, S. Odsen, S. Bartels, S. E. Macdonald, and J. R. Spence. 2017. Ecosystem memory of wildfires affects resilience of boreal mixedwood biodiversity after retention harvest. *Oikos* 126:1738–1747.
- Bergeron, Y. 2000. Species and Stand Dynamics in the Mixed Woods of Quebec's Southern Boreal Forest. *Ecology* 81:1500–1516.
- Bergerud, A. T. 1971. Abundance of forage on the winter range of Newfoundland caribou. *The Canadian Field-Naturalist* 85:39–52.
- Bjørneraas, K., E. J. Solberg, I. Herfindal, B. V. Moorter, C. M. Rolandsen, J.-P. Tremblay, C. Skarpe, B.-E. Sæther, R. Eriksen, and R. Astrup. 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. *Wildlife Biology* 17:44–54.

- Blattert, C., R. Lemm, O. Thees, M. J. Lexer, and M. Hanewinkel. 2017. Management of ecosystem services in mountain forests: Review of indicators and value functions for model based multi-criteria decision analysis. *Ecological Indicators* 79:391–409.
- Bose, A. K., B. D. Harvey, K. D. Coates, S. Brais, and Y. Bergeron. 2015. Modelling stand development after partial harvesting in boreal mixedwoods of eastern Canada. *Ecological Modelling* 300:123–136.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972a. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* 60:849–872.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972b. Rationale, limitations, and assumptions of a northeastern forest growth simulator. *IBM Journal of Research and Development* 16:101–116.
- Boudreault, C., Y. Bergeron, and D. Coxson. 2009. Factors controlling epiphytic lichen biomass during postfire succession in black spruce boreal forests. *Canadian Journal of Forest Research* 39:2168–2179.
- Bowd, E., W. Blanchard, L. McBurney, and D. Lindenmayer. 2021. Direct and indirect disturbance impacts on forest biodiversity. *Ecosphere* 12:e03823.
- British Columbia Data Catalogue. n.d. VRI - 2022 - Forest Vegetation Composite Polygons. <https://catalogue.data.gov.bc.ca/dataset/vri-2022-forest-vegetation-composite-polygons/resource/85724845-3973-4a26-b715-100306768bbc>.
- Brodo, I. M., S. D. Sharnoff, and S. Sharnoff. 2001. *Lichens of North America*. Yale University Press, New Haven and London.
- Brulisauer, A. R., G. E. Bradfield, and J. Maze. 1996. Quantifying organizational change after fire in lodgepole pine forest understorey. *Canadian Journal of Botany* 74:1773–1782.
- Bugmann, H. 2001. A review of forest gap models. *Climatic Change* 51:259–305.

- Bugmann, H., T. Cordonnier, H. Truhetz, and M. J. Lexer. 2017. Impacts of business-as-usual management on ecosystem services in European mountain ranges under climate change. *Regional Environmental Change* 17:3–16.
- Bugmann, H., and R. Seidl. 2022. The evolution, complexity and diversity of models of long-term forest dynamics. *Journal of Ecology* 110:2288–2307.
- Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere* 6:art70.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.
- Canham, C. D. 1988. An index for understory light levels in and around canopy gaps. *Ecology* 69:1634–1638.
- Canham, C. D., K. D. Coates, P. Bartemucci, and S. Quaglia. 1999. Measurement and modeling of spatially explicit variation in light transmission through interior cedar–hemlock forests of British Columbia 29:1775–1783.
- Canham, C. D., P. T. LePage, and K. D. Coates. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34:778–787.
- Canham, C. D., and L. E. Murphy. (n.d.). SORTIE-ND Documentation. <http://www.sortie-nd.org/help/manuals/index.html>.
- Canham, C. D., and M. Uriarte. 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. *Ecological Applications* 16:62–73.
- Canters, K. J., H. Schöllerj, S. Ott, and H. M. Jahns. 1991. Microclimatic influences on lichen distribution and community development. *The Lichenologist* 23:237–252.

- Carleton, T. J., and P. MacLellan. 1994. Woody vegetation responses to fire versus clear-cutting logging: a comparative survey in the central Canadian boreal forest. *Écoscience* 1:141–152.
- Carroll, S. B., and L. C. Bliss. 1982. Jack pine – lichen woodland on sandy soils in northern Saskatchewan and northeastern Alberta. *Canadian Journal of Botany* 60:2270–2282.
- Chen, H. Y. H., S. Légaré, and Y. Bergeron. 2004. Variation of the understory composition and diversity along a gradient of productivity in *Populus tremuloides* stands of northern British Columbia, Canada. *Canadian Journal of Botany* 82:1314–1323.
- Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* 5:74–86.
- Cichowski, D. 2010. Tweedsmuir-Entiako caribou project: Effects of a mountain pine beetle epidemic on northern caribou habitat use: final report. 77 pp.
- Cichowski, D. 2015. Tweedsmuir-Entiako caribou population status and background information summary. BC Ministry of Forests, Lands and Natural Resource Operations, Smithers, B.C. 145 pp.
- Cichowski, D. B. 1989. Seasonal movements, habitat use, and winter feeding ecology of woodland caribou in West-Central British Columbia. M.Sc. Thesis, University of British Columbia, Vancouver, B.C.
- Cichowski, D. B. 1993. Seasonal movements, habitat use, and winter feeding ecology of woodland caribou in west-central British Columbia. Research Branch, Ministry of Forests, Victoria, B.C. 65 pp.
- Cichowski, D. B. 1996. Managing woodland caribou in west-central British Columbia. *Rangifer* 16:119–126.
- Cichowski, D., and S. Haeussler. 2013. The response of caribou terrestrial forage lichens to mountain pine beetles and forest harvesting in the East Ootsa and Entiako areas.

Annual report – 2012/13 – year 11. Prepared for Bulkley Valley Centre for Natural Resources Research and Management, Habitat Conservation Trust Foundation, B.C. Min. FLNRO, Smithers, B.C. 55 pp.

Cichowski, D., and S. Haeussler. 2020. The response of caribou terrestrial forage lichens to mountain pine beetles, forest harvesting and fire in the East Ootsa and Entiako areas: 2016/17 (year 16) field season report. Bulkley Valley Centre for Natural Resources Research and Management, Habitat Conservation Trust Foundation, BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development, BC Parks, and Canadian Forest Products Ltd., Smithers, B.C. 97 pp.

Cichowski, D., G. D. Sutherland, R. S. McNay, and R. Sulyma. 2022. Direct and indirect effects of habitat disturbances on caribou terrestrial forage lichens in montane forests of British Columbia. *Forests* 13:251.

Clark, D. F., J. A. Antos, and G. E. Bradfield. 2003. Succession in sub-boreal forests of west-central British Columbia. *Journal of Vegetation Science* 14:721–732.

Coates, K. D., C. D. Canham, M. Beaudet, D. L. Sachs, and C. Messier. 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. *Forest Ecology and Management* 186:297–310.

Coates, K. D., C. D. Canham, and P. T. LePage. 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. *Journal of Ecology* 97:118–130.

Coates, K. D., S. Haeussler, S. Lindeburgh, R. Pojar, and A. J. Stock. 1994. Ecology and silviculture of interior spruce in British Columbia. FRDA Report, Canada/British Columbia Partnership Agreement on Forest Resource Development, Victoria, B.C. 190 pp.

- Coates, K. D., and E. C. Hall. 2005. Implications of alternate silvicultural strategies in mountain pine beetle damaged stands: Technical report for forest science program project y051161. Bulkley Valley Centre for Natural Resources Research and Management, Smithers, B.C. 31 pp.
- Coates, K. D., E. C. Hall, and C. D. Canham. 2018. Susceptibility of trees to windthrow storm damage in partially harvested complex-structured multi-species forests. *Forests* 9:199.
- Coates, K. D., E. B. Lilles, and R. Astrup. 2013. Competitive interactions across a soil fertility gradient in a multispecies forest. *Journal of Ecology* 101:806–818.
- Cordonnier, T., F. Berger, C. Elkin, T. Lämås, and M. Martinez. 2013. Models and linker functions (indicators) for ecosystem services. ARANGE Deliverable Report, ARANGE Advanced Multifunctional Management of European Mountain Forests Project. 94 pp.
- Cordonnier, T., F. Berger, C. Elkin, T. Lämås, and M. Martinez. 2014. ARANGE deliverable D2.2: Models and linker functions (indicators) for ecosystem services. ARANGE Deliverable Report, ARANGE Advanced Multifunctional Management of European Mountain Forests Project.
- Cornelissen, J. H. C., T. V. Callaghan, J. M. Alatalo, A. Michelsen, E. Graglia, A. E. Hartley, D. S. Hik, S. E. Hobbie, M. C. Press, C. H. Robinson, G. H. R. Henry, G. R. Shaver, G. K. Phoenix, D. Gwynn Jones, S. Jonasson, F. S. Chapin III, U. Molau, C. Neill, J. A. Lee, J. M. Melillo, B. Sveinbjörnsson, and R. Aerts. 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* 89:984–994.

- COSEWIC. 2002. COSEWIC assessment and update status report on the Woodland caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada. xi + 98 pp.
- COSEWIC. 2009. COSEWIC / COSEPAC - Guidelines for Recognizing Designatable Units. <https://www.cosewic.ca/index.php/en-ca/reports/preparing-status-reports/guidelines-recognizing-designatable-units.html>.
- COSEWIC. 2011. Designatable units for caribou (*Rangifer tarandus*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa. 88 pp.
- COSEWIC. 2014. COSEWIC assessment and status report on the caribou *Rangifer tarandus*: Northern Mountain population, Central Mountain population, Southern Mountain population in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 135 pp.
- Courbin, N., D. Fortin, C. Dussault, and R. Courtois. 2009. Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. *Landscape Ecology* 24:1375–1388.
- Courtois, R., A. Gingras, D. Fortin, A. Sebbane, B. Rochette, and L. Breton. 2008. Demographic and behavioural response of woodland caribou to forest harvesting. *Canadian Journal of Forest Research* 38:2837–2849.
- Courtois, R., J.-P. Ouellet, L. Breton, A. Gingras, and C. Dussault. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. *Écoscience; Sainte-Foy* 14:491–498.
- Coxson, D. S. 2015. Using partial-cut harvesting to conserve terrestrial lichens in managed landscapes. *Canadian Wildlife Biology & Management* 4:150–162.

- Coxson, D. S., and J. Marsh. 2001. Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. *Canadian Journal of Botany* 79:1449–1464.
- Crête, M., and R. Courtois. 1997. Limiting factors might obscure population regulation of moose (*Cervidae: Alces alces*) in unproductive boreal forests. *Journal of Zoology* 242:765–781.
- Cristal, I., A. Ameztegui, J. R. González-Olabarria, and J. Garcia-Gonzalo. 2019. A decision support tool for assessing the impact of climate change on multiple ecosystem services. *Forests* 10:440.
- Crites, S., and M. R. Dale. 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests 76:14.
- Cumming, H. G. 1987. Sixteen years of moose browse surveys in Ontario. *Alces* 23:125–155.
- DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, L. E. Morgantini, M. Wheatley, and M. Musiani. 2012. Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications* 22:1068–1083.
- DeMars, C. A., and S. Boutin. 2018. Nowhere to hide: Effects of linear features on predator-prey dynamics in a large mammal system. *Journal of Animal Ecology* 87:274–284.
- DeMars, C., and R. Serrouya. 2020. Tweedsmuir-Entiako primary prey strategy: phase 1. Caribou Monitoring Unit, Alberta Biodiversity Monitoring Institute. 41 pp.
- Denryter, K. A., R. C. Cook, J. G. Cook, and K. L. Parker. 2017. Straight from the caribou's (*Rangifer tarandus*) mouth: detailed observations of tame caribou reveal new insights into summer–autumn diets. *Canadian Journal of Zoology* 95:81–94.

- Dhar, A., N. Balliet, K. Runzer, and C. Hawkins. 2015. Impact of a mountain pine beetle outbreak on young lodgepole pine stands in central British Columbia. *Forests* 6:3483–3500.
- Dhar, A., L. Parrott, C. Hawkins, A. Dhar, L. Parrott, and C. D. B. Hawkins. 2016. Aftermath of mountain pine beetle outbreak in British Columbia: Stand dynamics, management response and ecosystem resilience. *Forests* 7:171.
- Dickie, M., R. Serrouya, R. S. McNay, and S. Boutin. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology* 54:253–263.
- Eastman, D. S. 1974. Habitat use by moose of burns, cutovers and forests in north-central British Columbia. Tenth North American Moose Conference and Workshop. Duluth, Minnesota. 19 pp.
- Eastman, D. S. 1977. Habitat selection and use in winter by moose in sub-boreal forests of north-central British Columbia, and relationships to forestry. PhD Thesis, University of British Columbia, Vancouver, B.C.
- Edwards, A. W. F. 1992. Likelihood. Page Likelihood—expanded edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Elkin, C., A. G. Gutiérrez, S. Leuzinger, C. Manusch, C. Temperli, L. Rasche, and H. Bugmann. 2013. A 2 °C warmer world is not safe for ecosystem services in the European Alps. *Global Change Biology* 19:1827–1840.
- Environment Canada. 2014. Recovery strategy for the woodland caribou, Southern Mountain population (*Rangifer tarandus caribou*) in Canada. Species at Risk Act Recovery Strategy Series., Environment Canada, Ottawa, Ontario. viii + 103 pp.

- Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Côté, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology* 89:419–434.
- Filotas, E., L. Parrott, P. J. Burton, R. L. Chazdon, K. D. Coates, L. Coll, S. Haeussler, K. Martin, S. Nocentini, K. J. Puettmann, F. E. Putz, S. W. Simard, and C. Messier. 2014. Viewing forests through the lens of complex systems science. *Ecosphere* 5:art1.
- Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Review* 35:51–81.
- Fortin, D., R. Courtois, P. Etcheverry, C. Dussault, and A. Gingras. 2008. Winter selection of landscapes by woodland caribou: behavioural response to geographical gradients in habitat attributes. *Journal of Applied Ecology* 45:1392–1400.
- Frazer, G. W., C. D. Canham, and K. P. Lertzman. 1999. Gap Light Analyzer (GLA), version 2.0: imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies, Millbrook, New York.
- Goffe, W. L., G. D. Ferrier, and J. Rogers. 1994. Global optimization of statistical functions with simulated annealing. *Journal of Econometrics* 60:65–99.
- Goudie, J. W. 1984. Height growth and site index curves for lodgepole pine and white spruce and interim managed stand yield tables for lodgepole pine in British Columbia. Unpubl. Rep., B.C. Min. For., Res. Branch., F.P.D.S. Section. 75 pp.
- Goulet, L. A. 1985. Winter habitat selection by moose in northern British Columbia. *Alces* 21:103–25.
- Greuel, R. J., G. É. Degré-Timmons, J. L. Baltzer, J. F. Johnstone, E. J. B. McIntire, N. J. Day, S. J. Hart, P. D. McLoughlin, F. K. A. Schmiegelow, M. R. Turetsky, A.

- Truchon-Savard, M. D. van Telgen, and S. G. Cumming. 2021. Predicting patterns of terrestrial lichen biomass recovery following boreal wildfires. *Ecosphere* 12:e03481.
- Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard, T. Grand, S. K. Heinz, G. Huse, A. Huth, J. U. Jepsen, C. Jørgensen, W. M. Mooij, B. Müller, G. Pe'er, C. Piou, S. F. Railsback, A. M. Robbins, M. M. Robbins, E. Rossmanith, N. Rüger, E. Strand, S. Souissi, R. A. Stillman, R. Vabø, U. Visser, and D. L. DeAngelis. 2006. A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* 198:115–126.
- Grimm, V., U. Berger, D. L. DeAngelis, J. G. Polhill, J. Giske, and S. F. Railsback. 2010. The ODD protocol: A review and first update. *Ecological Modelling* 221:2760–2768.
- Habitat Monitoring Committee. 1996. Procedures for environmental monitoring in range and wildlife habitat management Version 5.0. British Columbia Ministry of Environment, Lands and Parks and British Columbia Ministry of Forests, Victoria, B.C. 225 pp.
- Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin (1973-2006)* 25:173–182.
- Halpern, C. B., J. Halaj, S. A. Evans, and M. Dovčiak. 2012. Level and pattern of overstory retention interact to shape long-term responses of understories to timber harvest. *Ecological Applications* 22:2049–2064.
- Haughian, S. R., and P. J. Burton. 2015. Microhabitat associations of lichens, feathermosses, and vascular plants in a caribou winter range, and their implications for understory development. *Botany* 93:221–231.
- Hijmans, R. J. 2021. Raster: geographic data analysis and modeling.
- Hillman, A. C., and S. E. Nielsen. 2020. Quantification of lichen cover and biomass using field data, airborne laser scanning and high spatial resolution optical data: A case study from a Canadian boreal pine forest. *Forests* 11:682.

- Hodder, D. P., R. V. Rea, and S. M. Crowley. 2013. Diet content and overlap of sympatric mule deer, moose, and elk during a deep snow winter in north-central British Columbia, Canada. *Canadian Wildlife Biology & Management* 2:43–50.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Holt, R. D., S. W. Pacala, T. W. Smith, and J. Liu. 1995. Linking Contemporary Vegetation Models with Spatially Explicit Animal Population Models. *Ecological Applications* 5:20–27.
- Horstkotte, T., and J. Moen. 2019. Successional pathways of terrestrial lichens in changing Swedish boreal forests. *Forest Ecology and Management* 453:117572.
- Johnson, C. J., N. D. Alexander, R. D. Wheate, and K. L. Parker. 2003. Characterizing woodland caribou habitat in sub-boreal and boreal forests. *Forest Ecology and Management* 180:241–248.
- Johnson, C. J., L. P. W. Ehlers, and D. R. Seip. 2015. Witnessing extinction – Cumulative impacts across landscapes and the future loss of an evolutionarily significant unit of woodland caribou in Canada. *Biological Conservation* 186:176–186.
- Johnson, C. J., K. L. Parker, and D. C. Heard. 2000. Feeding site selection by woodland caribou in north-central British Columbia. *Rangifer*:158–172.
- Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. *Oecologia* 127:590–602.
- Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications* 12:1840–1860.

- Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology* 41:238–251.
- Johnson, E. A. 1981. Vegetation organization and dynamics of lichen woodland communities in the Northwest Territories, Canada. *Ecology* 62:200–215.
- Joly, K., B. W. Dale, W. B. Collins, and L. G. Adams. 2003. Winter habitat use by female caribou in relation to wildland fires in interior Alaska. *Canadian Journal of Zoology* 81:1192.
- Julianus, E., T. N. Hollingsworth, A. D. McGuire, and K. Kielland. 2019. Availability and use of moose browse in response to post-fire succession on Kanuti National Wildlife Refuge, Alaska. *Alces* 55:24.
- Keim, J. L., P. D. DeWitt, J. J. Fitzpatrick, and N. S. Jenni. 2017. Estimating plant abundance using inflated beta distributions: Applied learnings from a lichen-caribou ecosystem. *Ecology and Evolution* 7:486–493.
- Kielland, K., and C. Brown. 2015. Understanding the effects of wildfire severity on moose habitat characteristics and use in Interior, Alaska. University of Alaska Fairbanks, Fairbanks, Alaska.
- Kivinen, S., J. Moen, A. Berg, and Å. Eriksson. 2010. Effects of modern forest management on winter grazing resources for reindeer in Sweden. *AMBIO* 39:269–278.
- Kobe, R. K., and K. D. Coates. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia 27:10.
- Kranabetter, J. M., C. R. Dawson, and D. E. Dunn. 2007. Indices of dissolved organic nitrogen, ammonium and nitrate across productivity gradients of boreal forests. *Soil Biology and Biochemistry* 39:3147–3158.

- Kranabetter, J. M., and S. W. Simard. 2008. Inverse relationship between understory light and foliar nitrogen along productivity gradients of boreal forests. *Canadian Journal of Forest Research* 38:2487–2496.
- Lafond, V., T. Cordonnier, and B. Courbaud. 2015. Reconciling biodiversity conservation and timber production in mixed uneven-aged mountain forests: Identification of ecological intensification pathways. *Environmental Management* 56:1118–1133.
- Lafond, V., T. Cordonnier, Z. Mao, and B. Courbaud. 2017. Trade-offs and synergies between ecosystem services in uneven-aged mountain forests: evidences using Pareto fronts. *European Journal of Forest Research* 136:997–1012.
- Lance, A. N., and B. Mills. 1996. Attributes of woodland caribou migration habitat in west-central British Columbia. *Rangifer* 16:355–364.
- Leblond, M., Y. Boulanger, J. Pascual Puigdevall, and M.-H. St-Laurent. 2022. There is still time to reconcile forest management with climate-driven declines in habitat suitability for boreal caribou. *Global Ecology and Conservation* 39:e02294.
- Leblond, M., C. Dussault, and M.-H. St-Laurent. 2014. Development and validation of an expert-based habitat suitability model to support boreal caribou conservation. *Biological Conservation* 177:100–108.
- LePage, P. T., C. D. Canham, K. D. Coates, and P. Bartemucci. 2000. Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia 30:415–427.
- Lewis, K. J., C. J. Johnson, and M. N. Karim. 2019. Fire and lichen dynamics in the Taiga Shield of the Northwest Territories and implications for barren-ground caribou winter forage. *Journal of Vegetation Science* 0:13.

- Lilles, E. B., and R. Astrup. 2012. Multiple resource limitation and ontogeny combined: a growth rate comparison of three co-occurring conifers. *Canadian Journal of Forest Research*.
- Lilles, E., A. Dhar, K. D. Coates, and S. Haeussler. 2018. Retention level affects dynamics of understory plant community recovery in northern temperate hemlock-cedar forests. *Forest Ecology and Management* 421:3–15.
- Longton, R. E. 1992. The role of bryophytes and lichens in terrestrial ecosystems. Pages 32–76 in J. W. Bates and A. M. Farmer, editors. *Bryophytes and lichens in a changing environment*. Oxford University Press.
- Luttmerding, H. A., D. A. Demarchi, E. C. Lea, D. V. Meidinger, and T. Vold, editors. 1990. Describing ecosystems in the field. 2nd ed. Ministry of Environment in cooperation with Ministry of Forests, Victoria, B.C.
- MacCracken, J. G., and L. A. Viereck. 1990. Browse regrowth and use by moose after fire in interior Alaska. *Northwest Science* 64:11–18.
- Maikawa, E., and K. A. Kershaw. 1976. Studies on lichen-dominated systems. XIX. The postfire recovery sequence of black spruce – lichen woodland in the Abitau Lake Region, N.W.T. *Canadian Journal of Botany* 54:2679–2687.
- Mäkelä, A., M. del Río, J. Hynynen, M. J. Hawkins, C. Reyer, P. Soares, M. van Oijen, and M. Tomé. 2012. Using stand-scale forest models for estimating indicators of sustainable forest management. *Forest Ecology and Management* 285:164–178.
- Maleki, K., M. A. Gueye, B. Lafleur, A. Leduc, and Y. Bergeron. 2020. Modelling post-disturbance successional dynamics of the Canadian boreal mixedwoods. *Forests* 11:28.

- Maleki, K., B. Lafleur, A. Leduc, and Y. Bergeron. 2021. Modelling the influence of different harvesting methods on forest dynamics in the boreal mixedwoods of western Quebec, Canada. *Forest Ecology and Management* 479:118545.
- Marzluff, J. M., J. J. Millspaugh, K. R. Ceder, C. D. Oliver, J. Withey, J. B. McCarter, C. L. Mason, and J. Comnick. 2002. Modeling changes in wildlife habitat and timber revenues in response to forest management. *Forest Science* 48:191–202.
- Matlack, G. R. 1994. Vegetation dynamics of the forest edge -- trends in space and successional time. *Journal of Ecology* 82:113–123.
- McNay, R. S., D. Heard, R. Sulyma, and R. Ellis. 2008. A recovery action plan for northern caribou herds in north-central British Columbia. FORREX Forest Research Extension Partnership, Kamloops, B.C. 105 pp.
- Meidinger, D. V., and J. Pojar, editors. 1991. *Ecosystems of British Columbia*. Research Branch, Ministry of Forests, Victoria, B.C.
- Messier, C. C., K. J. Puettmann, and K. D. Coates. 2013. *Managing forests as complex adaptive systems: Building resilience to the challenge of global change*. Routledge, New York.
- Messier, C., K. Puettmann, R. Chazdon, K. P. Andersson, V. A. Angers, L. Brotons, E. Filotas, R. Tittler, L. Parrott, and S. A. Levin. 2015. From management to stewardship: Viewing forests as complex adaptive systems in an uncertain world. *Conservation Letters* 8:368–377.
- Metsaranta, J. M., and F. F. Mallory. 2007. Ecology and habitat selection of a woodland caribou population in west-central Manitoba, Canada. *Northeastern Naturalist* 14:571–588.

- Metsaranta, J. M., F. F. Mallory, and D. W. Cross. 2003. Vegetation characteristics of forest stands used by woodland caribou and those disturbed by fire or logging in Manitoba. *Rangifer* 23:255–266.
- Min. of Env. and Climate Change. 2018. Caribou herd locations for BC. <https://catalogue.data.gov.bc.ca/dataset/2b217585-f48d-4d9f-b7ba-746909ac35ca>.
- Mönkkönen, M., A. Juutinen, A. Mazziotto, K. Miettinen, D. Podkopaev, P. Reunanen, H. Salminen, and O.-P. Tikkanen. 2014. Spatially dynamic forest management to sustain biodiversity and economic returns. *Journal of Environmental Management* 134:80–89.
- Moran, E. V., N. Vannest, and M. Aubry-Kientz. 2021. Modeling the forest dynamics of the Sierra Nevada under climate change using SORTIE-ND. *Annals of Forest Science* 78:75.
- Morán-Ordóñez, A., A. Ameztegui, M. De Cáceres, S. de-Miguel, F. Lefèvre, L. Brotons, and L. Coll. 2020. Future trade-offs and synergies among ecosystem services in Mediterranean forests under global change scenarios. *Ecosystem Services* 45:101174.
- Mumma, M. A., M. P. Gillingham, S. Marshall, C. Procter, A. R. Bevington, and M. Scheideman. 2021. Regional moose (*Alces alces*) responses to forestry cutblocks are driven by landscape-scale patterns of vegetation composition and regrowth. *Forest Ecology and Management* 481:118763.
- Mumma, M. A., M. P. Gillingham, K. L. Parker, C. J. Johnson, and M. Watters. 2018. Predation risk for boreal woodland caribou in human-modified landscapes: Evidence of wolf spatial responses independent of apparent competition. *Biological Conservation* 228:215–223.
- Murphy, L. 2015. Likelihood package R documentation. <https://cran.r-project.org/web/packages/likelihood/likelihood.pdf>

- Mysterud, A., and E. Østbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildlife Society Bulletin (1973-2006)* 27:11.
- Nadeau Fortin, M.-A., L. Sirois, and M.-H. St-Laurent. 2016. Extensive forest management contributes to maintain suitable habitat characteristics for the endangered Atlantic-Gaspésie caribou. *Canadian Journal of Forest Research* 46:933–942.
- Nagy-Reis, M., M. Dickie, A. M. Calvert, M. Hebblewhite, D. Hervieux, D. R. Seip, S. L. Gilbert, O. Venter, C. DeMars, S. Boutin, and R. Serrouya. 2021. Habitat loss accelerates for the endangered woodland caribou in western Canada. *Conservation Science and Practice* 3:e437.
- Neilson, E. W., C. Castillo-Ayala, J. F. Beckers, C. A. Johnson, M. H. St-Laurent, N. Mansuy, D. Price, A. Kelly, and M. A. Parisien. 2022. The direct and habitat-mediated influence of climate on the biogeography of boreal caribou in Canada. *Climate Change Ecology* 3:100052.
- Nelson, C. R., and C. B. Halpern. 2005. Edge-related responses of understory plants to aggregated retention harvest in the Pacific Northwest. *Ecological Applications* 15:196–209.
- Nobert, B. R., T. A. Larsen, K. E. Pigeon, and L. Finnegan. 2020. Caribou in the cross-fire? Considering terrestrial lichen forage in the face of mountain pine beetle (*Dendroctonus ponderosae*) expansion. *PLOS ONE* 15:e0232248.
- Oliver, C. D., and B. C. Larson. 1990. *Forest stand dynamics*. McGraw-Hill, Inc.
- Osko, T. J., M. N. Hiltz, R. J. Hudson, and S. M. Wasel. 2004. Moose habitat preferences in response to changing availability. *The Journal of Wildlife Management* 68:576–584.

- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* 66:1–43.
- Payette, S., and A. Delwaide. 2018. Tamm review: The North-American lichen woodland. *Forest Ecology and Management* 417:167–183.
- Pec, G. J., J. Karst, A. N. Sywenky, P. W. Cigan, N. Erbilgin, S. W. Simard, and J. F. C. Jr. 2015. Rapid increases in forest understory diversity and productivity following a mountain pine beetle (*Dendroctonus ponderosae*) outbreak in pine forests. *PLOS ONE* 10:e0124691.
- Pecchi, M., M. Marchi, V. Burton, F. Giannetti, M. Moriondo, I. Bernetti, M. Bindi, and G. Chirici. 2019. Species distribution modelling to support forest management. A literature review. *Ecological Modelling* 411:108817.
- Peek, J. M. 2007. Habitat Relationships. Pages 351–375 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and management of the North American moose*. 2nd edition. University Press of Colorado, Boulder, Colorado, USA.
- Peek, J. M., D. L. Ulrich, and R. J. Mackie. 1976. Moose Habitat Selection and Relationships to Forest Management in Northeastern Minnesota. *Wildlife Monographs*:3–65.
- Pharo, E. J., and D. H. Vitt. 2000. Local Variation in Bryophyte and Macro-lichen Cover and Diversity in Montane Forests of Western Canada. *The Bryologist* 103:455–466.
- Province of British Columbia. 2010. Field manual for describing terrestrial ecosystems. 2nd ed. B.C. Ministry of Forests and Range and B.C. Ministry of Environment, Victoria, B.C.
- Province of British Columbia. 2023. Wildfire Season Summary. <https://www2.gov.bc.ca/gov/content/safety/wildfire-status/about-bcws/wildfire-history/wildfire-season-summary>.

- R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Racey, G. D., K. Abraham, W. R. Darby, H. R. Timmermann, and Q. Day. 1991. Can woodland caribou and the forest industry coexist: the Ontario scene. *Rangifer* 11:108–115.
- Racey, G. D., A. Harris, and R. F. Foster. 1996. Caribou winter habitat in the new forest: lessons from Lucy Lake. Ontario Ministry of Natural Resources, Thunder Bay, Ontario. 16 pp.
- Rea, R. V. 2014. A preliminary assessment of moose (*Alces alces*) winter diets in the Aleza Lake Research Forest in north-central British Columbia. *Wildlife Afield* 11:50–53.
- Rea, R. V., and A. L. Booth. 2011. Use of trembling aspen bark by moose in a browse-abundant habitat during winter. *Wildlife Afield* 8:104–107.
- Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466–478.
- Roloff, G. J., and B. J. Kernohan. 1999. Evaluating reliability of habitat suitability index models. *Wildlife Society Bulletin (1973-2006)* 27:973–985.
- Rowe, J. S. 1984. Lichen woodland in northern Canada. Pages 225–236 in R. Olson, R. Hastings, and F. Geddes, editors. *Northern ecology and resource management: Memorial essays honouring Don Gill*. The University of Alberta Press, Edmonton, Alberta.
- Russell, K. L. M., and C. J. Johnson. 2019. Post-fire dynamics of terrestrial lichens: Implications for the recovery of woodland caribou winter range. *Forest Ecology and Management* 434:1–17.

- Safranyik, L. 2004. Mountain pine beetle epidemiology in lodgepole pine. Mountain pine beetle symposium: challenges and solutions. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C. 287 pp.
- Sánchez, J. J., R. Marcos-Martinez, L. Srivastava, and N. Soonsawad. 2021. Valuing the impacts of forest disturbances on ecosystem services: An examination of recreation and climate regulation services in U.S. national forests. *Trees, Forests and People* 5:100123.
- Schaefer, J. A., and W. O. Pruitt. 1991. Fire and woodland caribou in southeastern Manitoba. *Wildlife Monographs*:3–39.
- Schrempp, T. V., J. L. Rachlow, T. R. Johnson, L. A. Shipley, R. A. Long, J. L. Aycrigg, and M. A. Hurley. 2019. Linking forest management to moose population trends: The role of the nutritional landscape. *PLOS ONE* 14:e0219128.
- Schwenk, W. S., T. M. Donovan, W. S. Keeton, and J. S. Nunery. 2012. Carbon storage, timber production, and biodiversity: comparing ecosystem services with multi-criteria decision analysis. *Ecological Applications* 22:1612–1627.
- Seidl, R., P. M. Fernandes, T. F. Fonseca, F. Gillet, A. M. Jönsson, K. Merganičová, S. Netherer, A. Arpaci, J.-D. Bontemps, H. Bugmann, J. R. González-Olabarria, P. Lasch, C. Meredieu, F. Moreira, M.-J. Schelhaas, and F. Mohren. 2011. Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling* 222:903–924.
- Seidl, R., T. A. Spies, D. L. Peterson, S. L. Stephens, and J. A. Hicke. 2016. REVIEW: Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology* 53:120–129.

- Seip, D., and E. Jones. 2010. Response of woodland caribou to partial retention logging of winter ranges attacked by mountain pine beetle: 2010. FIA/FSP Project # Y102010 2009-10, British Columbia Ministry of Forests and Range, Prince George, B.C. 33 pp.
- Serrouya, R., B. N. McLellan, S. Boutin, D. R. Seip, and S. E. Nielsen. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. *Journal of Applied Ecology* 48:935–942.
- Spies, T. A., B. C. McComb, R. S. H. Kennedy, M. T. McGrath, K. Olsen, and R. J. Pabst. 2007. Potential effects of forest policies on terrestrial biodiversity in a multi-ownership province. *Ecological Applications* 17:48–65.
- Spribille, T. 2018. Relative symbiont input and the lichen symbiotic outcome. *Current Opinion in Plant Biology* 44:57–63.
- Stevenson, S. K., and D. S. Coxson. 2015. Can partial-cut harvesting be used to manage terrestrial lichen habitat? A review of recent evidence. *Rangifer. Special Issue* 35:11–26.
- Steventon, J. D. 1996. Caribou habitat use in the Chelaslie River migration corridor and recommendations for management. Ministry of Forests, Research Program, Victoria, B.C. 17 pp.
- Stewart, F. E. C., J. J. Nowak, T. Micheletti, E. J. B. McIntire, F. K. A. Schmiegelow, and S. G. Cumming. 2020. Boreal caribou can coexist with natural but not industrial disturbances. *The Journal of Wildlife Management* 84:1435–1444.
- St-Laurent, M.-H., Y. Boulanger, D. Cyr, F. Manka, P. Drapeau, and S. Gauthier. 2022. Lowering the rate of timber harvesting to mitigate impacts of climate change on boreal caribou habitat quality in eastern Canada. *Science of The Total Environment* 838:156244.

- Stockdale, C., Q. Barber, A. Saxena, and M.-A. Parisien. 2019. Examining management scenarios to mitigate wildfire hazard to caribou conservation projects using burn probability modeling. *Journal of Environmental Management* 233:238–248.
- Street, G. M., A. R. Rodgers, T. Avgar, and J. M. Fryxell. 2015. Characterizing demographic parameters across environmental gradients: a case study with Ontario moose (*Alces alces*). *Ecosphere* 6:art138.
- Sturtevant, B. R., A. Fall, D. D. Kneeshaw, N. P. P. Simon, M. J. Papaik, K. Berninger, F. Doyon, D. G. Morgan, and C. Messier. 2007. A toolkit modeling approach for sustainable forest management planning: achieving balance between science and local needs. *Ecology and Society* 12.
- Sulyma, R., and D. S. Coxson. 2001. Microsite displacement of terrestrial lichens by feather moss mats in late seral pine-lichen woodlands of north-central British Columbia. *The Bryologist* 104:505–516.
- Sutherland, I. J., E. M. Bennett, and S. E. Gergel. 2016. Recovery trends for multiple ecosystem services reveal non-linear responses and long-term tradeoffs from temperate forest harvesting. *Forest Ecology and Management* 374:61–70.
- Suzuki, N., and K. L. Parker. 2016. Potential conflict between future development of natural resources and high-value wildlife habitats in boreal landscapes. *Biodiversity and Conservation* 25:3043–3073.
- Thom, D., and R. Seidl. 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews* 91:760–781.
- Thomas, D. C., S. J. Barry, and G. Alaie. 1996. Fire - caribou - winter range relationships in northern Canada. *Rangifer* 16:57–67.

- Thrower, J. S., A. F. Nussbaum, and C. M. Di Lucca. 1994. Site index curves and tables for British Columbia - interior species. 2nd edition. Land Management Handbook Field Guide Insert 6, B.C. Min. For. Res. Branch, Victoria, B.C. 50 pp.
- Timmermann, H. R., and J. G. McNicol. 1988. Moose habitat needs. *The Forestry Chronicle* 64:238–245.
- Triviño, M., T. Pohjanmies, A. Mazziotta, A. Juutinen, D. Podkopaev, E. Le Tortorec, and M. Mönkkönen. 2017. Optimizing management to enhance multifunctionality in a boreal forest landscape. *Journal of Applied Ecology* 54:61–70.
- United States Fish and Wildlife Service. 1981. Standards for the development of habitat suitability index models. Release No. 1-81, 103 ESM. Division of Ecological Services, U.S. Fish and Wildlife Service, Department of the Interior.
- Venier, L. A., I. D. Thompson, R. Fleming, J. Malcolm, I. Aubin, J. A. Trofymow, D. Langor, R. Sturrock, C. Patry, R. O. Outerbridge, S. B. Holmes, S. Haeussler, L. De Grandpré, H. Y. H. Chen, E. Bayne, A. Arsenault, and J. P. Brandt. 2014. Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. *Environmental Reviews* 22:457–490.
- Viereck, L. A., and L. A. Schandelmeier. 1980. Effects of fire in Alaska and adjacent Canada: a literature review. BLM-Technical Report, USDA Forest Service, Fairbanks, Alaska. 135 pp.
- Viljur, M.-L., S. R. Abella, M. Adámek, J. B. R. Alencar, N. A. Barber, B. Beudert, L. A. Burkle, L. Cagnolo, B. R. Campos, A. Chao, B. Chergui, C.-Y. Choi, D. F. R. Cleary, T. S. Davis, Y. A. Dechnik-Vázquez, W. M. Downing, A. Fuentes-Ramirez, K. J. K. Gandhi, C. Gehring, K. B. Georgiev, M. Gimbutas, K. B. Gongalsky, A. Y. Gorbunova, C. H. Greenberg, K. Hylander, E. S. Jules, D. I. Korobushkin, K. Köster, V. Kurth, J. D. Lanham, M. Lazarina, A. B. Leverkus, D. Lindenmayer, D. M. Marra,

- P. Martín-Pinto, J. A. Meave, M. Moretti, H.-Y. Nam, M. K. Obrist, T. Petanidou, P. Pons, S. G. Potts, I. B. Rapoport, P. R. Rhoades, C. Richter, R. A. Saifutdinov, N. J. Sanders, X. Santos, Z. Steel, J. Tavella, C. Wendenburg, B. Wermelinger, A. S. Zaitsev, and S. Thorn. 2022. The effect of natural disturbances on forest biodiversity: an ecological synthesis. *Biological Reviews* 97:1930–1947.
- Vitt, D. H., L. Finnegan, and M. House. 2019. Terrestrial bryophyte and lichen responses to canopy opening in pine-moss-lichen forests. *Forests* 10:233.
- Waterhouse, M. J., H. M. Armleder, and A. F. L. Nemec. 2011. Terrestrial lichen response to partial cutting in lodgepole pine forests on caribou winter range in west-central British Columbia. *Rangifer* 31:119–134.
- Webb, E. T. 1998. Survival, persistence, and regeneration of the reindeer lichens, *Cladina stellaris*, *C. rangiferina*, and *C. mitis* following clearcut logging and forest fire in northwestern Ontario. *Rangifer* 18:41–47.
- Westworth, D., L. Brusnyk, J. Roberts, and H. Veldhuzien. 1989. Winter habitat use by moose in the vicinity of an open-pit copper mine in north-central British Columbia. *Alces* 25:156–166.
- Whitman, E., M.-A. Parisien, D. T. Price, M.-H. St-Laurent, C. J. Johnson, E. R. DeLancey, D. Arseneault, and M. D. Flannigan. 2017. A framework for modeling habitat quality in disturbance-prone areas demonstrated with woodland caribou and wildfire. *Ecosphere* 8:e01787.
- Whittington, J., M. Hebblewhite, N. J. DeCesare, L. Neufeld, M. Bradley, J. Wilmshurst, and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach: Wolf-caribou encounter rates. *Journal of Applied Ecology* 48:1535–1542.

- Wittmer, H. U., B. N. McLellan, R. Serrouya, and C. D. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *Journal of Animal Ecology* 76:568–579.
- Wright, E. F., C. D. Canham, and K. D. Coates. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Canadian Journal of Forest Research* 30:10.
- Wright, E. F., K. D. Coates, C. D. Canham, and P. Bartemucci. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. *Canadian Journal of Forest Research* 28:16.

Personal Communication

Crowley, Shannon. February 6, 2019 and July 9, 2020. Ecological Monitoring Coordinator.
John Prince Research Forest. Fort St. James, B.C.

Hodder, Dexter. February 6, 2019 and July 9, 2020. Director of Research and Education.
John Prince Research Forest. Fort St. James, B.C.

Johnson, Chris. 2020. Professor. University of Northern British Columbia. Prince George,
B.C.

Attended half day meeting to workshop linker functions (March 27, 2019):

Cichowski, Debbie. March 27, 2019. Biologist. Caribou Ecological Consulting.
Smithers, B.C.

Clason, Alana. March 27, 2019. Research Associate and Ecologist. Bulkley Valley
Research Centre. Smithers, B.C.

Coates, Dave. March 27, 2019. Retired Research Silviculturist (British Columbia
Ministry of Forests). Smithers, B.C.

Elkin, Ché . March 27, 2019. Associate Professor. FRBC/Slocan Mixedwood
Ecology Chair. University of Northern British Columbia. Prince George, B.C.

Lilles, Erica. March 27, 2019. Research Generalist. British Columbia Ministry of
Forests. Smithers, B.C.

Appendix 1

SORTIE-ND: Model Description

<http://sortie-nd.org/help/manuals/index.html>

SORTIE-ND is an individual-tree, spatially explicit model. This appendix describes the model using the Overview, Design concepts, Details (ODD) protocol recommended by Grimm et al. (2006, 2010). This description of SORTIE-ND is sourced from SORTIE-ND online documentation (Canham and Murphy n.d.). SORTIE-ND can be parameterized to simulate and output the dynamics of a broad array of tree and stand variables.

Purpose: SORTIE-ND was developed to study neighbourhood processes and forest dynamics. It was initially developed as a small-scale disturbance model to study transitional oak-northern hardwood forests in the northeastern United States (Pacala et al. 1996). It has since been parameterized for Interior Cedar Hemlock moist cool (ICHmc2) and Sub-boreal Spruce moist cool Babine variant (SBSmc2) forests of northwest BC (Banner et al. 1993, Canham et al. 2004, Astrup et al. 2008a).

Entities, State Variables, and Scales: There are four hierarchical levels of the model, the individual (tree or grid cell), the neighbourhood (neighbouring trees within a specified radius of a target location), the subplot (a specified area within the plot), and the stand (the entire plot). There are three state entities: individual trees, grid cells (for substrate and light) and the plot. State variables for trees include: species, diameter at 10 cm above the ground, diameter at breast height (DBH, measured at 1.35 m above the ground), height, x and y coordinates (location), live or dead status, crown radius and depth, and years since death (if dead). State variables for substrate are cell size, substrate type, and time since substrate type was assigned. State variables for the plot include: length (in X and Y direction) and latitude. Numerous auxiliary variables can be calculated from state variables including measures of

tree volume, basal area, density, carbon, and light. These may be calculated at various scales (tree, grid cell, subplot and stand level). This description of variables pertains to the model set-up that has been established for northwest British Columbia. The specific variables that are available for a model scenario are dependent on the model behaviours that are selected (i.e., the ecological and biological processes selected for incorporation into the model).

Basic plot and scenario set-up options include timestep, timeframe and plot and grid cell size. The typical timestep and minimum timeframe is 1 year; there is no maximum timeframe. The minimum plot size is 100 m by 100 m. There is no maximum plot size however plot size typically reflects the computational intensity of the simulation, computing capacity, and the research question. 200 x 200-m or 300 x 300-m are typical plot sizes. The default setting for grid cell size (pixel) is typically set at 8 x 8- m. A plot can be conceptualized as a torus (or donut) where a tree on the west ‘edge’ of the plot is modelled as the neighbour of a tree on the east ‘edge’ of the plot at the same latitude. Thus a 9-ha plot set up as a clearcut (9-ha clearcut) models the interior condition of a stand with no neighbouring mature trees or edge effect (i.e., all trees in the plot are surrounded by trees regenerating in the same clearcut conditions).

Process overview and scheduling: A SORTIE-ND simulation flows in the following process order: 1. harvest and disturbance activity, 2. light calculation, 3. growth, 4. mortality, 5. substrate dynamics, 6. snag dynamics, 7. seed dispersal, 8. seedling establishment, 9. planting activity, 10. output generation.

Design concepts: SORTIE-ND was initially designed to model neighbourhood interactions, that is, the interactions of trees with their nearest neighbours to study local ecosystem dynamics. SORTIE-ND extrapolates from measurable fine-scale and short-term interactions among individual trees to large-scale and long-term dynamics of forest communities (Coates

and Hall 2005). SORTIE-ND was initially designed to study ecological processes but has since been developed to also address questions regarding forest management, natural disturbance, climate change and carbon dynamics.

Each tree is modelled as an individual with an explicit location; the establishment, growth, mortality, and regeneration dynamics of each individual is determined by its neighbourhood and the ecological processes included in the simulation. These processes are modelled in SORTIE-ND by 'behaviours'. Researchers can parameterize existing behaviours or develop new ones specific to their forest type and research question. Different behaviours can be applied to different tree species and tree life stages. The intent with the design of SORTIE-ND was the development of a flexible model with a simple structure that provides the user with the opportunity to control almost every aspect of the model. The description of state variables and behaviours of SORTIE-ND in this appendix describe the model as parameterized for the SBS.

The design of SORTIE-ND results in emergent properties. The interaction of behaviours specific to size and species of individual trees results in changes in species composition of multi-species stands over time that reflects observed successional processes (Maleki et al. 2020). Light dynamics occurring within stands over time are also emergent properties of the model and reflect the interaction of species-specific tree establishment, growth and mortality behaviours.

Behaviours can incorporate stochasticity; currently mortality, snag fall, seed dispersal and seedling establishment are behaviours with stochastic elements.

Initialization: Initialization of the model involves establishing the state variables for the plot and initializing the tree population. Trees can be initialized in three ways: 1) a stem map that identifies the location, species and DBH of each tree, 2) specifying initial densities of trees by

species and either height class (for seedlings) or DBH class (for trees with a DBH) or 3) the tree planting behaviour. Height and DBH classes are established by the user. Trees are initialized at random locations unless locations are specified with a stem map. Grid cell pixel size can be specified for substrate and light. Substrate features of grid cells are initialized from the input parameters.

Input data: Tree maps can be input for starting conditions. The current version of SORTIE-ND in use in northwest B.C. does not incorporate other external inputs.

Submodels: Grimm et al. (2010) state that it is important to describe sub-models in detail with respect to model parameters, parameter dimensions, decisions guiding model form selection, and parameter testing and validation. Behaviours can be viewed as submodels. Extensive work has been conducted to develop each behaviour and parameterize those that are applied to forests of northwest B.C. The online SORTIE-ND manual provides detailed information regarding each behaviour (Canham and Murphy n.d.).

Appendix 2

Linker Functions: Model Description

Linker functions have been used to extend the ability of stand dynamics models to predict not only tree related variables but also habitat elements (e.g. Cordonnier et al. 2013, Mönkkönen et al. 2014, Bugmann et al. 2017). The linker functions developed in this study described, in a mathematical form, the relationship between specific stand-level variables and habitat elements. For example, one linker function described the relationship between understory light and suitability for forage lichen. Mönkkönen et al. (2014) and Cordonnier et al. (2013) provide examples of the development of linker functions to describe the suitability of a site to provide habitat for a specific species or guild of species.

The Grimm et al. (2006, 2010) ODD protocol was developed to describe complex models but can also be applied to simple models such as the linker functions in this study. In this context, the purpose of linker functions was to link stand variables (e.g., light, tree, or site variables) to habitat variables (e.g., relative suitability of a stand to support forage lichen or moose shrub communities). Variables included understory light, time since disturbance, edaphic site condition (indices of soil moisture and nutrients), conifer basal area and broadleaf basal area. These variables can be acquired from SORTIE-ND output. The process overview and scheduling can be described by describing the nested structure of the model. The full lichen or moose shrub linker function represents the interactions and relationship between all the identified stand variables and the habitat variable. The full linker function is comprised of component linker functions. A component linker function is developed specific to each stand variable and defines the relationship between the stand variable and the habitat variable. Component linker functions are combined into a full linker function. Scheduling requires the following order of calculation: first the component linker function and second the linker

function. The design concept behind the development of linker functions is that they are developed through a combination of available literature, data and expert knowledge. They can further be refined through field studies targeting the areas where data is least available or analysis indicates further study is required. The mathematical form of each function was selected on the principle that they should be simple but also flexible enough to represent the hypothesized potential relationship.

The first step of the project was an extensive literature review. Informal meetings were then organized with local experts in the fields of ecology, moose and caribou forage, and lichen ecology to discuss and draft the linker and component functions. A half-day meeting was held with Deb Cichowski, Dr. Ché Elkin, Dr. Alana Clason, Erica Lilles, and Dr. Dave Coates and a shorter meeting occurred with Dexter Hodder, Shannon Crowley and Dr. Ché Elkin. I also met with Dr. Darwyn Coxson. At these meetings we identified appropriate predictor and response variables and hypothesized the appropriate functional forms for the component and full linker functions.

Terrestrial lichen and moose shrub species were determined to be the primary forage groups that determined the value of a stand for caribou winter habitat. Terrestrial lichens make up the majority of northern caribou diet during the winter (Miller 1976, Thomas and Hervieux 1986, Cichowski 1989, Thompson et al. 2015). Woody shrubs comprise the majority of moose winter diet (Eastman 1977, Rea and Booth 2011, Hodder et al. 2013).

The linker functions were developed following a process similar to the habitat suitability functions described in Mönkkönen et al. (2014). That is, for each forage type (lichen or moose shrub) a linker function was developed that represented the relationship of each stand variable to the index of habitat suitability (i.e., for terrestrial lichens, stand variables include light availability and proportion of broadleaf trees in the stand). The interactions between

component linker functions were either multiplicative (if each component was fundamentally non-replaceable) or additive (if each item could be considered an alternative to the other) (see Whitman et al. 2017).

In developing component linker functions, it was important to keep in mind that each component linker function represented solely the relationship between one stand variable and the resultant response variable. For example for lichen, the component linker function for understory light represented only the influence of understory light on the relative suitability for lichen. It did not reflect any differences in soil moisture or vegetation community that could occur at different light levels.

Personal Communication

Cichowski, Debbie. March 27, 2019. Biologist. Caribou Ecological Consulting. Smithers, BC

Clason, Alana. March 27, 2019. Research Associate and Ecologist. Bulkley Valley Research Centre. Smithers, B.C.

Coates, Dave. March 27, 2019. Retired Research Silviculturist (British Columbia Ministry of Forests). Smithers, B.C.

Coxson, Darwin. March 25, 2019. Professor. University of Northern British Columbia. Prince George, B.C.

Crowley, Shannon. February 6, 2019 and July 9, 2020. Ecological Monitoring Coordinator. John Prince Research Forest. Fort St. James, B.C.

Elkin, Ché . March 27, 2019. Associate Professor. FRBC/Slocan Mixedwood Ecology Chair. University of Northern British Columbia. Prince George, B.C.

Hodder, Dexter. February 6, 2019 and July 9, 2020. Director of Research and Education. John Prince Research Forest. Fort St. James, B.C.

Lilles, Erica. March 27, 2019. Research Generalist. British Columbia Ministry of Forests. Smithers, B.C.

Appendix 3

Linker Function Calibration Figures

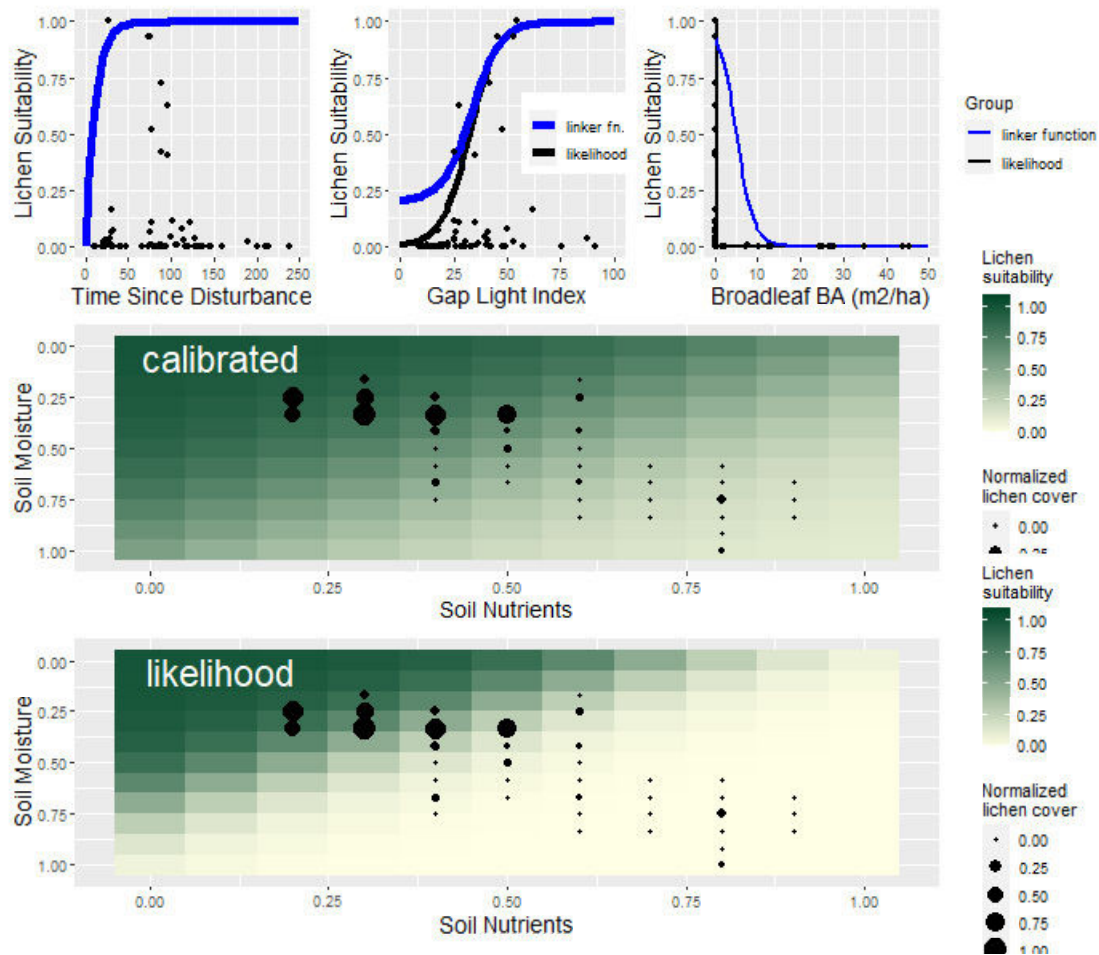


Figure 13. Comparison of the linker functions for lichen parameterized with the calibrated parameters (blue) versus parameterized with the maximum likelihood estimates (black). BA = basal area (m^2/ha). Where only a blue line is present, the maximum likelihood estimate was used in the final function. Empirical data are represented by black dots ($n=76$) and were collected during the summer of 2019 in sub-boreal forests of west-central British Columbia.

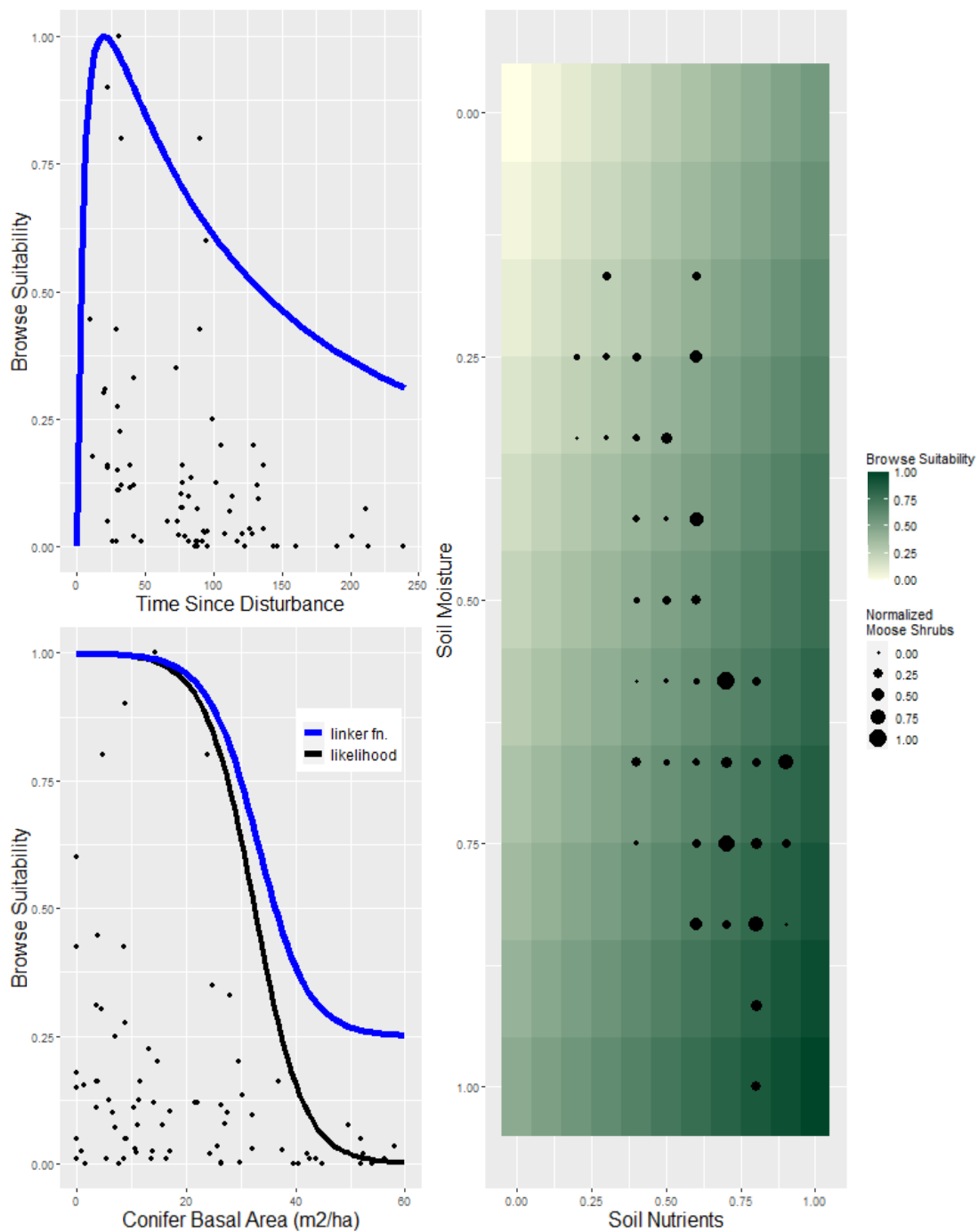


Figure 14. Comparison of the linker functions for moose shrubs used for forage parameterized with the calibrated parameters (blue) versus parameterized with the maximum likelihood estimates (black). Where only a blue line is present, the maximum likelihood estimate was used in the final function. Empirical data are represented by black dots (n=76) and were collected during the summer of 2019 in sub-boreal forests of west-central British Columbia.

Appendix 4

Empirical Data Distribution Figures

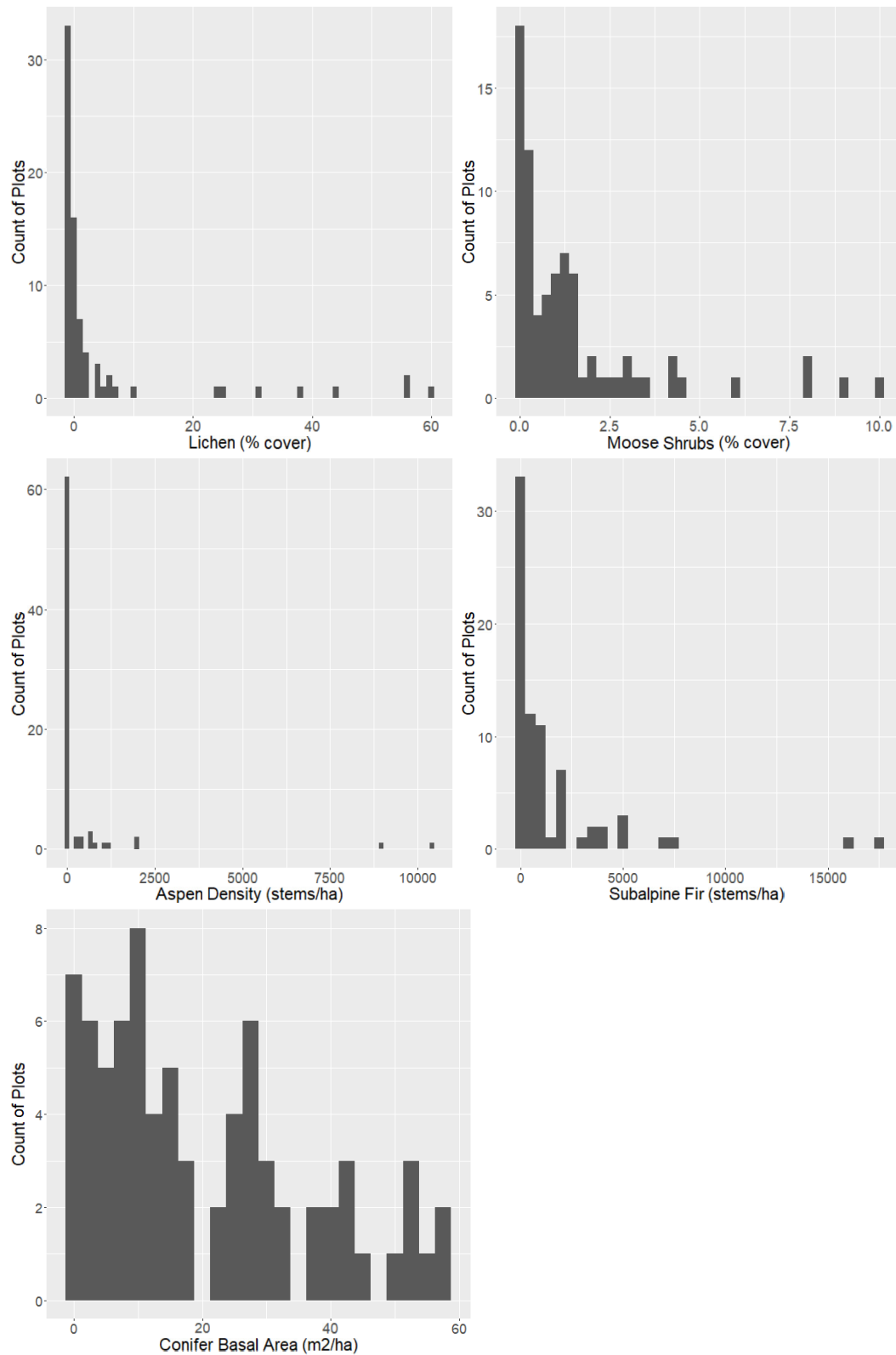


Figure 15. Distribution of the abundance of forage lichen, moose shrubs, aspen (0.5 - 3 m in height), subalpine fir (0.5 - 3 m in height), and conifer basal area in the empirical dataset ($n = 76$). Data were collected during the summer of 2019 in sub-boreal forests of west-central British Columbia.

Appendix 5

Linker Component Function Figures

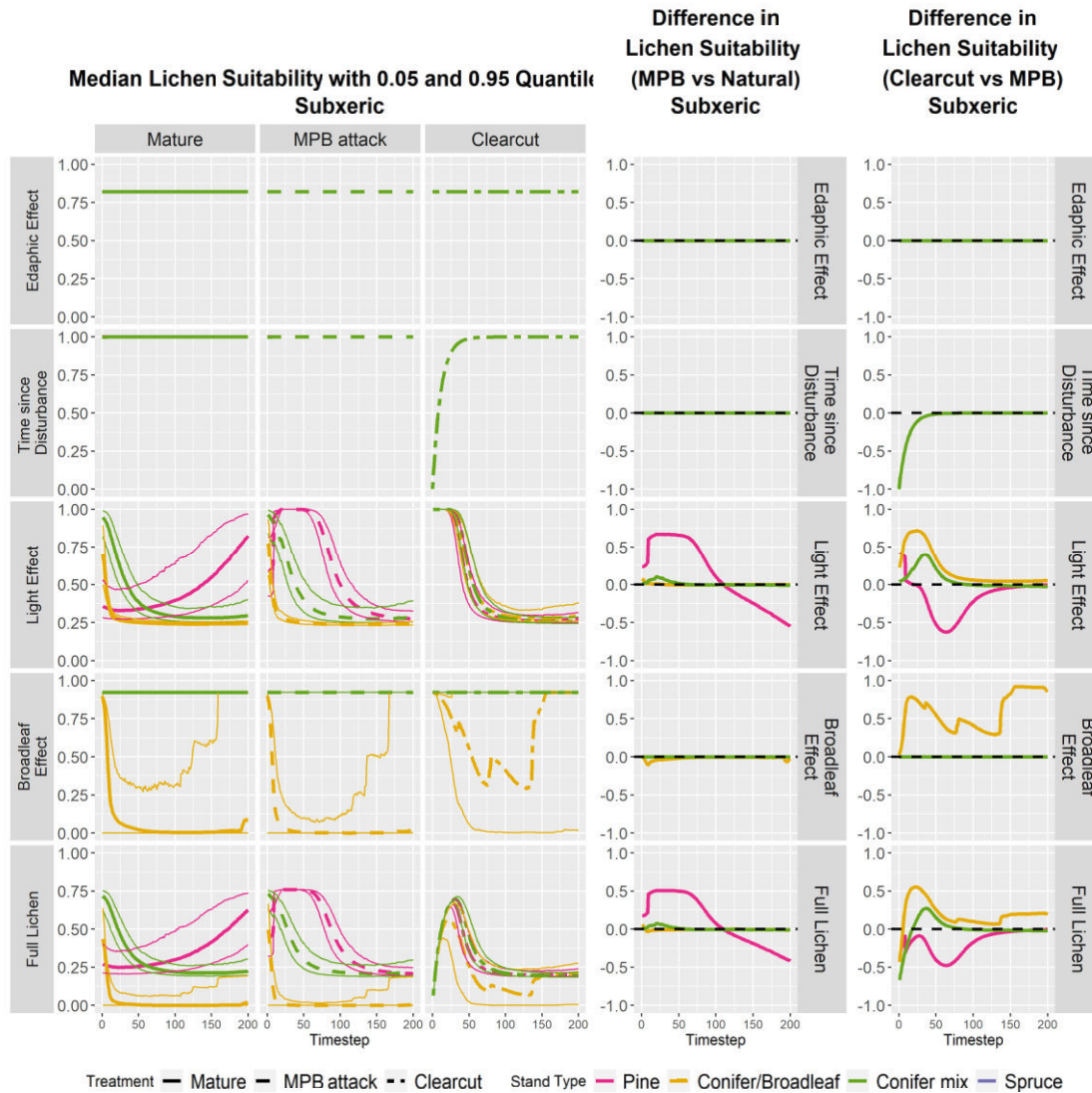


Figure 16. Output of the component linker functions for forage lichen in three different stand types (colours) on subxeric sites. The top four rows present the output of the component linker functions, with the full suitability index for forage lichen shown in row five. Coloured lines represent different stand types. Where only the *conifer mix* stand suitability appears on the figure, the other stand types have the same suitability (e.g., the broadleaf effect for the mature *pine* stand is the same as the *conifer mix* stand). The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand. The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

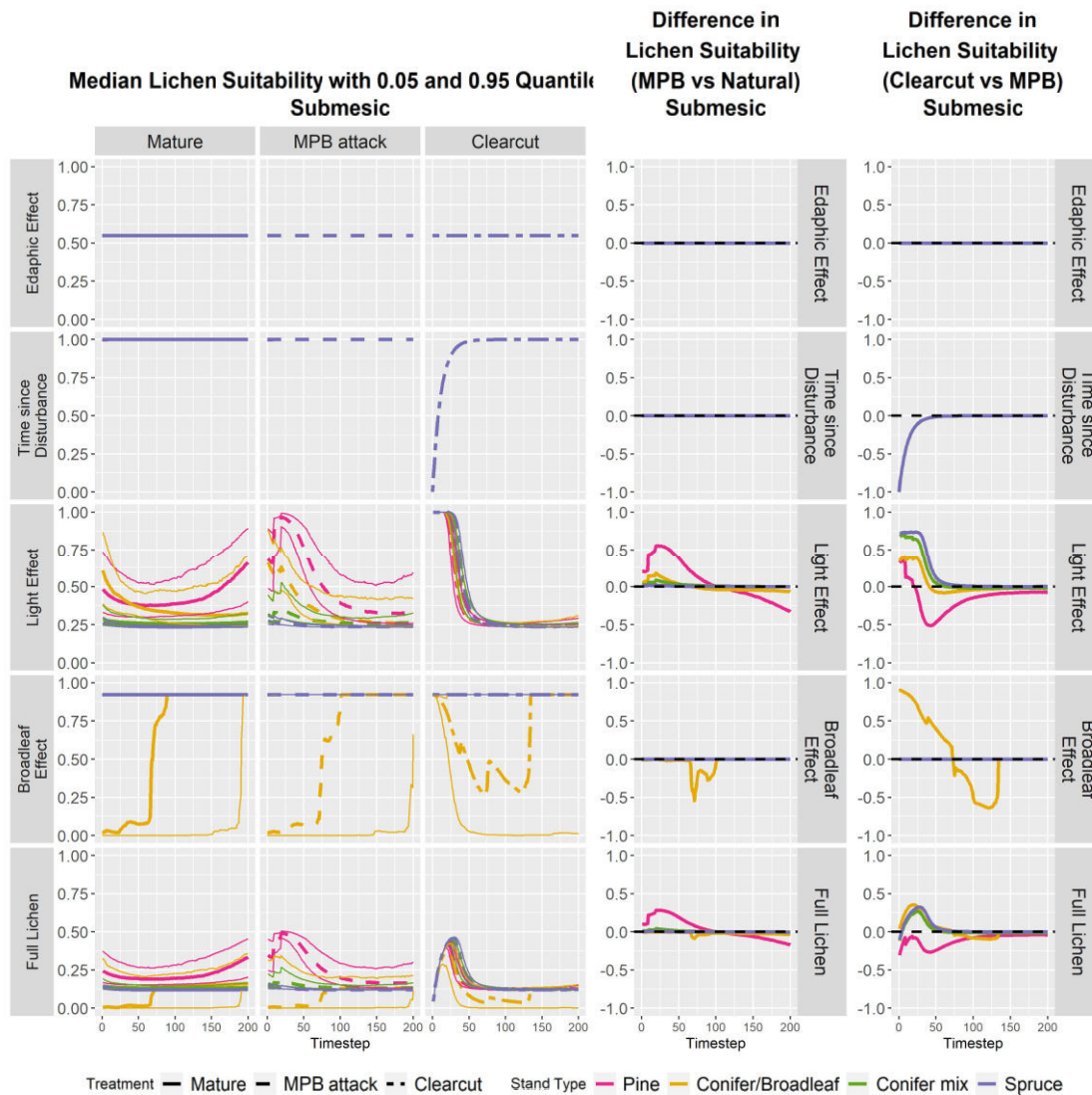


Figure 17. Output of the component linker functions for forage lichen in four different stand types (colours) on submesic sites. The top four rows present the output of the component linker functions, with the full suitability index for forage lichen shown in row five. Where only the *spruce* stand suitability appears on the figure, the other stand types have the same suitability (e.g., the broadleaf effect for the mature *pine* stand is the same as the *spruce* stand). The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand. The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

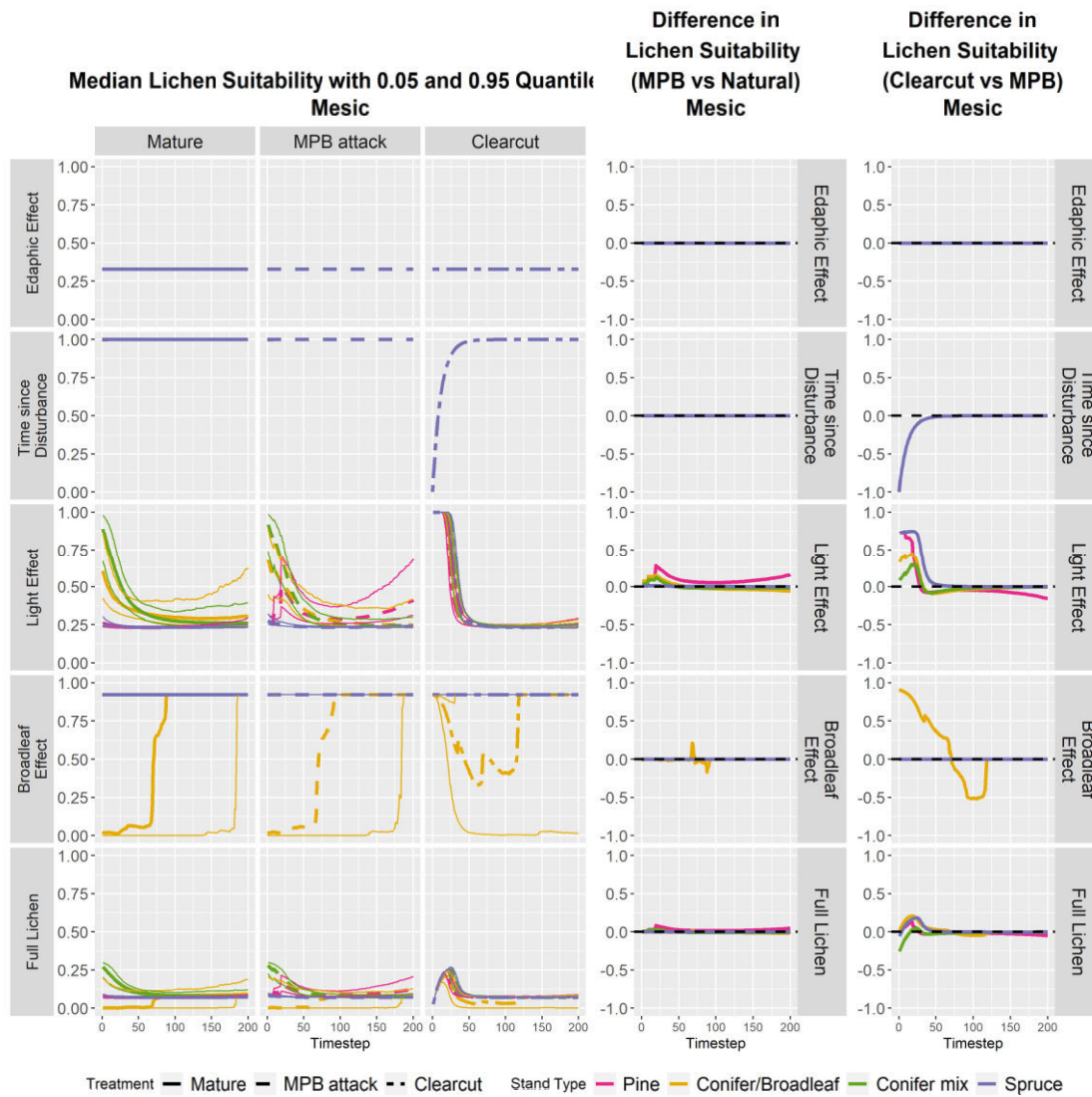


Figure 18. Output of the component linker functions for forage lichen in four different stand types (colours) on mesic sites. The top four rows present the output of the component linker functions, with the full suitability index for forage lichen shown in row five. Where only the *spruce* stand suitability appears on the figure, the other stand types have the same suitability (e.g., the broadleaf effect for the mature *pine* stand is the same as the *spruce* stand). The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand. The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

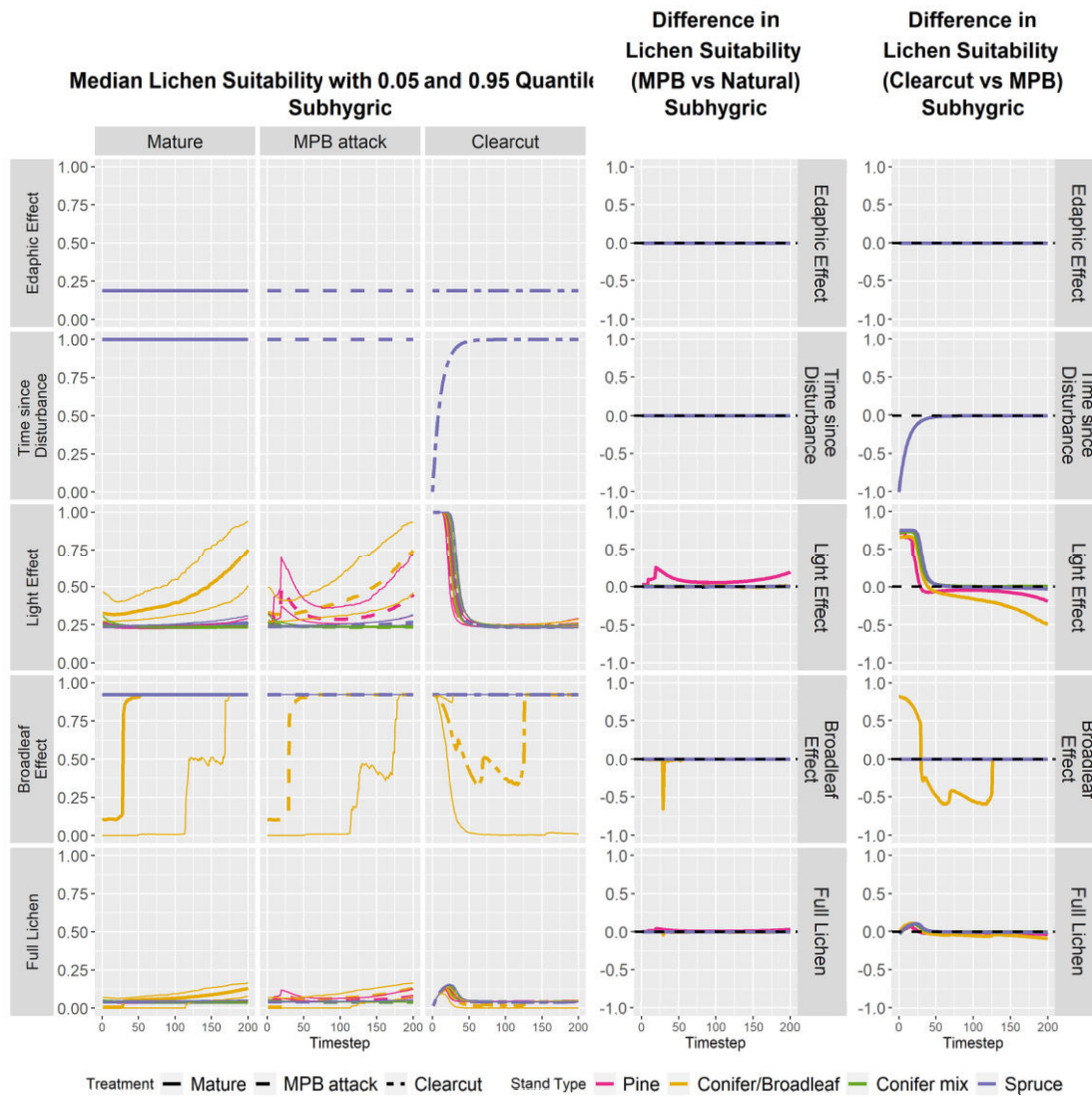


Figure 19. Output of the component linker functions for forage lichen in four different stand types (colours) on subhygric sites. The top four rows present the output of the component linker functions, with the full suitability index for forage lichen shown in row five. Where only the *spruce* stand suitability appears on the figure, the other stand types have the same suitability (e.g., the broadleaf effect for the mature *pine* stand is the same as the *spruce* stand). The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand. The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

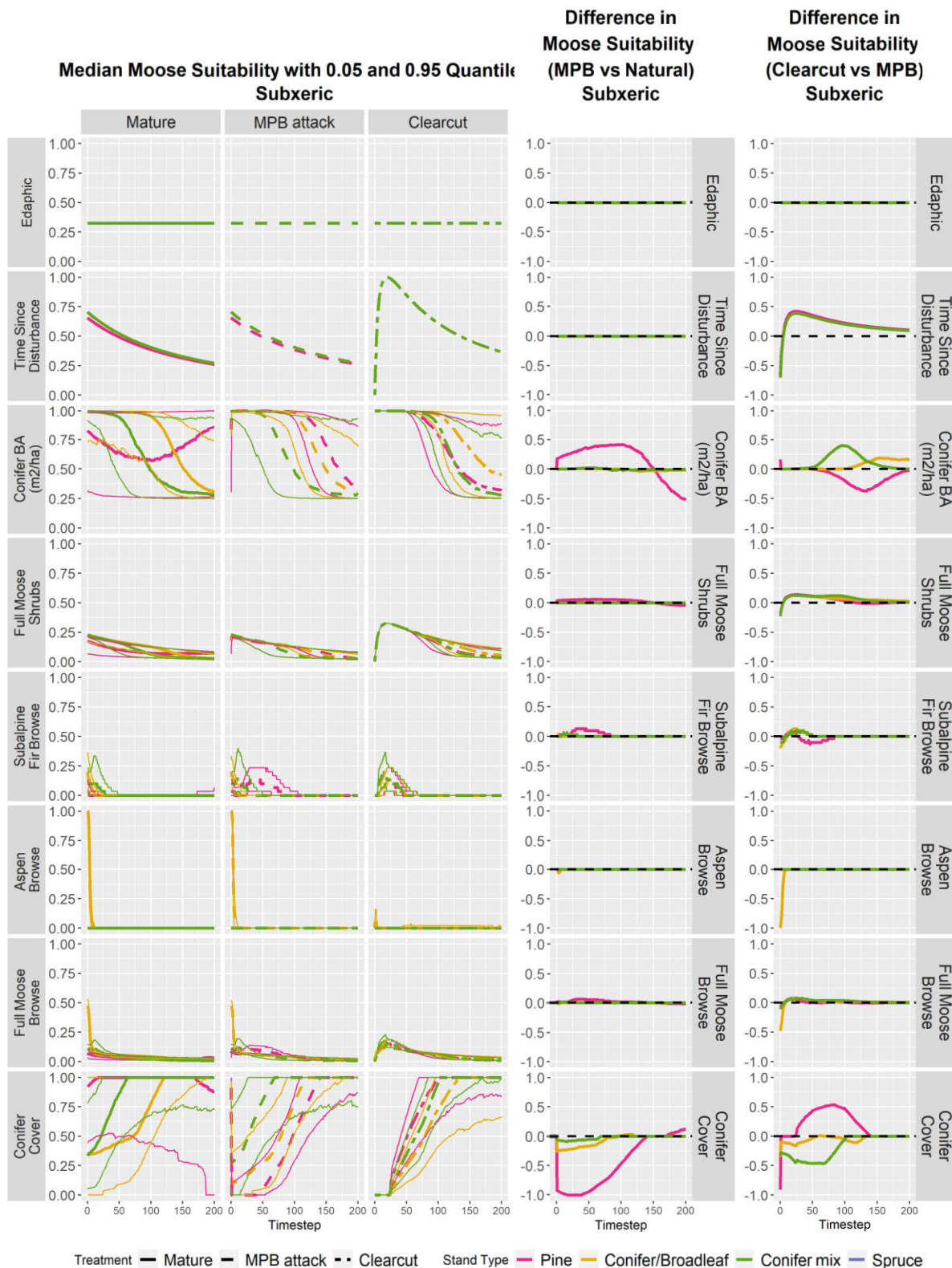


Figure 20. Output of the component linker functions for moose browse in three different stand types (colours) on subxeric sites. The top three rows present the output of the component linker functions for moose shrubs, with the full suitability index for moose shrubs shown in row four. The suitability of a stand for subalpine fir and aspen browse are presented in rows five and six and the total moose browse suitability of a stand in row seven. The bottom row illustrates the suitability of a stand to

provide vertical cover. Coloured lines represent different stand types. Where only the *conifer mix* stand suitability appears on the figure, the other stand types have the same suitability (e.g., aspen browse for the mature *pine* stand is the same as the *conifer mix* stand). The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand. The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

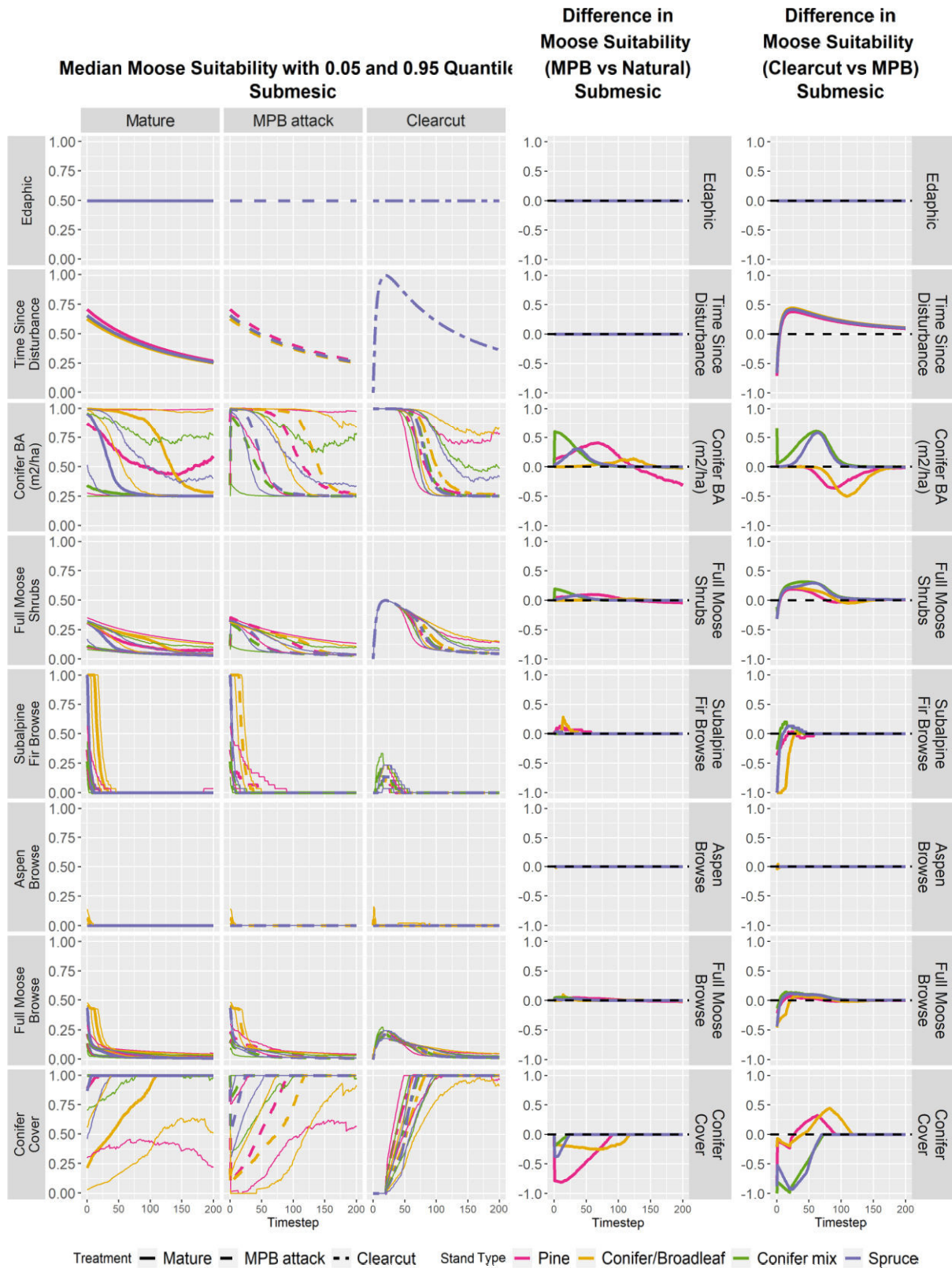


Figure 21. Output of the component linker functions for moose browse in four different stand types (colours) on submesic sites. The top three rows present the output of the component linker functions for moose shrubs, with the full suitability index for moose shrubs shown in row four. The suitability

of a stand for subalpine fir and aspen browse are presented in rows five and six and the total moose browse suitability of a stand in row seven. The bottom row illustrates the suitability of a stand to provide vertical cover. Coloured lines represent different stand types. Where only the *spruce* stand suitability appears on the figure, the other stand types have the same suitability (e.g., aspen browse for the mature *pine* stand is the same as the *spruce* stand). The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand. The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

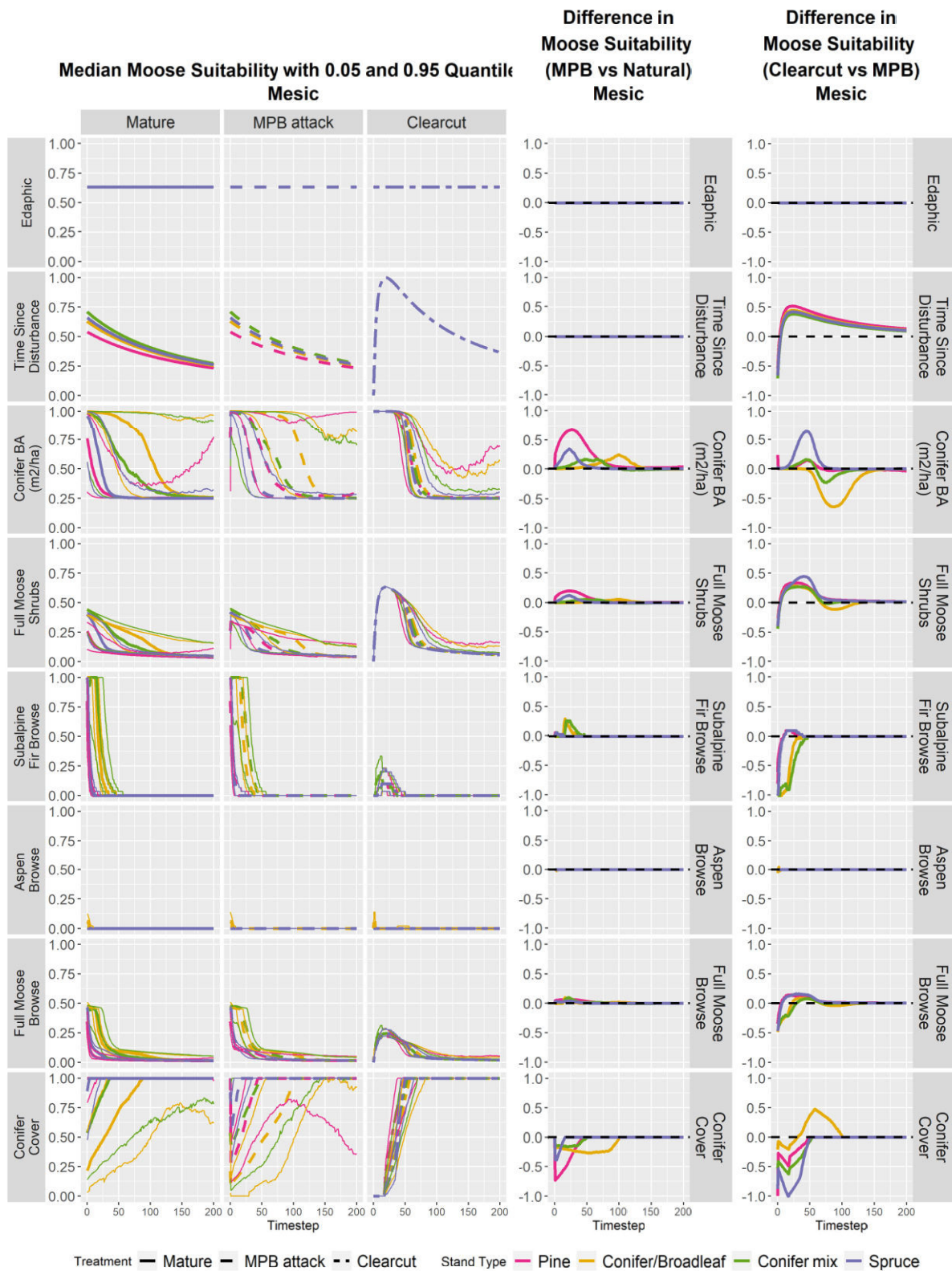


Figure 22. Output of the component linker functions for moose browse in four different stand types (colours) on mesic sites. The top three rows present the output of the component linker functions for moose shrubs, with the full suitability index for moose shrubs shown in row four. The suitability of a stand for subalpine fir and aspen browse are presented in rows five and six and the total moose browse suitability of a stand in row seven. The bottom row illustrates the suitability of a stand to

provide vertical cover. Coloured lines represent different stand types. Where only the *spruce* stand suitability appears on the figure, the other stand types have the same suitability (e.g., aspen browse for the mature *pine* stand is the same as the *spruce* stand). The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand. The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

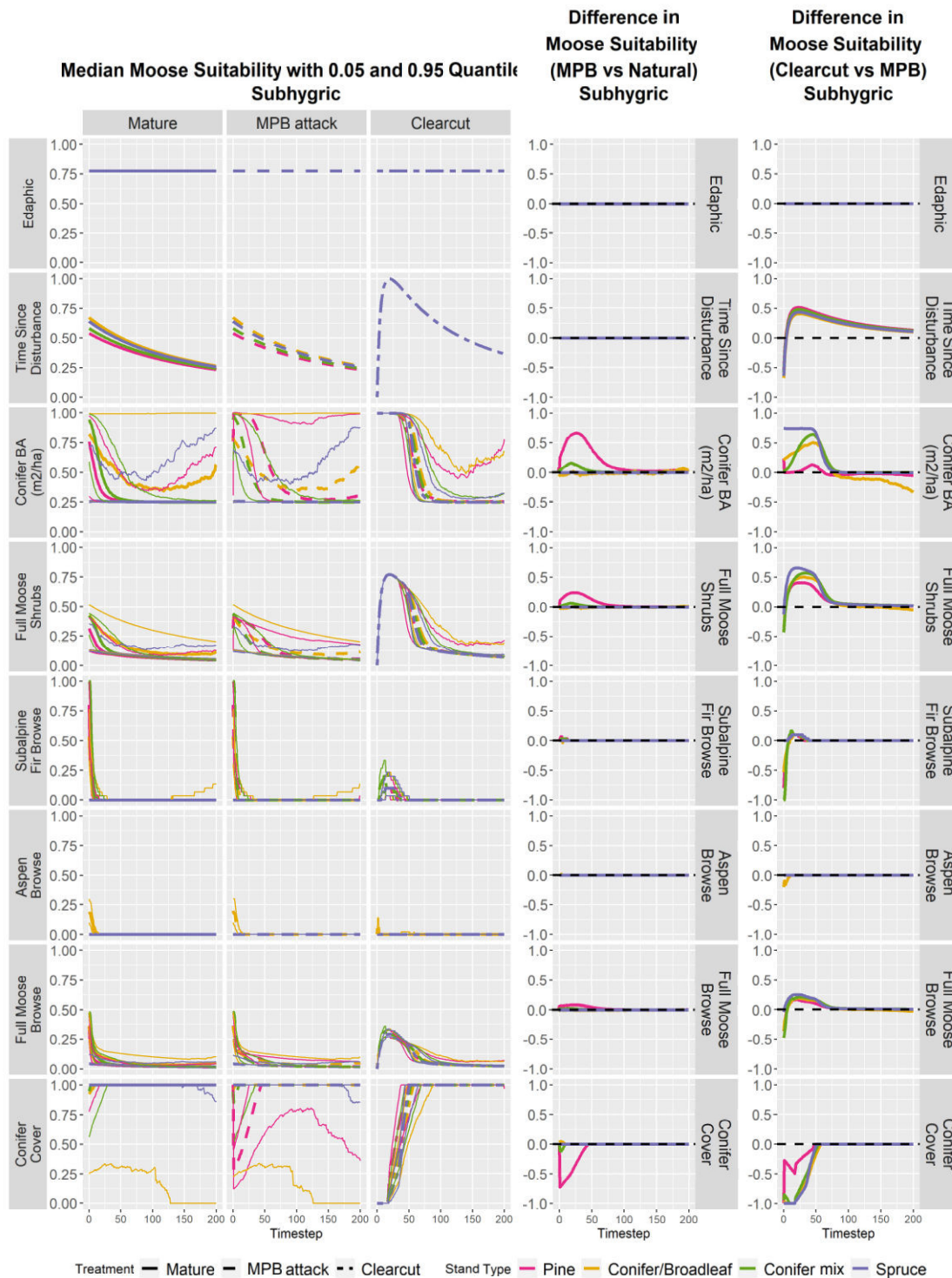


Figure 23. Output of the component linker functions for moose browse in four different stand types (colours) on subhygric sites. The top three rows present the output of the component linker functions for moose shrubs, with the full suitability index for moose shrubs shown in row four. The suitability of a stand for subalpine fir and aspen browse are presented in rows five and six and the total moose browse suitability of a stand in row seven. The bottom row illustrates the suitability of a stand to provide vertical cover. Coloured lines represent different stand types. Where only the *spruce* stand suitability appears on the figure, the other stand types have the same suitability (e.g., aspen browse for the mature *pine* stand is the same as the *spruce* stand). The 5th and 95th quantiles (thin lines) provide

measures of the variability in suitability within the stand. The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand.

Appendix 6

Figures of Suitability Indices for all Stand Types and all Sites

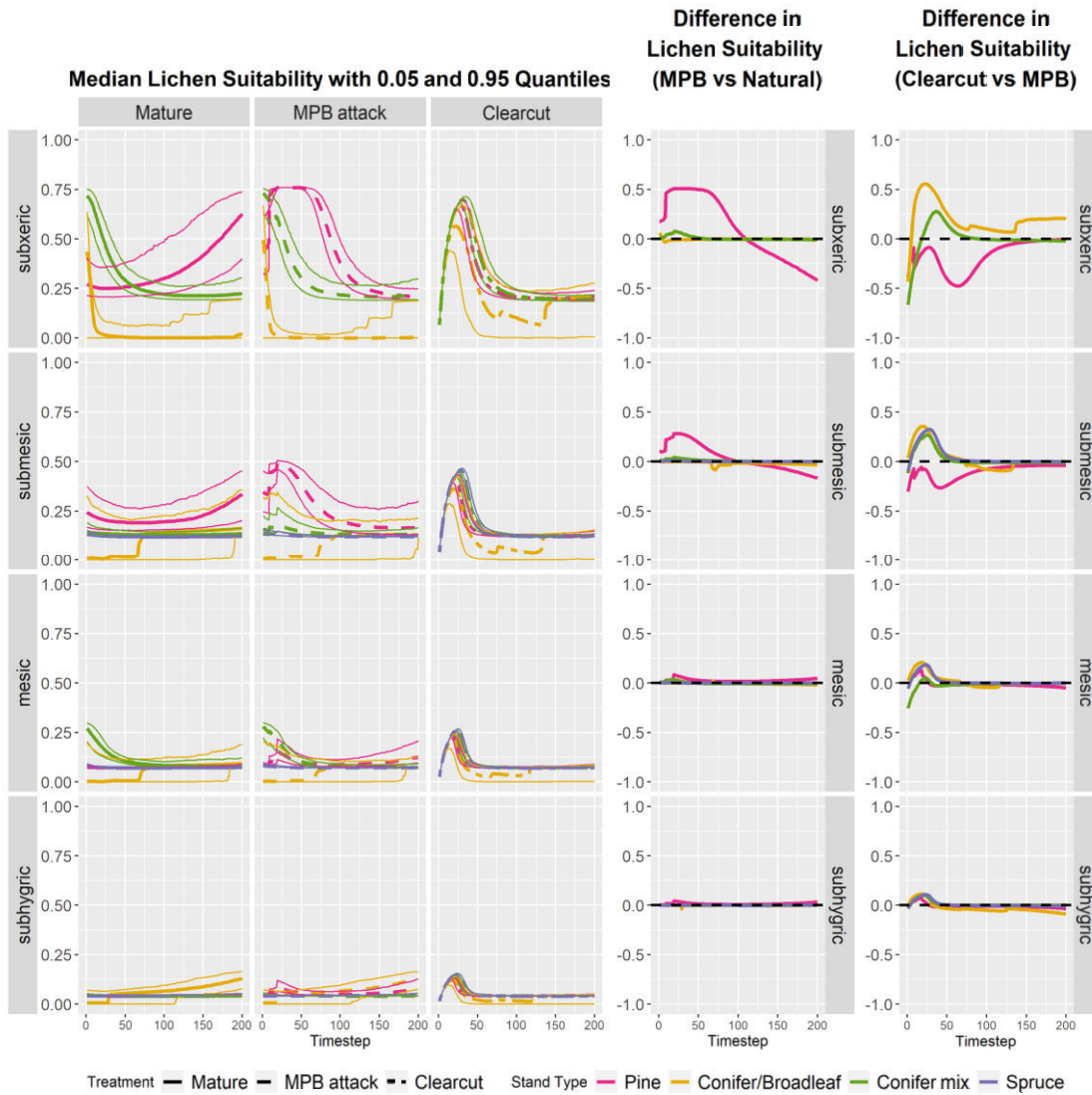


Figure 24. The projected response of lichen suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours). The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand. The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand.

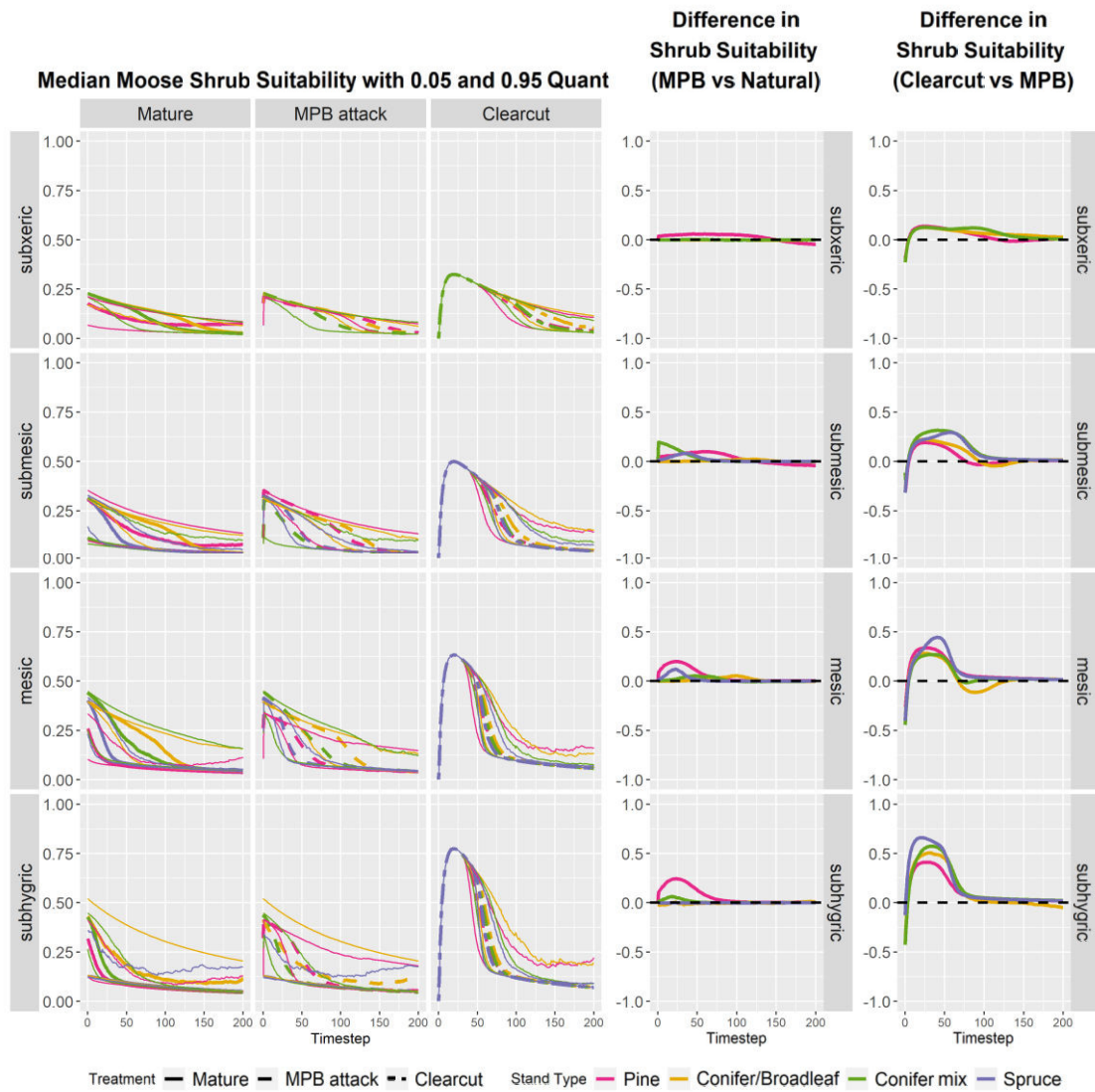


Figure 25. The projected response of moose shrub suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours). The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand. The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand.

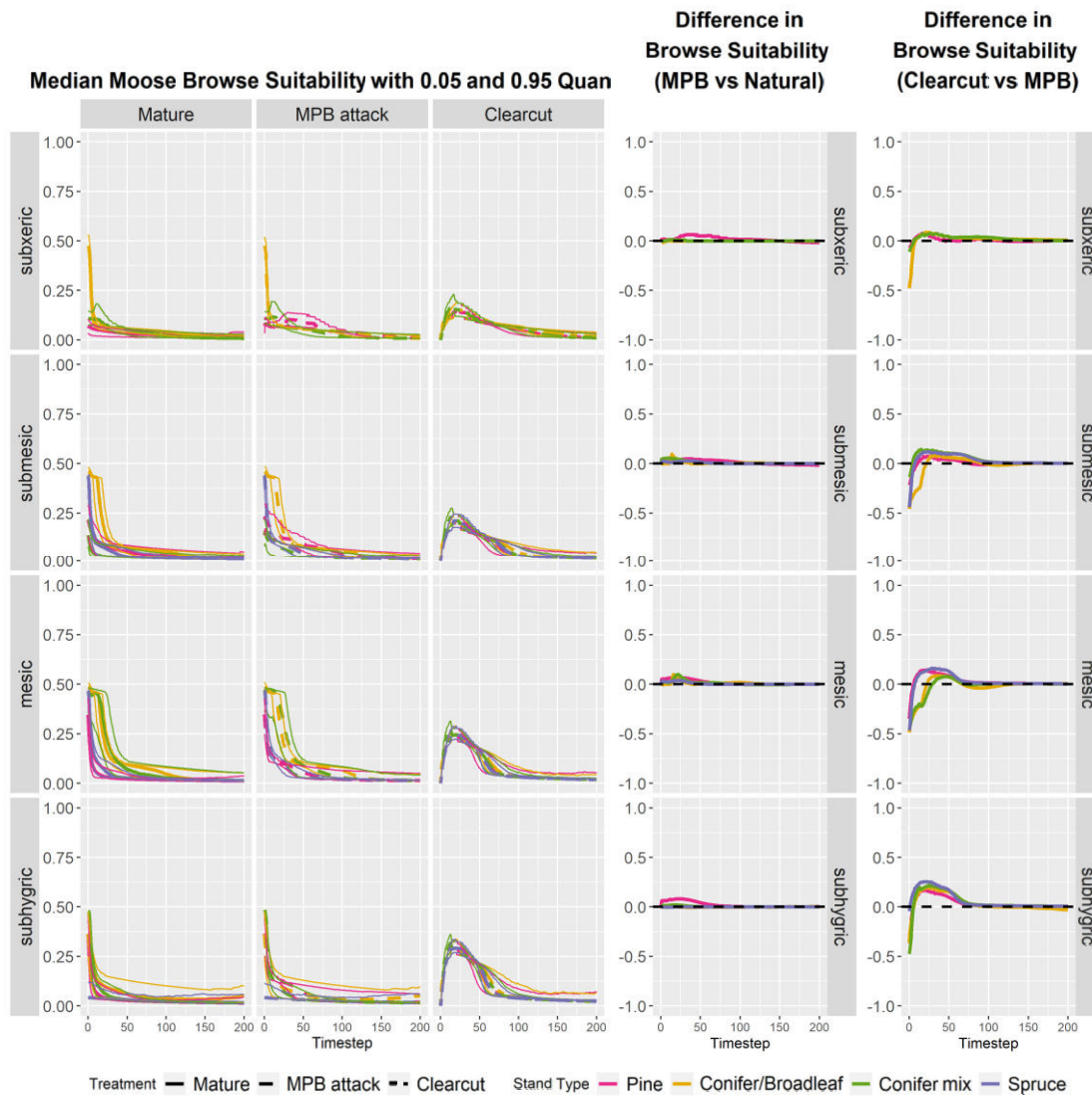


Figure 26. The projected response of moose browse suitability (includes aspen and subalpine fir 0.5 – 3 m in height and moose shrubs) over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours). The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand. The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand.

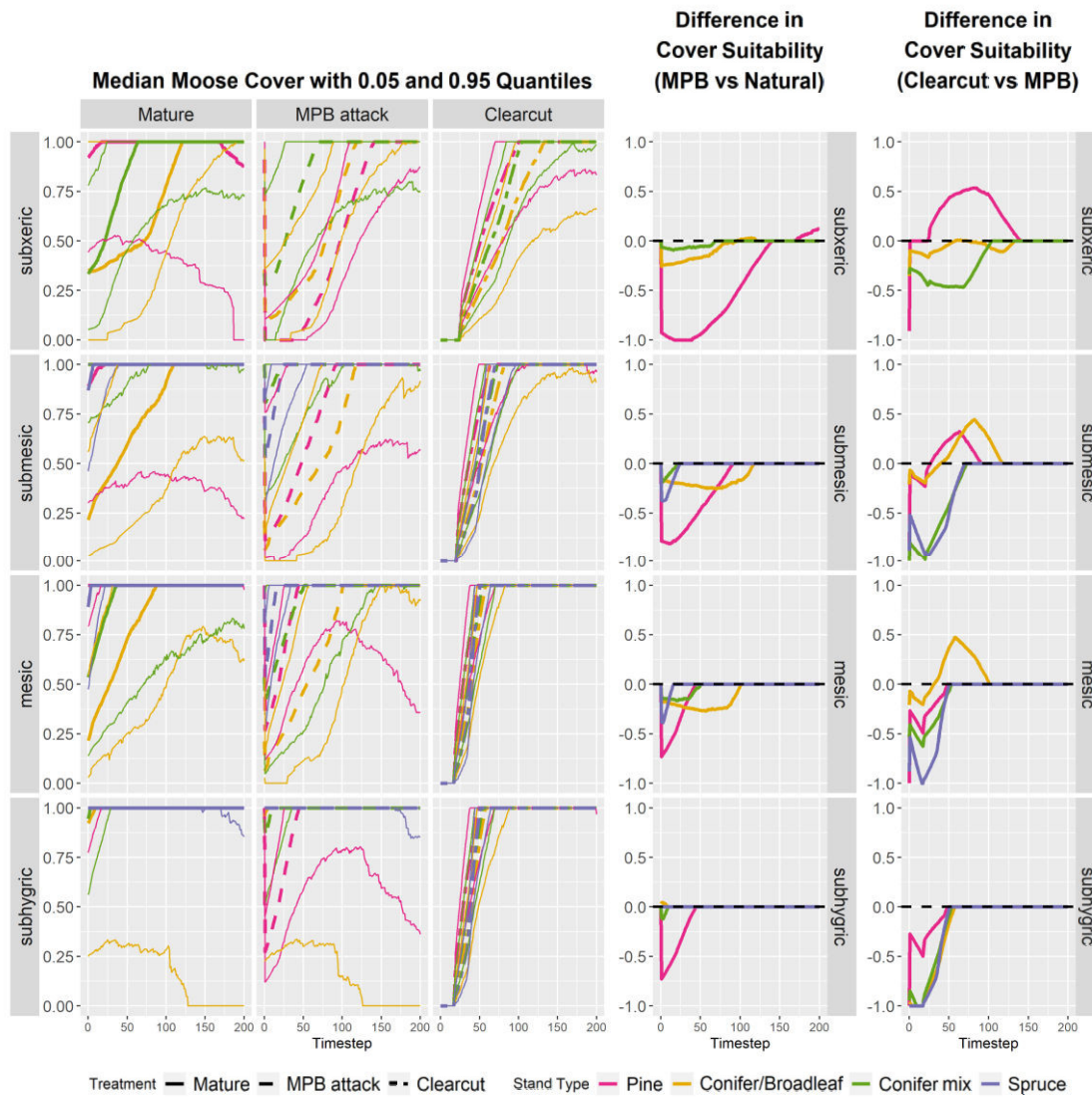


Figure 27. The projected response of the suitability of a stand to provide vertical cover over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (rows) and four stand types (colours). The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand. The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand.

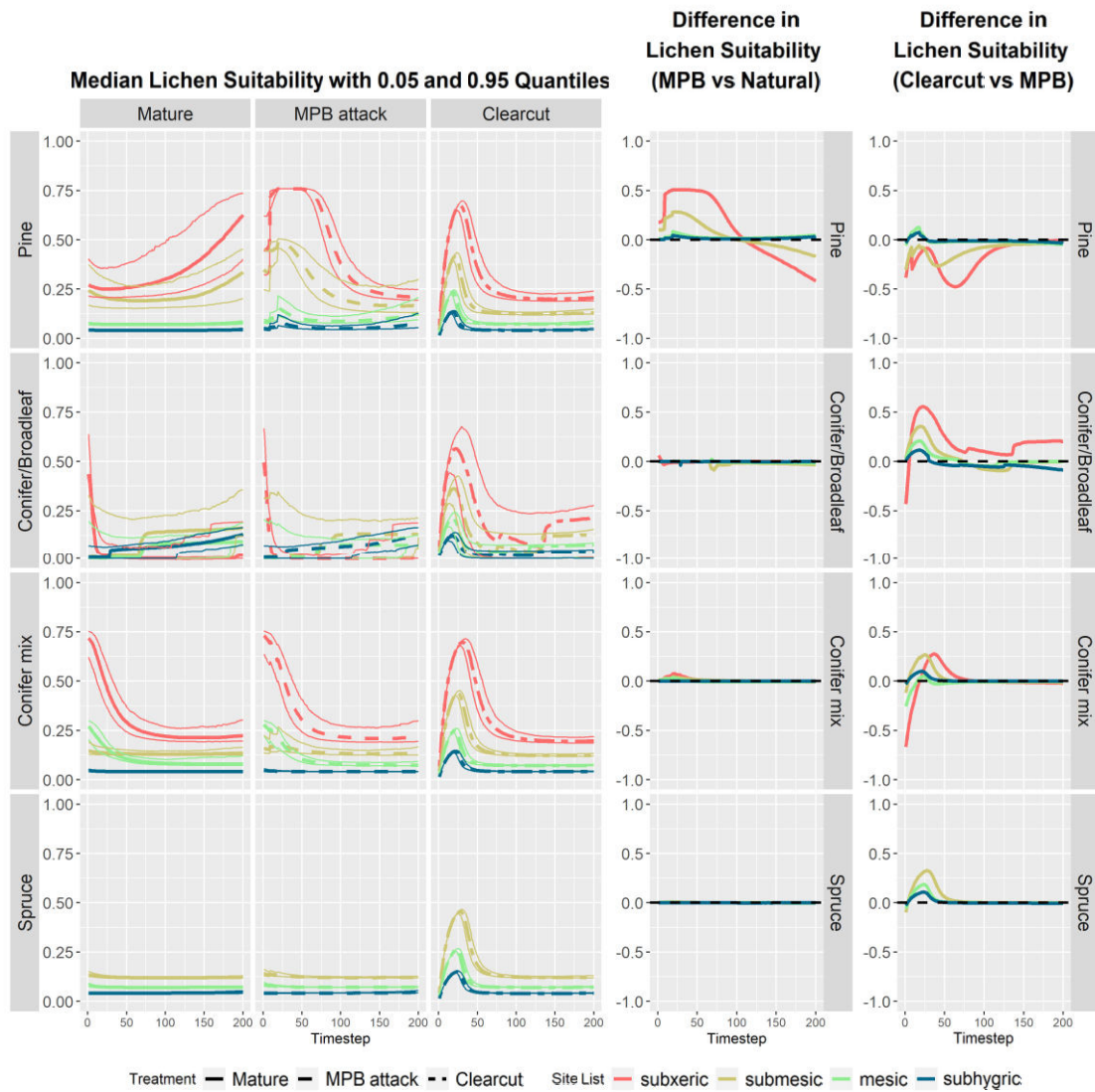


Figure 28. The projected response of lichen suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (colours) and four stand types (rows). The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand. The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand.

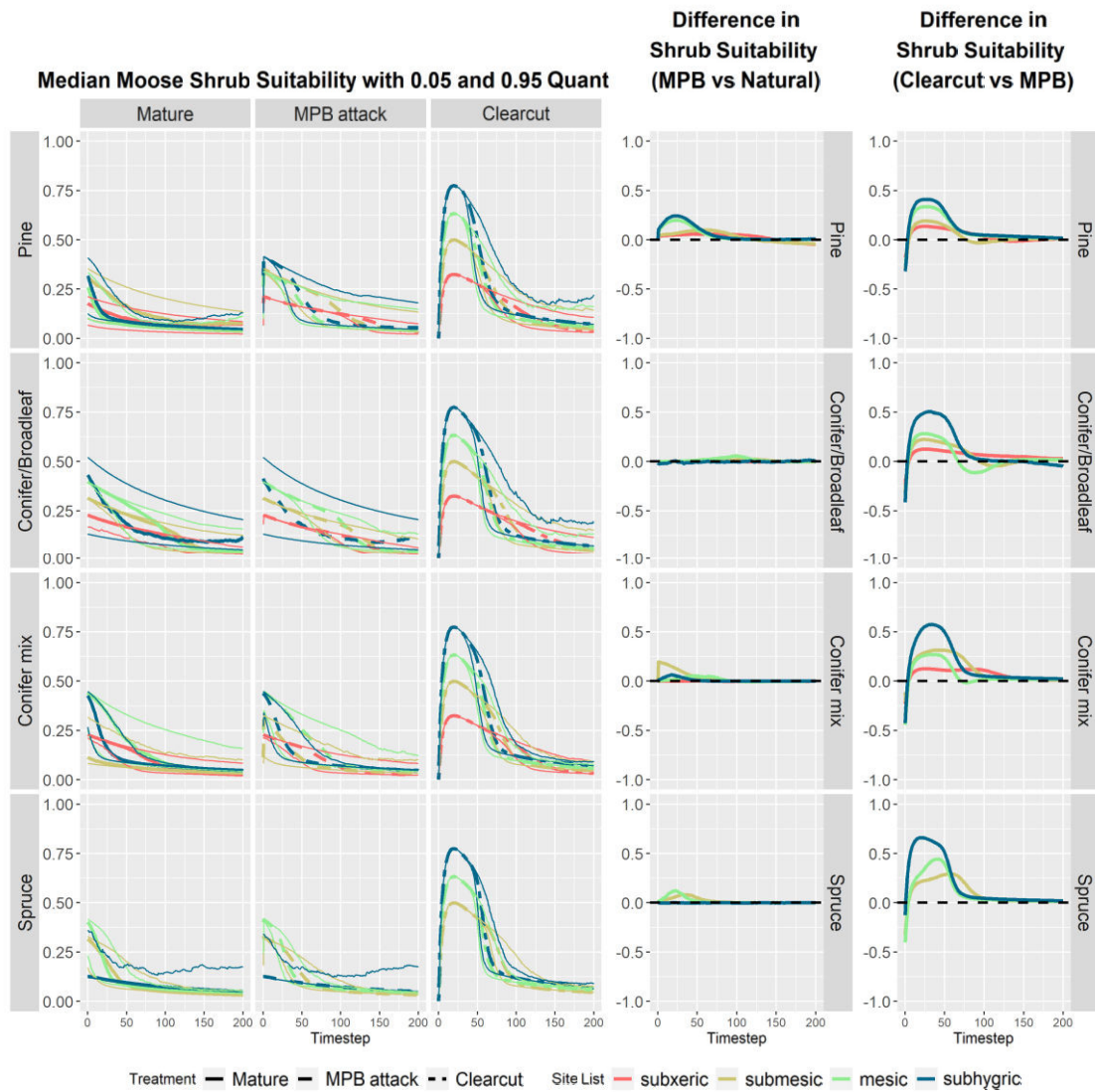


Figure 29. The projected response of moose shrub suitability over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (colours) and four stand types (rows). The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand. The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand.

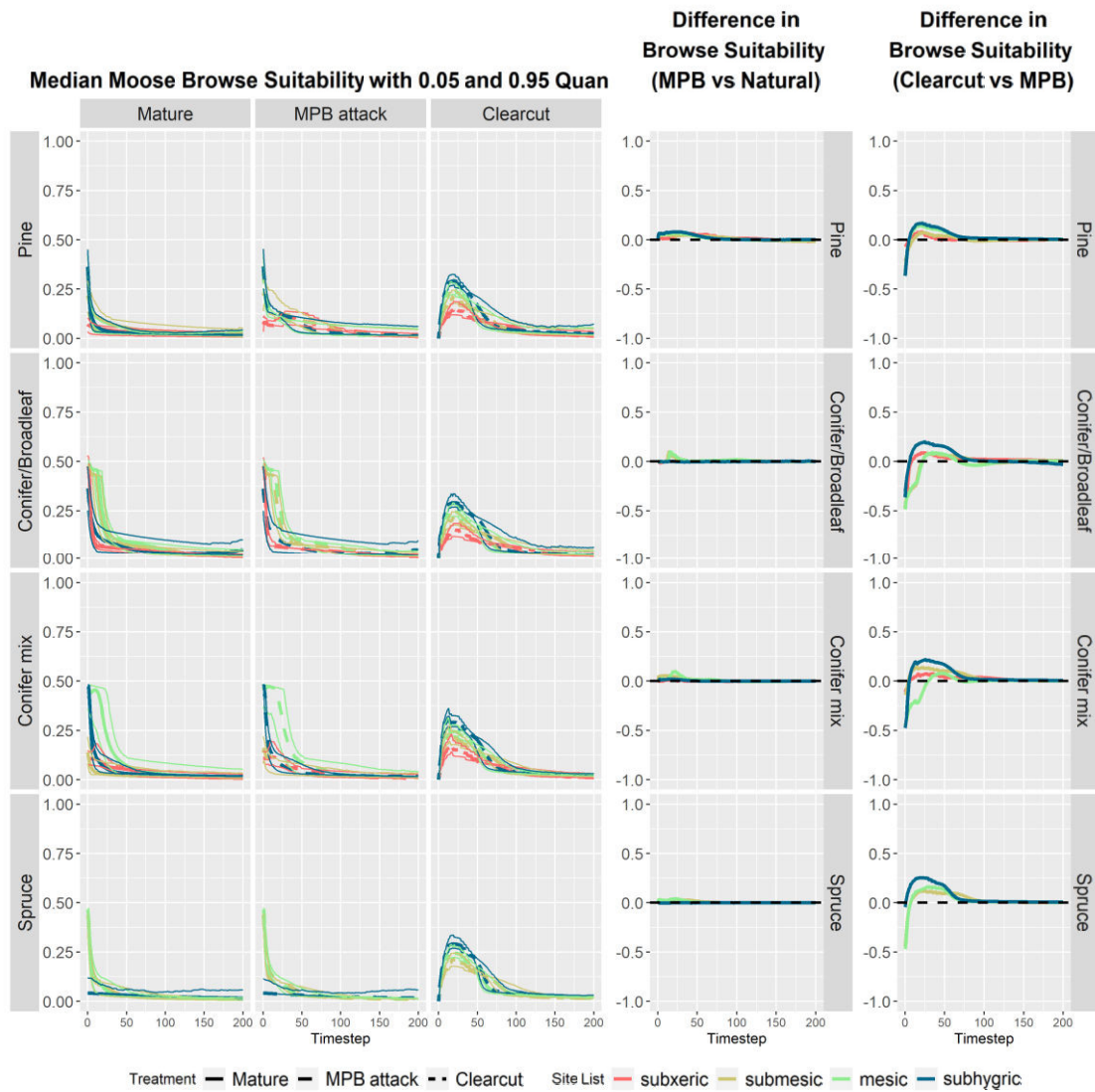


Figure 30. The projected response of moose browse suitability (includes aspen and subalpine fir 0.5 – 3 m in height and moose shrubs) over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (colours) and four stand types (rows). The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand. The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand.

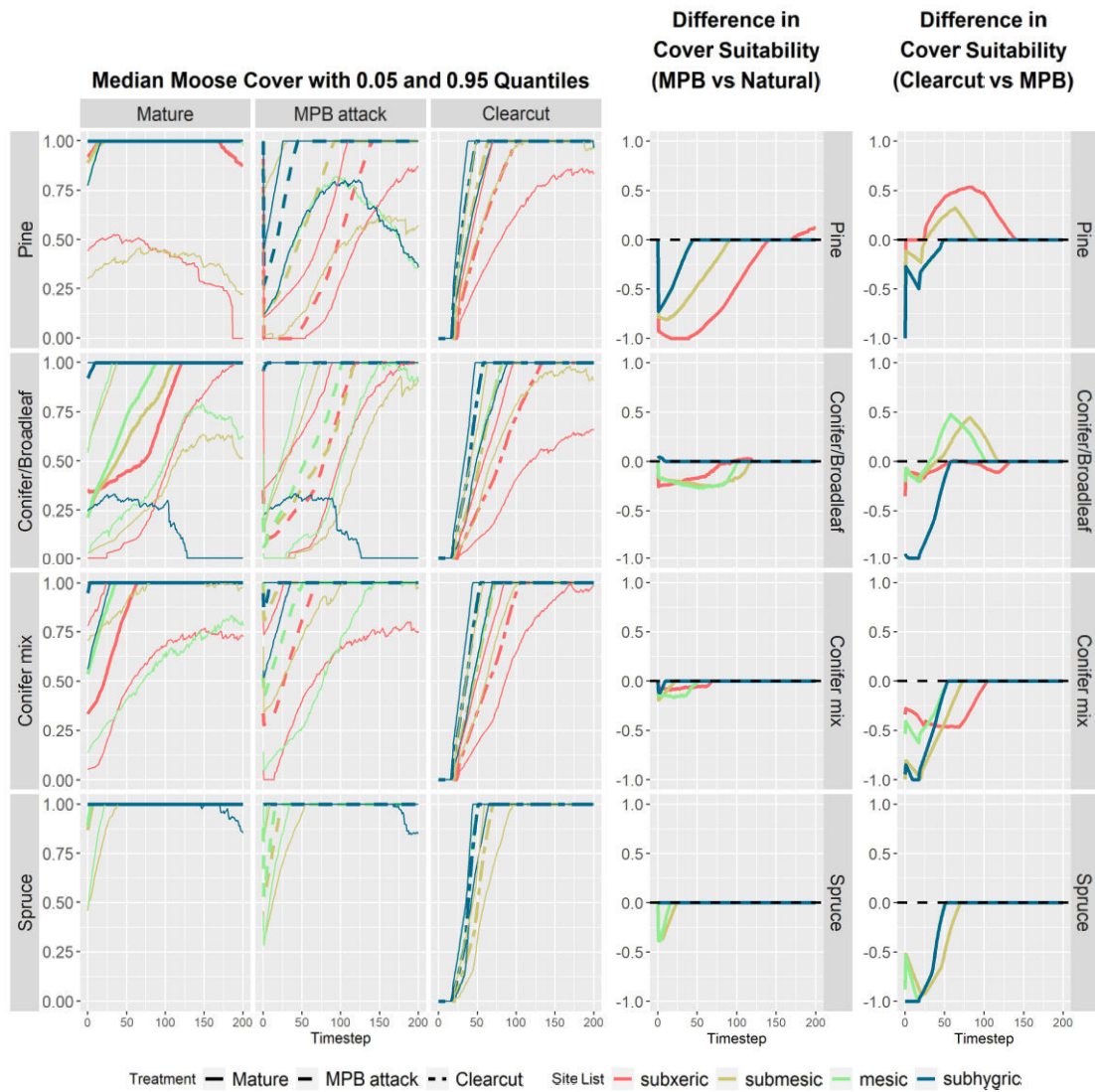


Figure 31. The projected response of the suitability of a stand to provide vertical cover over time in undisturbed mature forest (1st column), after MPB disturbance (2nd column) and after clearcut (3rd column) across four edaphic sites (colours) and four stand types (rows). The 4th column illustrates the difference in suitability between a MPB attacked stand and an undisturbed stand and the 5th column shows the difference between a clearcut stand and a MPB attacked stand. The 5th and 95th quantiles (thin lines) provide measures of the variability in suitability within the stand.

Appendix 7

Figures Comparing Variability in Suitability across Stand Types and Edaphic Sites

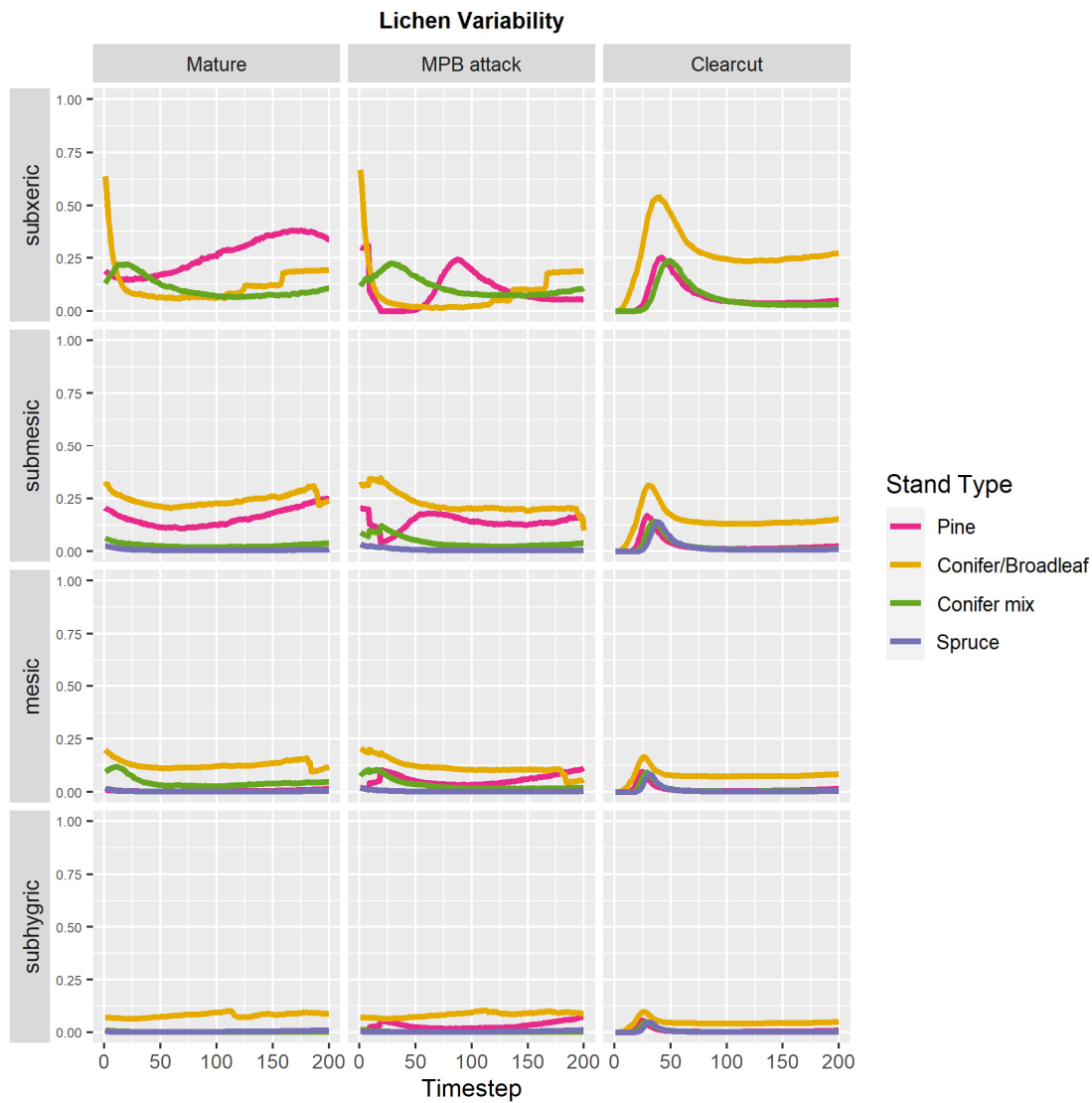


Figure 32. Comparison of the variability in lichen suitability for four stand types (colours) on four edaphic sites (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep.

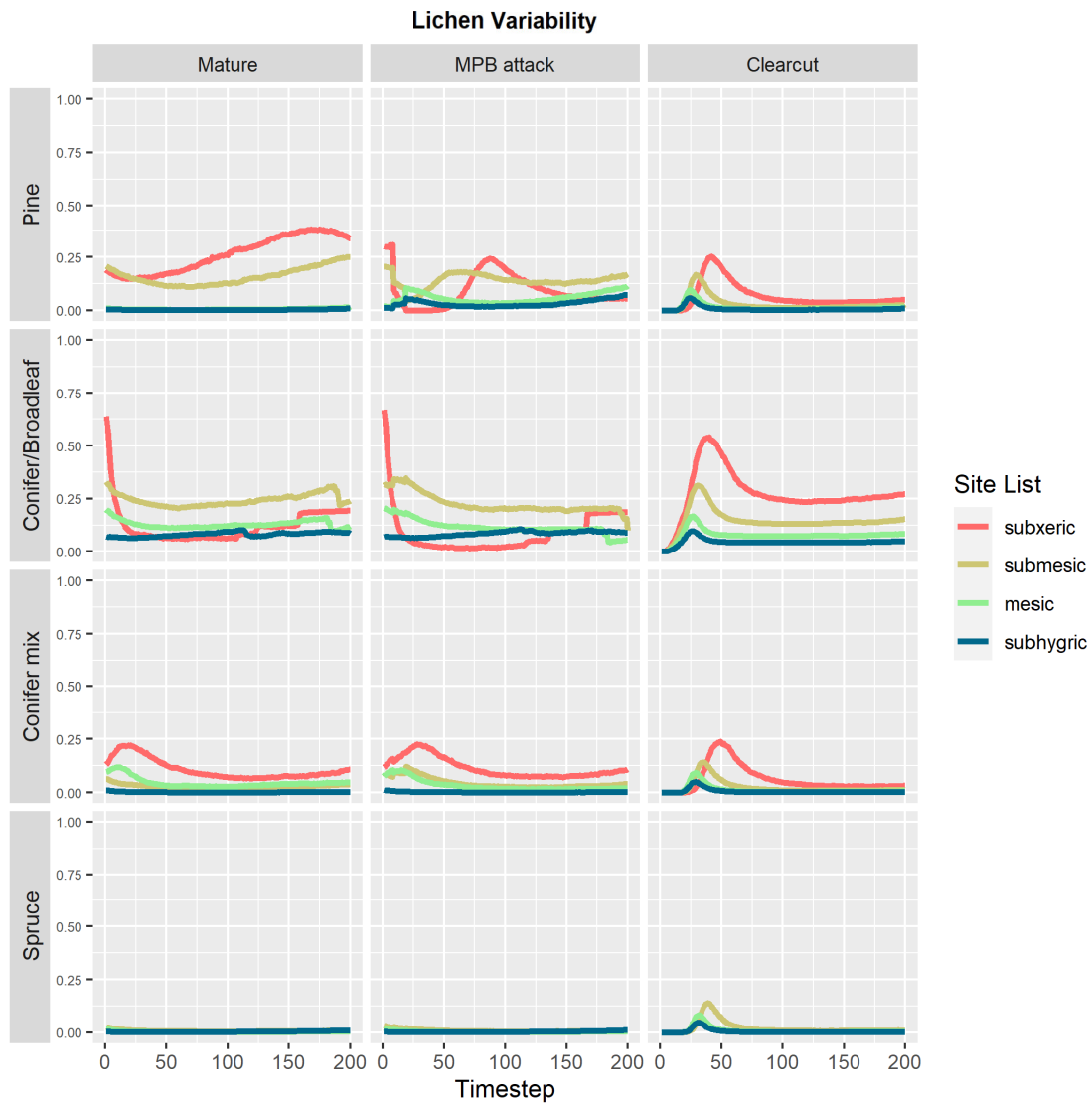


Figure 33. Comparison of the variability in lichen suitability between four edaphic sites (colours) for four stand types (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep.

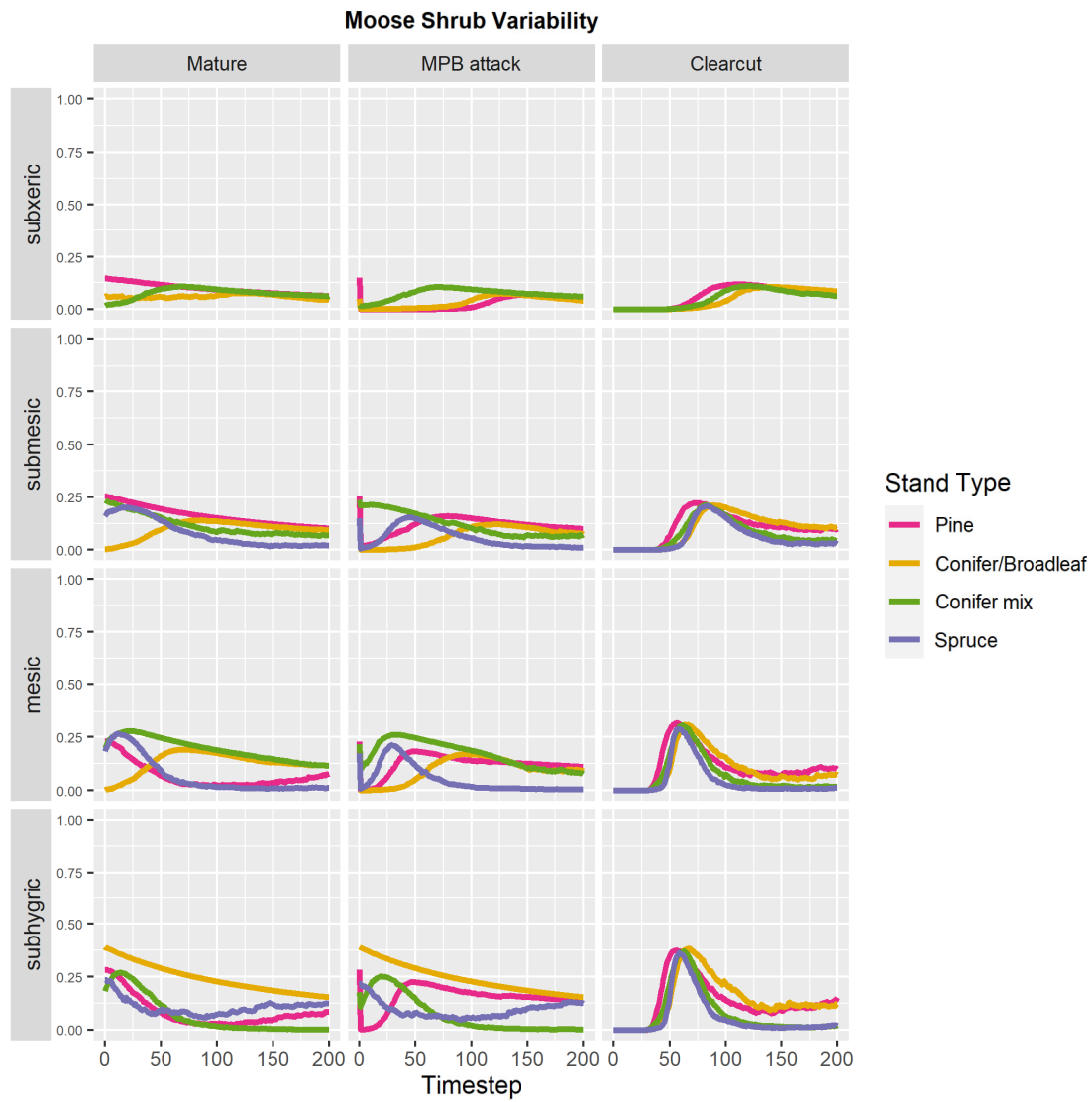


Figure 34. Comparison of the variability in moose shrub suitability for four stand types (colours) on four edaphic sites (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep.

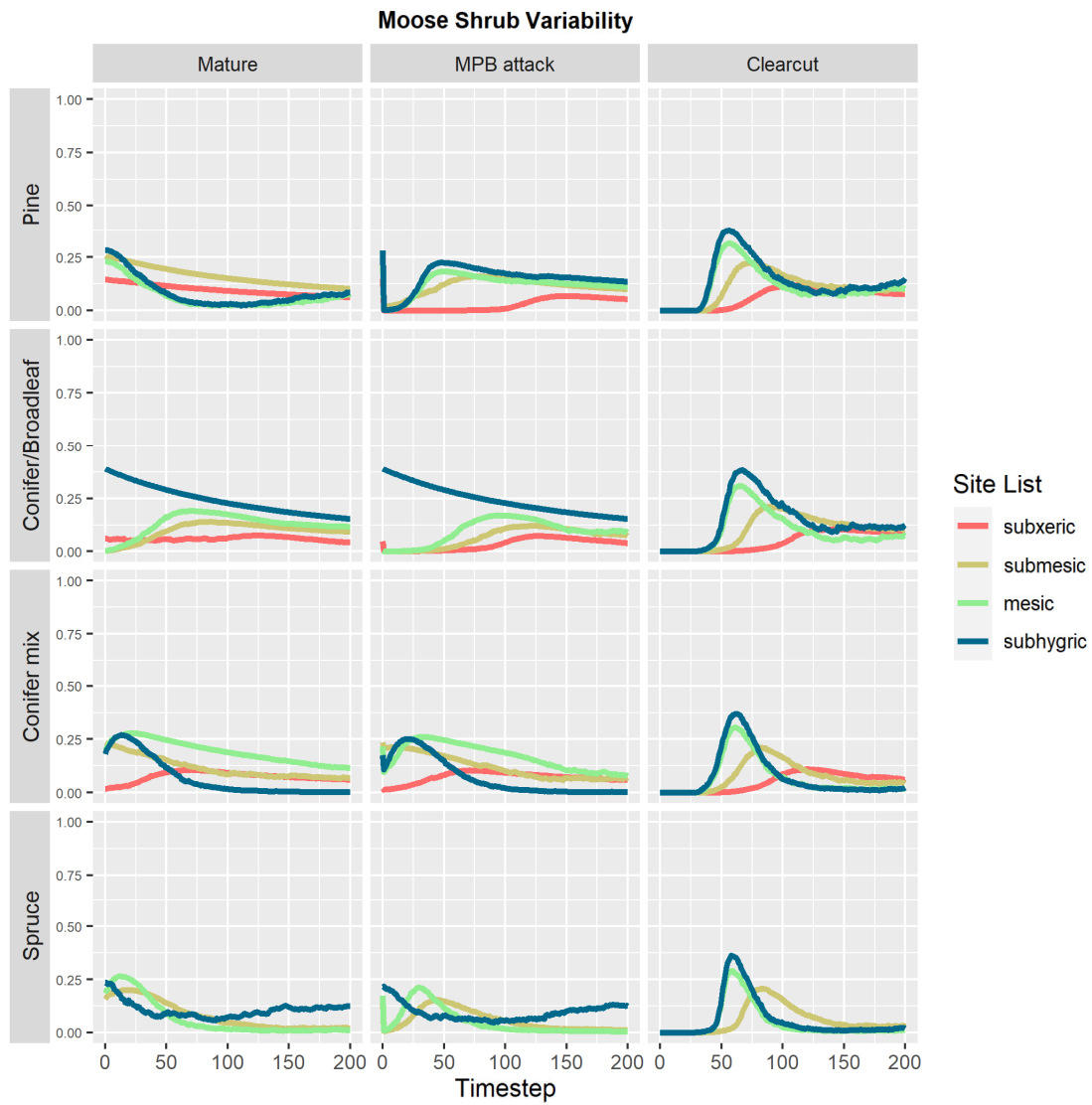


Figure 35. Comparison of the variability in moose shrub suitability between four edaphic sites (colours) for four stand types (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep.

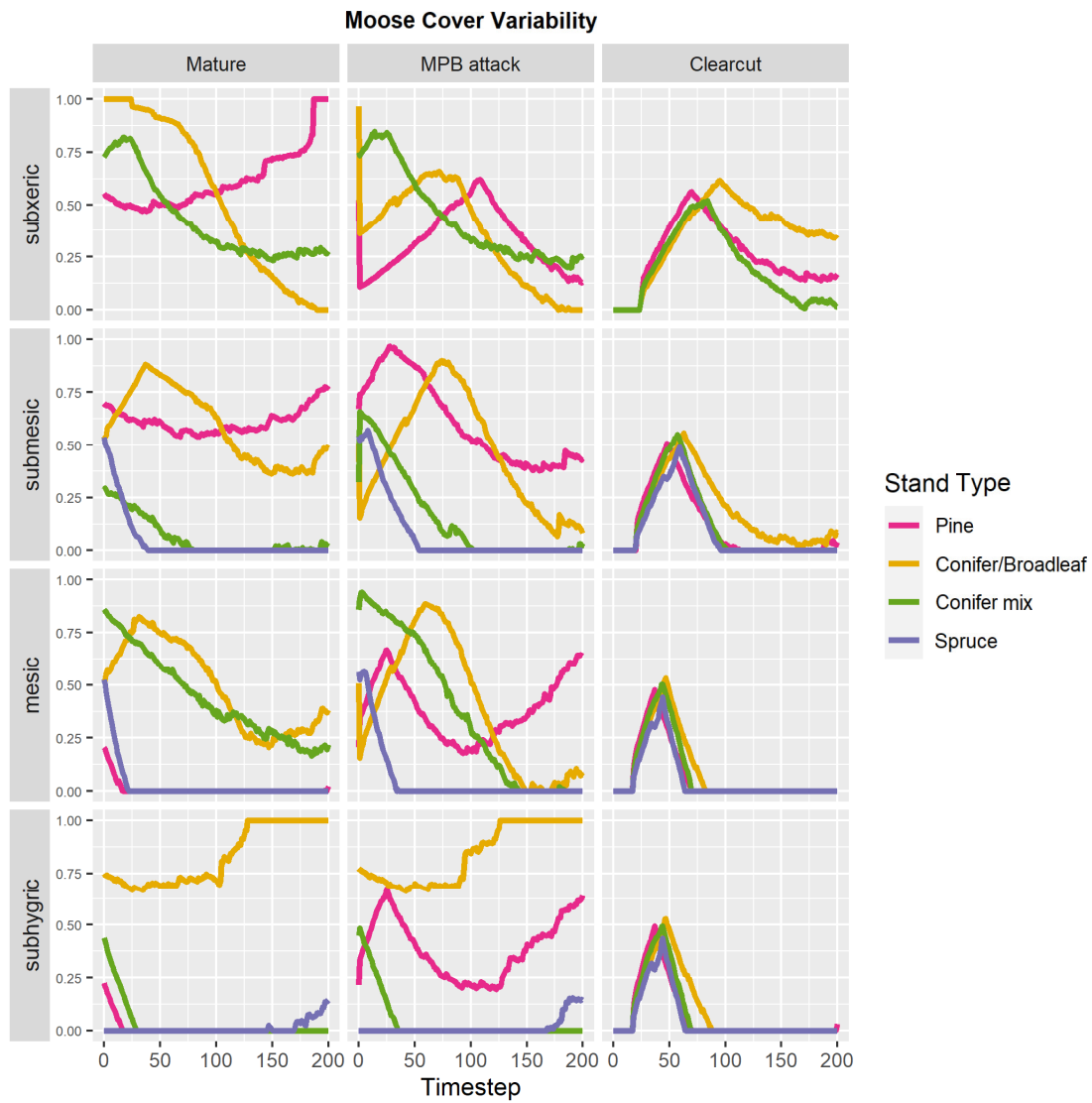


Figure 36. Comparison of the variability in suitability of a stand to provide vertical cover for four stand types (colours) on four edaphic sites (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep.

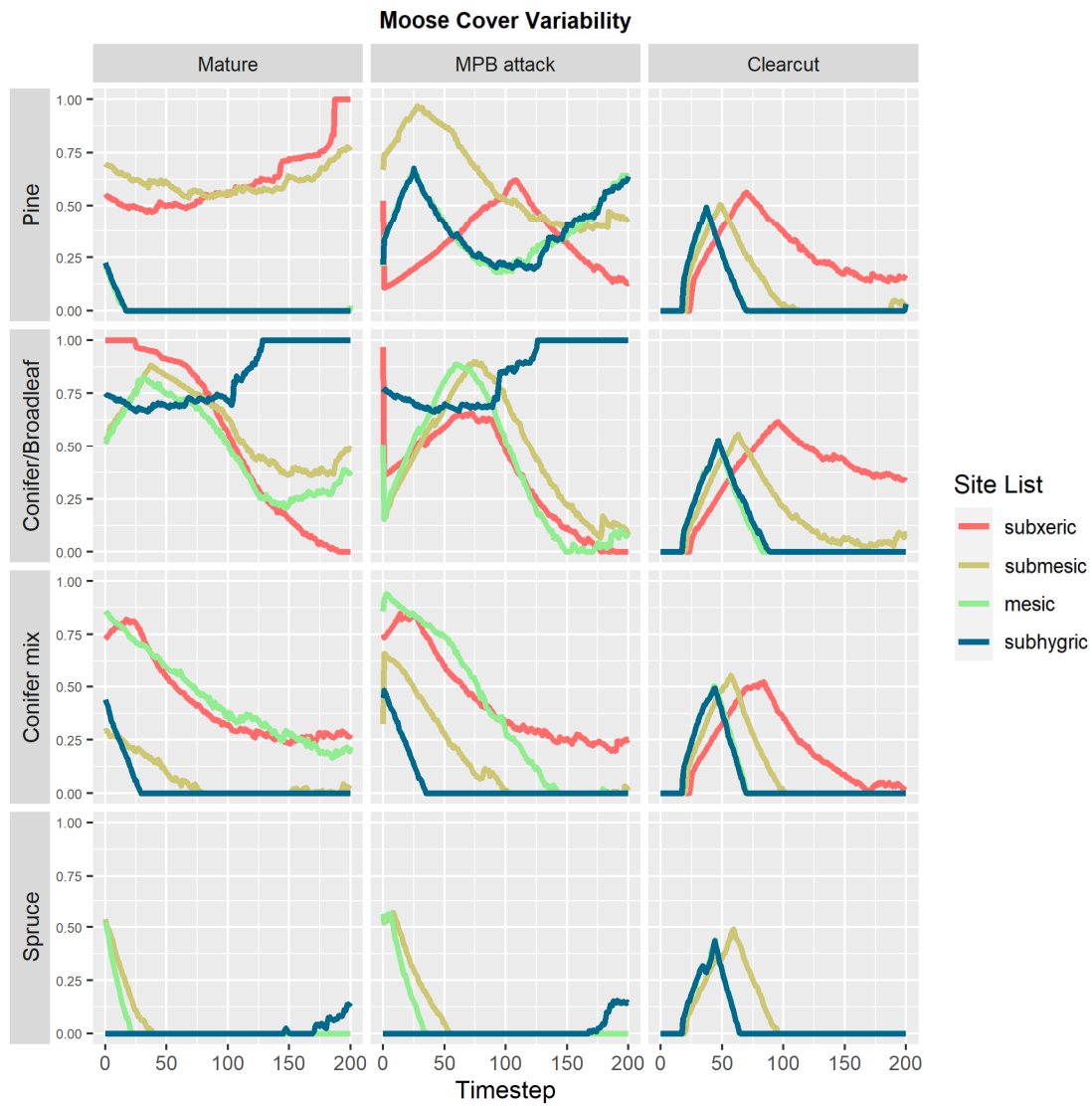


Figure 37. Comparison of the variability in suitability of a stand to provide vertical cover between four edaphic sites (colours) for four stand types (rows) as represented by the difference between the 95th suitability quantile and the 5th suitability quantile at each timestep.