A FUNCTIONAL TRAIT ANALYSIS OF SUCCESSIONAL PATHWAY DYNAMICS

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Abstract

The study of plant community re-assembly following disturbances in anthropogenically managed landscapes is a necessity in today's climate. The measurement of plant functional traits is a tool that can be of great help in understanding how individual plants and entire communities respond to shifts in disturbance regimes and environmental characteristics that are directly or indirectly under human influence. In Eastern Newfoundland, two distinct successional pathways may be initiated depending on fire severity. Fires of high severity in *Picea mariana*-dominated forests will initiate a forest succession; fires of low severity can cause a state shift where an ericaceous heath dominated by *Kalmia angustifolia* will succeed where a *P. mariana*-dominated forest once stood.

To enhance understanding of community response to varying disturbance regimes, I applied a functional trait analysis to two distinct successional pathways with the aim of (i) assessing the functional diversity (FD) of both pathways, (ii) identifying the causes of the observed FD, and (iii) using the functional traits of both communities to predict future successional pathways. Alpha functional diversity (α-FD) was calculated as functional dispersion (FDis) and beta functional diversity (β-FD) was mean pairwise distance (D_{PW}) and mean distance to nearest neighbour (D_{NN}). Identifying significant drivers of FD in both communities was performed by linking soil characteristics with plant traits via a combine RLQ-fourth corner approach. Finally, prediction of post-fire succession was made possible by constructing a model based on fuzzy logic that incorporated community flammability and regeneration strategy of dominant plants, along with environmental variables.

In Chapter 2, I found that a community succeeding to heath had lower α-FD and β-FD than that succeeding to forest. This I attributed to niche space being unavailable to two out of the three major functional groups (trees and herbs) in heaths. The constriction in the functional space (α-FD loss) in heath leads to the functional homogenization (β-FD loss) of heath sites and of the landscape in general. The niche space restriction responsible for the FD loss after heath formation occurs in the form of belowground nutrient limitation; I found heath soils to be significantly lower in available N and P, and lower in pH. The combined RLQ-fourth corner method (described in Chapter 3) revealed what traits related to nutrient acquisition and use are favoured in the nutrient poor heath soils. In acidic soils where N and P are limited, associating with ericoid mycorrhizae imparts effective nutrient acquisition and high leaf dry matter content represents an efficient nutrient use strategy. Forest soils are not as limiting and therefore species which do not possess the above-mentioned traits are not filtered out. The model developed in Chapter 4 identified the environmental conditions that could lead to a forest to undergoing a state shift to a heath, and conditions that create habitat filters and lead to a loss of FD. Interactions between climate, community flammability, organic matter levels, and propagule density may occur by which *P. mariana* forests will inevitably be succeeded by *K. angustifolia* heaths. The model can be employed to further study post-fire community assembly when two distinct successional pathways are possible; it can also be employed in decision making when alterations to natural disturbance regimes, such as fire suppression are being considered.

In short, this dissertation employs a functional trait approach to examine community assembly along two distinct successional pathways. The novelty of this research lies in that, through a functional lens, it examines how the response and effect traits of two distinctive functional groups act to initiate and maintain divergent post-fire communities. It contributes to the further understanding of two important ecological processes: how pre-disturbance conditions and the nature of the disturbance itself interact with distinct regeneration strategies to drive community assembly, and how trait-mediated interspecific interactions act to either promote or limit co-existence in post-disturbance communities.

Keywords: Assembly; disturbance; ericoid mycorrhizae; fourth corner; functional dispersion; functional homogenization; fuzzy logic; LDMC; RLQ; soil nutrients; succession

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Chapter 1

General Introduction

This dissertation continues the work which began over a century ago, when plant communities were viewed as dynamic entities, a view championed by Frederic Clements and Henry Gleason. While critical of each other's work, they both shared a view that interactions existed not only between individual plant species but also between species and their environments (Clements 1916; Gleason 1917). This complex web of interactions produced discernable patterns across temporal and spatial scales which became known as succession (Odum 1969).

The concept of functional traits existed since the time of Charles Darwin, yet only recently has it begun to play a prominent role in ecological studies. Studies based on functional traits benefit from a simplification of information, the complexity of systems with hundreds of species can be broken down to a much smaller set of functional traits related to the questions being posed (Keddy 1992; Dray and Legendre 2008). Using this simplified functional data set, investigators can gain insights into the adaptive ability of species and their competitive ability in intra-and interspecific interactions (MacArthur and Levins 1967; Violle et al. 2012), as well as their ability to cope with fluctuating habitat conditions (Tilman 1985; Chen and Taylor 2012). The phenotypic trait expression of a genome can vary depending on biotic and abiotic conditions of an environment meaning that the value of a single trait can be expressed at many points along a range within an individual, population, or community. Studying how traits vary at one (or all) of these scales, in conjunction with the environments in which they occur, is where the immense strength of a functional trait analysis lies (Calow 1987; Suding et al. 2008; Zhang et al. 2018).

Trait variation at the community scale can reveal ecosystem properties (Díaz and Cabido 2001; Weisser et al. 2017). Similar to taxonomic diversity, functional diversity can be divided into components: richness and evenness, or alpha and beta diversity. The alpha functional diversity of traits in a system is an indication of niche space utilization; a greater dispersion of functional traits within a community implies more resources are being used by member species (Laliberté and Legendre 2010). A system that has high dispersion in its functional trait space is likely to be a highly productive one. This metric is often weighted by abundance for two reasons: the effect a species has on its habitat is in relation to its biomass (Grime 1998), and the realized niche of dominant species is likely to be greater than that of a subordinate one. Beta functional diversity represents the level of similarity between two plots or sites in respect to their functional composition; it is a good indication of the resilience of a system in the event of environmental perturbations (Olden et al. 2004). A community with greater functional heterogeneity (or low similarity) is more likely to contain species able to positively respond to disturbances (Olden 2006; Clavel et al. 2011). Other ecosystem properties can be identified through the traits of the resident species. Species (especially dominant species) can change characteristics of the habitat; species effect traits are those which can modify habitat functions (Naeem and Wright 2003).

Trait variation that occurs along an environmental gradient (e.g. disturbance intensity, population density, soil nutrient status) can reveal community assembly processes at work and population dynamics within the community (Keddy 1992; Gotelli and McCabe 2002). By classifying species according to their functional traits and linking traits to environmental gradients, one can identify abiotic habitat filters. Habitat filters work to restrict the entry of some species to the system; species lacking the particular traits or having trait values outside a certain range will be sieved out and fail to establish (Cornwell et al. 2006; Raevel et al. 2012). The failure to establish can be due to the inability to perform under certain habitat conditions (abiotic filter) or the inability to compete with other species for resources (biotic filter). Biotic habitat filters can be viewed in terms of competitive, or even facilitative, interactions (Bowker et al. 2010). Dominant plant species can modify their habitat and generate positive feedbacks that increase their fitness at the expense of other species (Kardol et al. 2013; Revilla et al. 2013). These habitat modifications can be aboveground (varying light levels) or belowground (altered soil nutrient availability) and can facilitate, rather than inhibit, some species (Michalet et al. 2006). Whenever environmental conditions change (whether it is an abiotic or biotic form), the success of species in coping with these changes is dependent on what is known as their response traits (Naeem and Wright 2003).

The goal of this dissertation is to apply a functional trait approach to investigate community assembly mechanism in post-fire sites in eastern Newfoundland (Table 1). I will examine variations in functional traits at the community scale with the aim of understanding how the inherent differences in environmental conditions of two distinct successional pathways (*Picea mariana* dominated forest or *Kalmia angustifolia* dominated heath) shape the functional composition of their respective communities. The initiation of either pathway is dependent on the nature of the disturbance, specifically how it impacts the amount of residual organic matter (ROM) and consequently what type of regeneration strategy is promoted. Low levels of ROM favour seed regeneration and will initiate forest succession while high levels of ROM favours vegetative sprouting and leads to a heath succession (Figure 1.1).

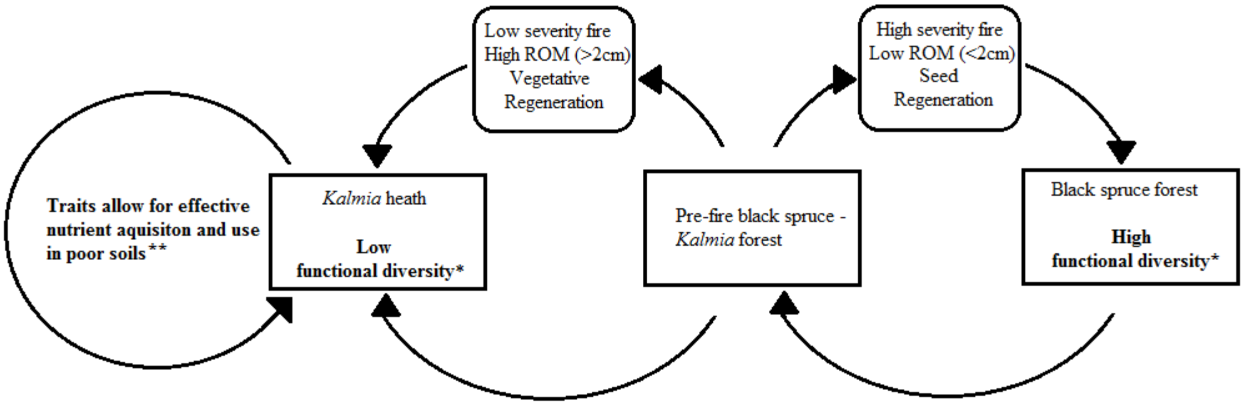


Figure 1.1. Conceptual model of system used to attain the objectives of this dissertation. Fire severity selects for regeneration traits (vegetative vs. seed) and dictates direction of succession based on residual organic matter (ROM). Hypotheses of Chapters 2 and 3 are denoted by asterisks. *Hypothesis 1: *Kalmia* heaths have lower functional diversity than post-fire black spruce forests. **Hypothesis 2: Shrubs possess traits which allow them to maintain dominance over trees in nutrient poor soils.

Table 1.1. Site characteristics of post-fire heath and forest sites. Modified in part from Kravechenko (2016). Stem density represents all tree species in all size classes.

Community type	**Site Name**	**GPS coordinates**	**Time since fire (yrs)**	**Burn area (ha)**	**Fire severity**	**Tree density (stems·ha^{-1})**	**OM depth (cm)**
Heath	Rocky Pond	N 48° 31' 662" W 53° 29' 334"	13	85	-	330	4 ± 2
	Triton Brook	N 48° 40' 477" W 54° 29' 334"	16	>500	800	130	8 ± 5
	Spracklin Road	N 48° 31' 953" W 54° 03' 091"	18	75	466	230	5 ± 3
	Thorburn	N 48° 18' 073" W 54° 09' 997"	24	67	200	1150	9 ± 3
	Blue Hill	N 48° 35' 211" W 53° 59' 760"	27	24	188	370	9 ± 3
	Charlottetown	48° 27' 140" W 53° 59' 923"	30	28	412	230	11 ± 1
	Terra Nova Road	48° 30' 487" W 54° 07' 143"	36	33	412	770	7 ± 2
	Terra Nova Dump	N 48° 31' 638" W 54° 09' 082"	37	34	412	440	4 ± 2
	Pitt's Pond	N 48° 26' 822" W 54° 08' 716"	52	800	216	4170	14 ± 3
Forest	Buchan's Junction	N 48° 47' 682" W 56° 38' 098"	13	-	-	7800	6 ± 5
	Gambo	N 48° 44' 048" W 54° 11' 016"	35	23 045	3948	3963	6 ± 2
	Traytown	N 48° 39' 026" W 53° 57' 044"	44	10	-	2738	8 ± 2
	Arnold's Pond	N 48° 34' 022" W53° 58' 021"	>100	-	-	3550	12 ± 4

My first objective (Chapter 2) was to measure the alpha and beta functional diversity of forests and heaths with the aim of revealing the functional response of communities regenerating after fires of varying severity. The second objective (Chapter 3) was to link the functional composition of the two successional pathways to belowground habitat characteristics, thereby identifying optimal traits as dictated by any abiotic filters that may be in place. The final objective (Chapter 4) was to design a model based on functional traits related to fire with the aim of predicting post-fire regeneration. Community flammability (effect trait) and regeneration type (response trait) were incorporated into a model based on fuzzy logic that can identify conditions needed to initiate either forest or heath succession.

1.2 References

Bowker, M.A., Soliveres, S., Maestre, F.T. 2010. Competition increases with abiotic stress and regulates the diversity of biological soil crusts. *Journal of Ecology*, **98**, 551–560.

Calow, P. 1987. Towards a definition of functional ecology. *Functional Ecology*, **1**, 57–61.

Chen, H.Y.H., Taylor, A.R. 2012. A test of ecological succession hypotheses using 55-year time-series data for 361 boreal forest stands. *Global Ecology and Biogeography*, **21**, 441–454.

Clavel, J., Julliard, R., Devictor, V. 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*, **9**, 222–228.

Clements, F. E. 1916. *Plant succession*. Carnegie Institute of Washington **242**. 512 pp.

Cornwell, W.K., Schwilk, D.W., Ackerly, D.D. 2006. A trait-based test for habitat filtering: Convex hull volume. *Ecology*, **87**, 1465–1471.

Díaz, S., Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646-655.

Dray, S., Legendre, P. 2008. Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology*, **89**, 3400–3412.

Gleason, H. A. 1917. The structure and development of the plant association. *Bulletin of the Torrey Botanical Club*, **43**, 463-481.

Gotelli, N.J., McCabe, D.J. 2002. Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology*, **83**, 2091–2096.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, **3**, 157–164.

Kravechenko, D. 2012. Role of safe sites in black spruce recruitment and growth release in post-fire *Kalmia* heath. M. Sc. Thesis, Lakehead University, Thunder Bay, Canada.

Laliberté, E., Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299-305.

MacArthur, R. H., Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. *American Naturalist*, **101**, 377–385.

Michalet, R., Brooker, R. W., Cavieres, L. A., Kikvidze, Z., Lortie, C. J., Pugnaire, F. I., Valiente-Banuet, A., Callaway, R. M., 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, **9**, 767–773.

Naeem, S., Wright, J. P. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, **6**, 567–579.

Odum, E. P. 1969. The strategy of ecosystem development. *Science*, **164**, 262-270.

Olden, J. D., LeRoy Poff, N., Douglas, M. R., Douglas, M. E., Fausch, K. D. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, **19**, 18–24.

Olden, J. D. 2006. Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, **33**, 2027–2039.

Raevel, V., Violle, C., Munoz, F. 2012. Mechanisms of ecological succession: insights from plant functional strategies. *Oikos*, **121**, 1761–1770.

Revilla, T. A., Veen, G. F. (Ciska), Eppinga, M. B., Weissing, F. J. 2013. Plant–soil feedbacks and the coexistence of competing plants. *Theoretical Ecology*, **6**, 99–113.

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D. U., Jackson, S. T., Navas, M.-L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125–1140.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *The American Naturalist*, **125**, 827–852.

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V., Messier, J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution*, **27**, 244–252.

Weisser, W. W., Roscher, C., Meyer, S. T., Ebeling, A., Luo, G., Allan, E., Beßler, H., Barnard, R. L., Buchmann, N., Buscot, F., Engels, C., Fischer, C., Fischer, M., Gessler, A., Gleixner, G., Halle, S., Hildebrandt, A., Hillebrand, H., de Kroon, H., Lange, M., Leimer, S., Le Roux, X., Milcu, A., Mommer, L., Niklaus, P. A., Oelmann, Y., Proulx, R., Roy, J., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Tscharntke, T., Wachendorf, M., Wagg, C., Weigelt, A., Wilcke, W., Wirth, C., Schulze, E.-D., Schmid, B., Eisenhauer, N.

2017. Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. *Basic and Applied Ecology*, **23**, 1–73.

Zhang, H. Chen, H. Y. H., Lian, J., John, R., Ronghua, L., Liu, H., Ye, W., Beringer, F., Ye, Q. 2018. Using functional trait diversity patterns to disentangle the scale-dependent ecological processes in a subtropical forest. *Functional Ecology*, **00**, 1-11.

Chapter 2

Alternate successional pathway yields alternate pattern of functional diversity

2.1. Abstract

Impacts of disturbance on functional diversity (FD) have been studied largely in terms of single post-disturbance communities, but rarely applied to post-fire alternate successions leading to forests and heaths. In Eastern Canada, low severity fires often turn *Picea mariana* forests into *Kalmia angustifolia* dominated heaths. This alternate end-point from forest to heath can have implications for biodiversity and ecosystem function and provides an opportunity to test assumptions concerning alternate successional trajectories. I hypothesized that post-fire *Kalmia* heaths possess lower FD than forest communities, and heath formation selects for a narrow range of species traits resulting in biotic homogenization. I tested the hypothesis by measuring alpha and beta FD and functional composition of trees, shrubs and herbs in post-fire heath and forest communities to determine if an alternate successional pathway causes a decline in FD. Based on five functional traits of vascular plants, I measured trait dispersion in the functional trait space (α-FD), as well as the distance separating species in the functional trait space between sites (β-FD). I measured the three functional diversity metrics in nine heath and four forest sites in Terra Nova National Park, Newfoundland, Canada (Lat. 48'33N, Long. 53'58.8W). I found a significant difference in α and β FD, depending on the successional pathway and the life form considered. A loss of α-FD for trees and herbs in heaths indicates filtering of particular traits. Overall β-FD was lower in heath than forest. It was also lower for trees and herbs, indicating an increase in functional similarity (functional homogenization) of the majority of life forms. Individual traits of three life forms (trees, shrubs and herbs) indicate possible mechanisms driving the loss of FD. The promotion of heath formation by low severity fires restricts functional dispersion of tree and herb traits and leads to the functional homogenization of post-fire communities. The lower alpha and beta FD in heaths provide strong evidence supporting my hypothesis that this disturbance-driven alternate succession is associated with lower FD resulting in functional homogenization.

Keywords: Community assembly; Disturbance; Functional dispersion; Functional homogenization; Heath; Trait filtering

2.2. Introduction

Increased anthropogenic disturbance and climate change have been affecting ecosystems worldwide, and ecologists are trying to understand the functional response of ecosystems to these disturbances. Several studies have shown that in order to understand how changes in disturbance regimes may impact key ecosystem processes, one must detect signals from aspects of functional diversity (FD) rather than taxonomic diversity (Mokany et al. 2008; Mayfield et al. 2008). While it is known that species richness is often linked to increased productivity (Cardinale et al. 2007), functional trait analyses provide direct insight into mechanisms driving the properties of ecosystems (ecosystem function, *sensu* Reiss et al. 2009) (Díaz and Cabido 2001; Cadotte et al. 2011). Ecosystem function includes stability when faced with environmental perturbation (Sankaran and McNaughton 1999; Chillo et al. 2011; Sonnier et al. 2014; Mokany et al. 2015), site fertility (Wardle and Zackrisson 2005) and overall productivity (Petchey 2003; Paquette and Messier 2011). Functional diversity can also provide insights in community assembly mechanisms such as habitat filtering (Keddy 1992; Cornwell et al. 2006; Kumordzi et al. 2015), biotic interactions such as facilitation (Gavinet et al. 2016; Montesinos-Navarro et al. 2016), competition, or niche complementarity (MacArthur and Levins 1967; Stubbs and Wilson 2004; Staples et al. 2016).

Anthropogenic effects on land use and disturbance regimes, such as suppression of wildfires, can alter the functional and compositional diversity of communities in many forms and at many scales: it may be a loss of species or FD at the plot or site level (α-diversity), or taxonomic and functional homogenization across sites (β-diversity; Olden and Rooney 2006). A greater range of functional traits and more functional dissimilarity between communities ensures ecosystem functions are more likely to be preserved in the face of environmental change, and therefore, provides higher ecosystem stability (Laliberté et al. 2010). While patterns of functional convergence and divergence have been associated with site productivity and disturbance regime respectively (Grime 2006), it has been shown that abiotic habitat filters acting on species regeneration traits alone can yield communities with distinct functional compositions (Siegwart-Collier and Mallik 2010; Mallik et al. 2010). A post-disturbance community is often composed of species whose response traits are favored by filters imposed by the disturbance or by legacy effects of the pre-disturbance dominant species (Jasinski and Payette 2005; Wirth et al. 2008; Johnstone et al. 2010; Shenoy *et al.* 2011). If a post-disturbance community differs significantly from the pre-disturbance community in its suite of effect traits, then a change in biodiversity and ecosystem function may occur (Suding *et al*. 2008). It is particularly important to investigate this in the boreal forest of eastern Newfoundland because, unlike studies conducted elsewhere (Urza and Sibold 2017; Vítová et al. 2017; Johnstone *et al.* 2010), the pre-disturbance community here can potentially be replaced by a community dominated by a significantly different life form (tree vs. shrub) resulting in the conversion of forests in to heaths (Mallik 2003).

The formation of ericaceous heaths dominated by a native understory shrub *Kalmia angustifolia* L. (hereafter referred to as *Kalmia*) occur following canopy-removing disturbance such as wildfire in boreal forests of eastern Canada. In post-fire heaths organic soil is left relatively undisturbed, a condition created by low and often patchy fire severity (Siegwart-Collier and Mallik 2010). The high levels of residual organic matter favor vegetative regeneration of ericaceous shrubs such as *Kalmia* and *Vaccinium* spp*.,* which quickly dominate the post-fire sites and inhibit tree colonization (Mallik 2003; Mallik et al. 2010). The phenomenon has been studied in-depth from the forest regeneration perspective because *Kalmia* heaths provide little value in terms of timber products (Mallik and Inderjit 2001; Thiffault et al. 2012). The effect of anthropogenic disturbance on biodiversity of European ericaceous heaths dominated by *Calluna vulgaris* (L.), Hull, *Erica cinerea* L. and *E. tetralix* L. has been studied well from a conservation point of view (Gimingham 1972; Roem and Berendse 2000; Britton and Fisher 2007; Calo et al. 2007), yet heaths of Eastern Canada dominated by *Kalmia* have received very little attention (but see Bloom and Mallik 2004). It is necessary to determine the impact of long-lasting (multiple decades) *Kalmia* heaths on biodiversity. Land management decisions in this ecosystem such as suppression of wildfires often result in small, low severity burns leading to heath formation as opposed to wildfires that are often large, burn with high severity and lead to forest succession (Mallik 2003). With regards to these two successional pathways I asked the question as to how FD varies with forest vs. heath succession. I hypothesize that heath formation will result in a loss of both α- and β- FD leading to functional homogenization.

2.3 Materials and Methods

2.3.1 Study site description

I conducted this study in and around Terra Nova National Park (Lat. 48’33N, Long. 53’58.8W) in the Central Newfoundland ecoregion of the Boreal Shield ecozone (Damman 1983). Mean summer and winter temperatures are 13 °C and -5 °C respectively and the area receives average annual precipitation of 801 to 1200 mm, of which approximately 30% is snowfall (Environment Canada 2017). The soils of the area are nutrient poor podzolic gravel-loam (Soil Classification Working Group 1998). Forests are dominated by trees such as *P. mariana, Abies balsamea* (L.) Mill., mixed with *Betula papyrifera* Marsh., *Populus tremuloides* Michx., and to a lesser extent, *Larix laricina* (du Roi), Koc, and *Acer rubrum* L. with understory ericaceous shrubs such as *R. groenlandicum* (Oeder) Kron & Judd, and *Vaccinium angustifolium*

Aiton. Herbaceous plants such as *Gaultheria hispidula* (L.), Muhl. ex Bigelow, *Linnaea borealis* L., *Cornus canadensis* L., *Clintonia borealis* (Aiton) Raf., mosses such as *Pleurozium schreberi* (Brid.) Mitt., *Dicranum* spp. Hedw., *Ptilium crista-castrensis* (Hedw.) De Not., *Hylocomium splendens* (Hedw.) Schimp., and *Cladina* spp. lichens constitute the ground vegetation (Damman 1964). A combined effect of active fire suppression and low-severity wildfires created many *Kalmia* dominated heaths in the study area (Mallik 1995; Siegwart Collier and Mallik 2010). *Kalmia* heaths are interspersed with *P. mariana* and *Larix laricina* Koch seedlings and saplings. *Rhododendron canadense* (L.) Torr, *R. groenlandicum* (Oeder) Kron and Judd, and *Vaccinium angustifolium* (Aiton) are subordinate to *Kalmia*. Ground cover is dominated by fruticose lichens such as *Cladonia cristatella* Tuck, and *Cladina rangiferina* (Aiton) Raf. (Damman 1964).

2.3.2 Site selection and sampling protocol

I selected study sites based on time since fire, dominant vegetation type and residual organic matter depth (*sensu* Siegwart Collier and Mallik 2010). This method of site selection resulted in two types of study systems: naturally regenerating forest and *Kalmia* heath, both of which were dominated by *P. mariana* before fire (as determined from the composition of adjacent unburned stands of each site). I selected sites representing the two successional pathways (heath and forest): nine heath sites aged 13 to 52 years since fire and four forest sites aged 12 to 100 years since fire (Table 1.1). Time since fire and fire severity data based on pre-fire drought code and number of burn days were obtained from Power (2000). Due to a low frequency of high severity fires in the area, naturally regenerating forest sites were very few forcing me to select a disproportionate number of heath and forest sites. In each site I placed 10 randomly located 2 x 2 m quadrats and determined species cover visually using the nomenclature of VASCAN (Database of Vascular Plants in Canada, Canadensys 2015). Since my objective was to determine abundance weighted species diversity of heath and forest sites I used the same protocol (2 x 2 m quadrats) in the forest sites. Although usually forest vegetation is sampled using 10 x 10 m or larger plots, the assessment of abundance of understory plants would have been difficult in large plots and also result in inconsistency compared to those sampled in heaths. From the abundance weighted cover data, I compiled three separate species-abundance matrices by classifying plant species in broad functional groups: trees, shrubs and herbs. This was necessary as the heath and forest sites were dominated by different functional groups, shrubs and trees respectively. This separation allowed for the detection of differences in functional diversity and composition that may have been masked by the inherent differences in trait syndromes of the two groups. Therefore, metrics were calculated overall for forests and heaths, as well as separately for trees, shrubs, and herbs within each successional pathway. Comparisons were made within functional groups and between community types. For each site, sampling was repeated in the adjacent unburned stands as a reference to determine the degree of change in post-fire functional diversity and composition. Age and species composition of adjacent unburned stands were typical of mature to over-mature boreal black spruce forests of Atlantic Canada.

I selected four aboveground traits: specific leaf area (SLA), leaf dry matter content (LDMC), seed mass, and maximum height, and one below ground trait: specific root length (SRL). The selected traits represented nutrient acquisition and reproductive strategies employed by plants in post-fire community assembly (Appendix I). Based on the site-by-species abundance matrix, 25 species representing > 90% of total cover in the total observed species pool were selected for trait measurement and FD calculations (Appendix II). Traits were measured on seven individuals of each species during the final week of July (peak growing period), 2015. I measured SLA as the ratio of fresh leaf area to leaf dry mass; LDMC as the ratio of fresh leaf mass to dry leaf mass; height as distance from the ground to the highest photosynthetic tissue and SRL as the ratio of length of absorptive roots with diameter < 2 mm to dry root mass. To ensure roots belonged to the target species, root samples were collected by following the aboveground stem to underground structures. This was especially necessary for shrub species as they have extensive root systems that are quite similar in appearance. A detailed protocol for trait measurement can be found in Cornelissen *et al*. (2003). Seed mass was obtained from Bonner and Karrfalt (2008). Cryptogam species were not included in the study due to the difficulty in incorporating cryptogamic traits analogous to those possessed by vascular plants (St. Martin and Mallik, 2017).

2.3.3 Functional diversity and composition

In calculating FD metrics and community-weighted mean values, I used a subset of species containing those comprising > 85% abundance (Appendix II). *Kalmia* heaths are relatively species-poor in terms of vascular plants and when a subset of those species is used, the number of species present dropped below the number of traits used. This renders certain measures of α-FD unusable, such as the convex hull volume (Cornwell et al. 2006). However, calculation of functional dispersion (FDis) requires only two species and if only one species is present it would be zero (Laliberté and Legendre 2010). Measures of incidence based similarity used for β-FD lose information if rare species are not considered as they would influence mean distances separating species in the functional trait space. For these reasons I used abundance-weighted indices.

I employed several indices to study functional diversity and composition of each successional pathway, heath and forest. Functional α-diversity (α-FD) was calculated using functional dispersion (FDis), which measures the distribution of species from the abundance-weighted center of the occupied trait space (Laliberté and Legendre 2010). Functional β-diversity (β-FD) was calculated using the β-diversity analogues of functional pairwise dissimilarity (D_{PW}) (equation 1) and nearest neighbor dissimilarity (D_{NN}) (equation 2).

D_{PW} measures the mean distance between pairs of species in two communities (Swenson *et al.* 2012), and is best suited for detecting large-scale functional turnover within community types.

$$D_{PW} = \sum_{i=1}^{Sa} f_i \overline{\delta_{ib}} + \sum_{j=1}^{Sb} f_j \overline{\delta_{ja}} \qquad \text{(eqn. 1)}$$

Where S_a is the number of species in community A and S_b is the number of species in community B, f_i is the relative abundance of species *i* and f_j is the relative abundance of species *j*. δ_{ib} is the mean pairwise functional distance between species *i* in community A and all other species in community B, and δ_{ja} is the mean pairwise functional distance of species *j* in community B to all other species in community A.

D_{NN} measures the mean distance between a species and its nearest neighbour in the functional space of two communities (Ricotta and Burrascano 2009) (equation. 2) and is best suited to detecting fine scale functional similarity within community types.

$$D_{NN} = \sum_{i=1}^{Sa} f_i min\delta_{ib} + \sum_{j=1}^{Sb} f_j min\delta_{ja} \qquad \text{(eqn. 2)}$$

Where $min\ \delta_{ib}$ is the functional distance between species *i* in community A and its nearest neighbour in community B and $min\ \delta_{ja}$ is the functional distance of species *j* in community B to its nearest neighbour in community A.

These two metrics provided a measure of dissimilarity between pairs of heath communities and pairs of forest communities and I employed both metrics to obtain information at different functional resolutions. To obtain distances separating species in the functional space, traits were first standardized to mean 0 and unit variance, then the species-trait matrix was transformed to a species-species Gower distance matrix. All diversity metrics were calculated for the entire species set as well as for three subsets based on maximum height; 'Trees' greater than 3 m, 'Shrubs' between 3 and 0.5 m, and 'Herbs' less than 0.5 m. I calculated the community-weighted mean (CWM) trait values to determine the functional composition of each community type and the three life form groups (trees, shrub and herbs). All calculations were performed using the "vegan" package (Oksanen *et al*. 2013) and the "FD" package (Laliberté and Shipley 2013), for R using R version 2.15.3 (R Core Team, 2013).

2.3.4. Post-fire ecosystem properties

To determine the change in post-fire functional diversity and functional composition, adjacent unburned mature forest stands were sampled as a replacement of pre-fire conditions in the same manner as the post-fire sites. To avoid edge effect, I sampled the unburned stands 80 - 100 m from the margin of the burned area. In this ecosystem, forests regenerating following severe fires achieve canopy closure around 50 years. In the oldest forest site (> 80 years since fire) the boundary between burned and unburned forest was undetectable because burned and unburned areas appeared similar. Therefore, only the three youngest forest sites were used for this particular analysis. Diversity metrics for the adjacent stands were calculated as described above.

2.4. Results

2.4.1. Functional diversity of forest and heath succession

There was no significant pattern in FD along the time since fire gradient therefore, mean values for forest and heath FD were reported. Overall, mean functional dispersion (FDis; α-FD) was significantly higher in forest sites than heath sites when the entire species set was considered (Kruskal-Wallis test, $\alpha = 0.05$; Fig 2.1.) When the species set was separated into life form groups and metrics were considered for each group separately, the results were less defined. When comparing the same group in different community types, tree and herb groups had significantly higher α-FD in forests than in heaths. For shrubs, α-FD between heaths and forests was not significantly different. In terms of β-FD, represented by the mean-pairwise functional distance (D_{PW}) as well as the functional distance to the nearest neighbor (D_{NN}), trees and herbs showed significantly higher values in forest sites than in heath sites. The shrub group β-FD did not follow the same pattern as shrub α-FD. The beta diversity for shrubs was significantly higher in heaths than in forests (Fig. 2.1). When comparing the three life form groups within a community type, shrub diversity (α and β) was highest in heaths, whereas tree diversity was highest in forests.

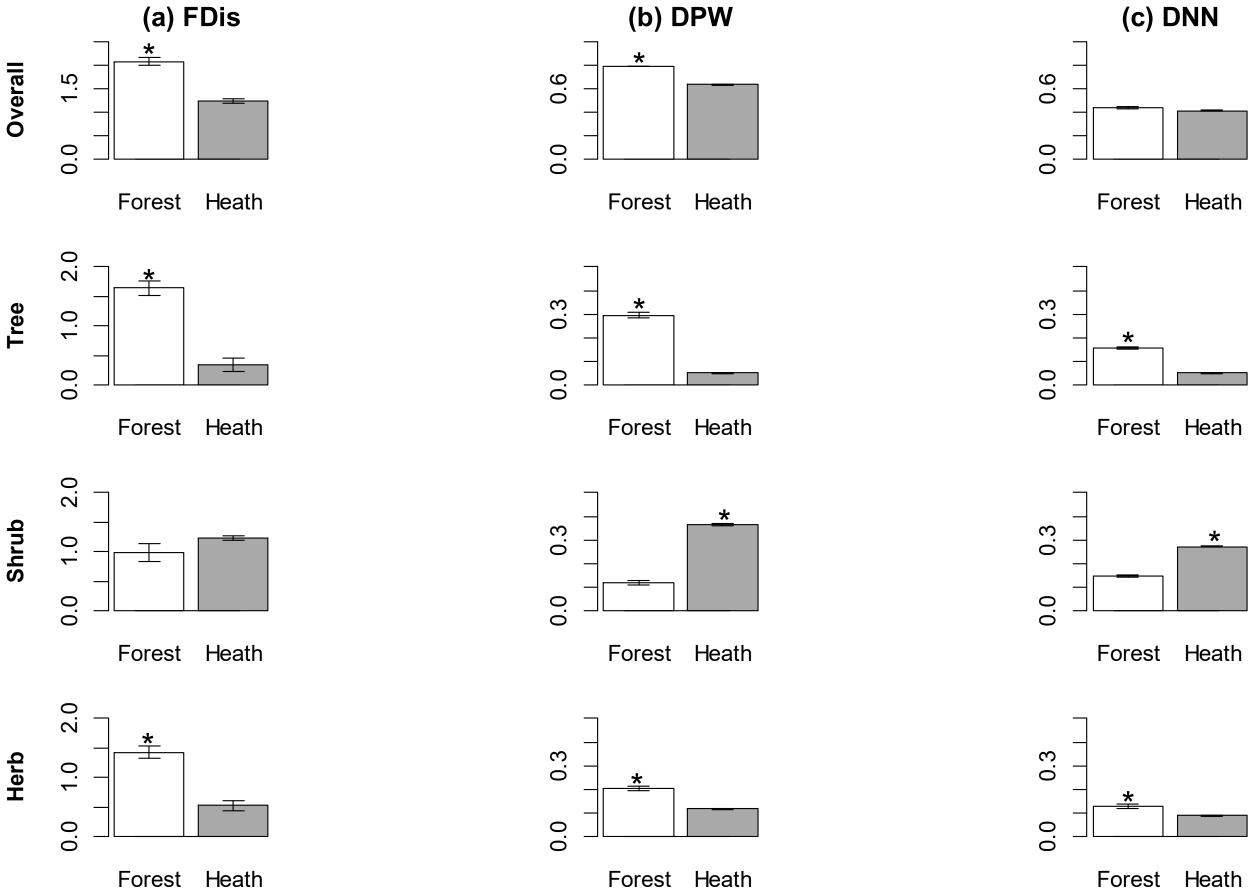


Figure 2.1. Mean functional diversity values for the three life forms in both forest and heath sites (n = 130). Functional dispersion (FDis) represents functional alpha diversity, and mean pairwise distance (D_{PW}) and distance to nearest neighbour (D_{NN}) represent functional beta diversity. Asterisk represent a significantly higher value ($p < 0.05$), error bars represent 95% confidence interval.

When post-fire FD was compared with adjacent unburned stands, overall FDis was greater in post-fire forest sites than adjacent unburned forests, although only the youngest site was significantly higher (Wilcoxon signed rank test, $\alpha = 0.05$; Fig. 2.2). In contrast, eight out of nine post-fire heath sites had significantly lower FDis than those of adjacent unburned sites. The response of group specific FDis varied for both forest and heath sites. Tree functional dispersion in forest sites was greatly enhanced following fire across all sites, whereas it varied among the heath sites with no significant differences among them. Missing values for some sites were due to only a single species being present, resulting in zero dispersion. Shrub FDis was significantly greater in one forest site; in heath sites, there was a consistent pattern of higher FDis but the differences were not significant. Similar to the tree group, herb FDis was enhanced in post-fire forest sites (but not significantly), and varied less predictably in the heath sites (Fig. 2.2).

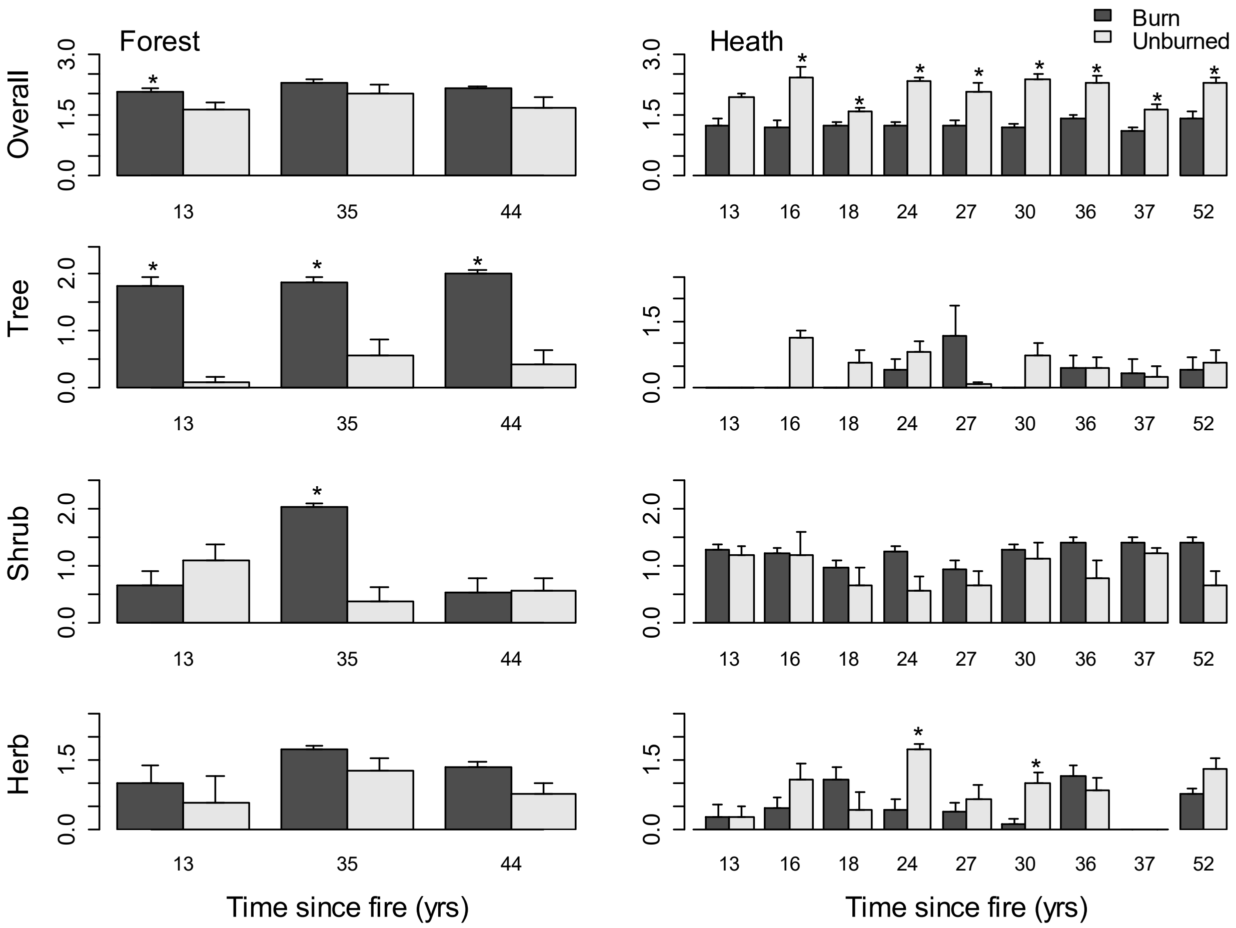


Figure 2.2. Functional dispersion (FDis) of forest and heath sites and their respective adjacent unburned stands. Asterisks represent a significantly higher value ($p < 0.05$); error bars represent 95% confidence interval. The oldest forest site (> 100 yrs) was excluded from this analysis because the boundary between burned and unburned stand was undetectable.

The response of β-FD following fire was consistent between post-fire forest and heath sites for both mean pairwise functional distance (D_{PW}) and functional distance to nearest neighbor (D_{NN}). No significant difference was observed in the forest sites for D_{PW} (Fig. 2.3) nor for D_{NN} (Fig. 2.4) in overall values or lifeform-specific values. Post-fire heath sites had lower values than unburned stands for both β-FD metrics (Figs. 2.3, 2.4) with the exception being herbs in the 18 year old heath, and shrubs in all heaths.

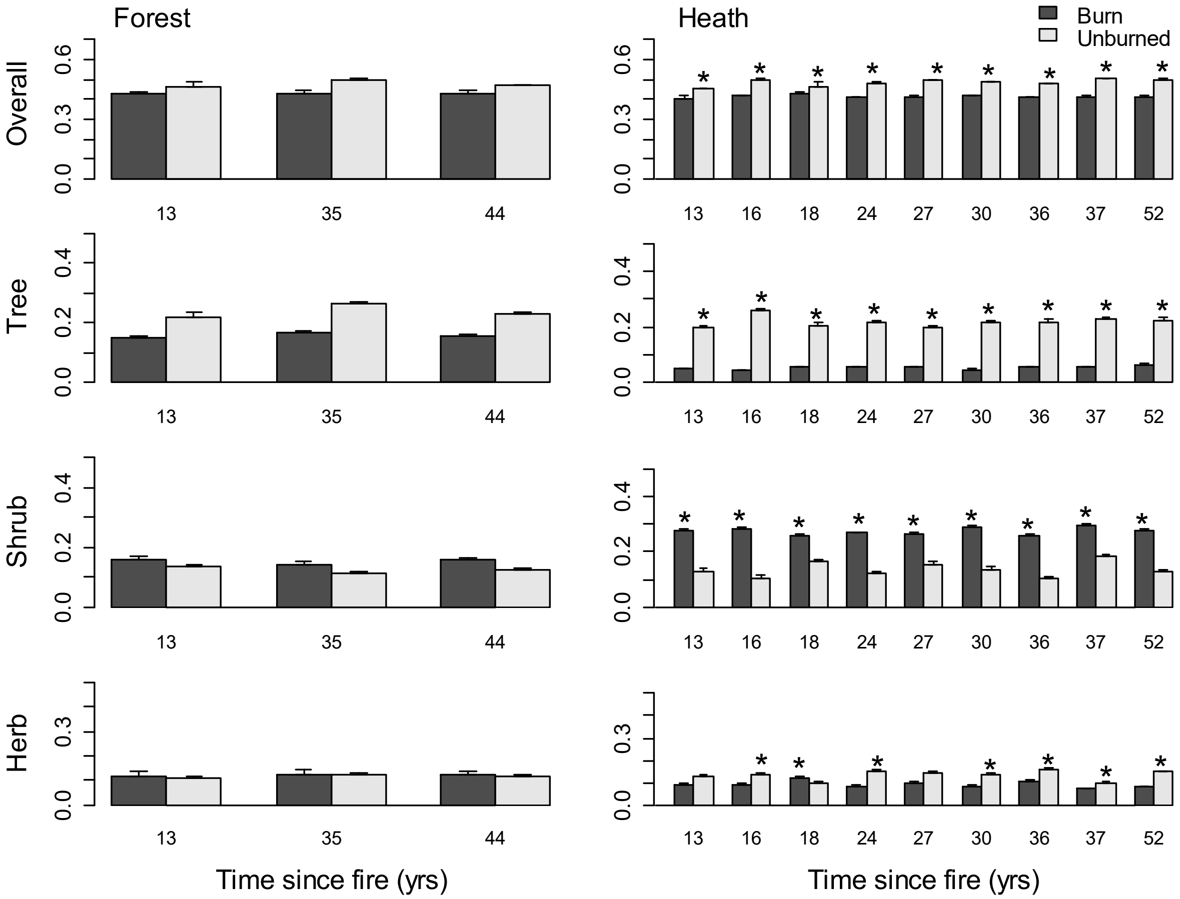


Figure 2.3. Mean pairwise functional distance (D_{PW}) of forest and heath sites and their respective adjacent unburned stands. Asterisks represent a significantly higher value ($p < 0.05$); error bars represent 95% confidence interval. The oldest forest site (>100 yrs) was excluded from this analysis because the boundary between burned and unburned stand was undetectable.

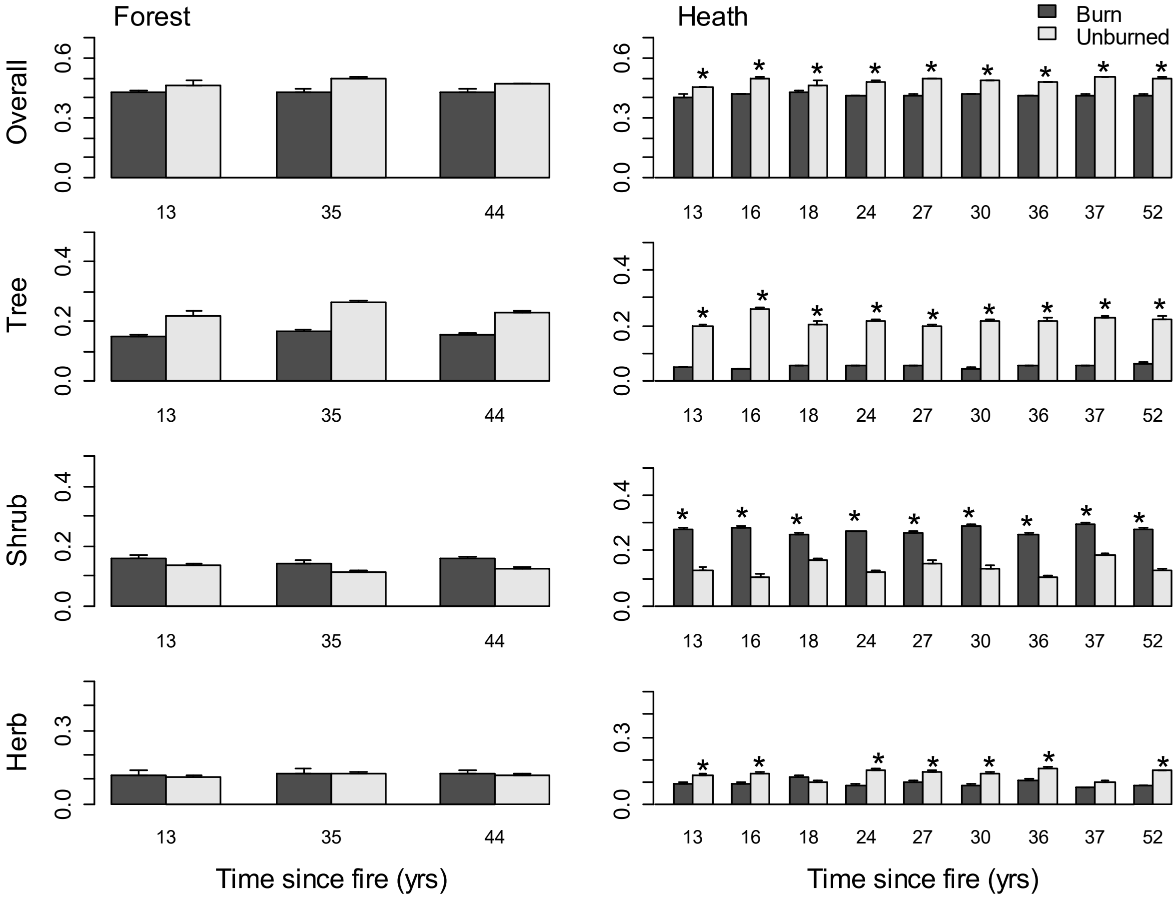
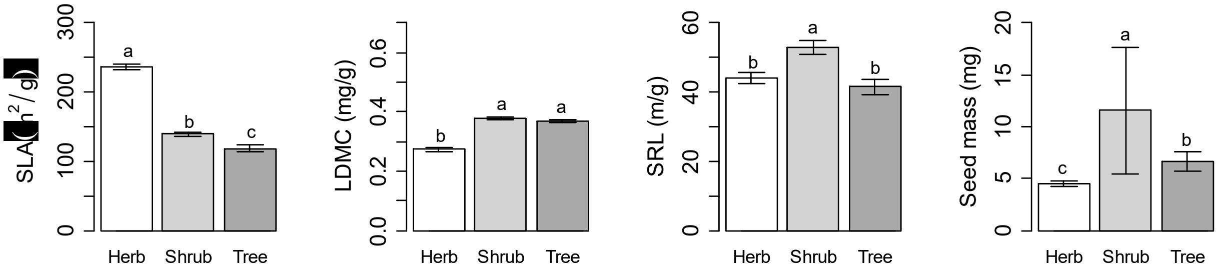


Figure 2.4. Functional distance to nearest neighbor (D_{NN}) of forest and heath sites and their respective adjacent unburned stands. Asterisks represent a significantly higher value ($p < 0.05$); error bars represent 95% confidence interval. The oldest forest site (>100 yrs) was excluded from this analysis because the boundary between burned and unburned stand was undetectable.

2.4.2. Functional composition of life form groups

Mechanisms driving the functional diversity of a system can often be revealed by examining the functional composition of the system. I separated functional composition of forests and heaths into three groups (Fig. 2.5). Specific leaf area (SLA) and leaf dry matter content (LDMC) often display an inverse relationship but this was not the case when mean trait values were examined for each life form group. Herbs showed a significantly higher SLA, followed by shrubs, then trees. The LDMC of herbs was the lowest (as expected from an inverse relationship) however shrubs and trees had a very similar mean LDMC. Herbs had a significantly higher SLA than shrubs and trees and a significantly lower SRL than shrubs. Seed mass was significantly different between all three groups, with shrubs having the highest seed mass, followed by trees, then herbs (Kruskal-Wallis test followed by Dunn's test, α = 0.05; Fig. 2.5). Community-weighted mean height of the groups was not compared as height was a characteristic used to separate the life form groups.


(a) Forest


(b) Heath

Figure 2.5. Community-weighed mean values of four traits used in this analysis for the three life forms in both forest and heath sites: specific leaf area (SLA), leaf dry matter content (LDMC), specific root length (SRL), and seed mass. Error bars represent 95% confidence interval. Letters denote significant difference ($p \leq 0.05$).

2.5. Discussion

2.5.1. Functional diversity of forests and heaths

Using abundance weighted diversity indices I found differences between the two successional pathways in overall FD as well as differences within life form groups. Siegwart Collier and Mallik (2010) reported that low severity suppressed fires fail to destroy the belowground sprouting centers and rhizomes of ericaceous plants promoting vegetative regeneration immediately after fire. This leads to high abundance of shrubs and formation of heaths. On the other hand, high severity fires, by consuming the organic matter and destroying belowground organs of shrubs, create favourable seedbeds and enhance tree seed germination and seedling establishment, leading to forest succession. The promotion of one type of reproductive trait over another (i.e. vegetative vs. seed) leads to two distinct successional pathways. Here I show that this also plays a role in determining functional diversity of the post-fire plant communities.

Overall, forest sites had significantly higher dispersion of species in the functional trait space than heaths, and trees and herbs were more dispersed in forest functional space. Tree abundance in heaths was low and the two most abundant species were *P. mariana* and *L. laricina*, both of which are conifers. In forest sites, however, tree abundance was more evenly shared among conifer and deciduous species, leading to a higher dispersion within the functional trait space. Deciduous contributions to high dispersion included high SLA in *P. pensylvatica* and high seed mass of *A. rubrum* compared to coniferous species. Herb functional dispersion also displayed a similar response to the two successional pathways. *Clintonia borealis* was present in only one out of nine heath sites and *Aralia nudicaulis* was absent from all of them. The relative absence of these two functionally distinct species (in terms of SLA, SRL, and height; Appendix

III) from heaths is a main driver of the lower functional dispersion of herbs of heaths compared to forests. Dispersion of shrubs was not significantly different between forests and heaths, likely due to the high redundancy of trait values in this particular group (Appendix III). Four members of Ericaceae (*K. angustifolia, R. canadense, R. groenlandicum, V. angustifolia*) were abundant in heaths contributing > 60% cover. While some members were rare in the forest sites, the presence of others ensured that shrub functional dispersion in forests remained high. One might argue that my selection of a subset of plants consisting of only the most abundant species is a limitation of this study. However, studies have shown that patterns of FD are often driven by the traits of the dominant species as per the Mass-Ratio hypothesis (Grime 1998; Mokany et al. 2008; Li et al. 2015). Forests and heaths in eastern Newfoundland are heavily influenced by the dominant species therefore, I used abundance-weighted diversity metrics, which would have made the impact of rare species negligible had they been included. Nevertheless, I acknowledge that the omission of rare vascular plants and cryptogams may have resulted in the loss of information, such as the impact to functional dispersion if rare species occupied a position on the edge of the trait space.

In examining the β-FD of forests and heaths, I found that greater functional dissimilarity existed among forest sites than among heath sites. Higher D_{PW} in forest sites indicates that tree and herb species therein were separated from all other species in the functional space of forests by a greater distance than species in the heath functional space. Higher D_{NN} in forest sites means that any tree-tree or herb-herb species pair in one forest site was separated by a greater distance than any particular heath species pair. Considering the β-FD at both resolutions (D_{NN} and D_{PW}), we can confidently conclude that heaths are functionally more homogenized systems than forests and that this homogenization is driven by a reduction in dissimilarity within tree and herb life forms. Shrubs do not face a similar reduction in beta diversity; in fact they show greater dissimilarity in heaths than in forest sites. Shrub species that favour open areas (i.e. heaths) such as *Amelanchier interior* and *Ilex mucronata* have distinct trait syndromes relative to ericaceous shrub species and contribute to the high dispersion and dissimilarity of the shrub group in the heaths. For example, both *A. interior* and *I. mucronata* have a maximum height twice that of the ericads, produce seeds with a much higher mass, and form associations with endomycorrhizae rather than ericoid mycorhizzae (Appendix II). These results of lower α and β-FD of the majority of the groups in heaths provide support for my hypothesis that this disturbance-driven alternate successional pathway (i.e., heath) is associated with lower FD, and is subject to functional homogenization. Velle et al. (2014) found prescribed burning of *Calluna* heathlands enhanced taxonomic heterogeneity by creating habitat for specialist species. Although the authors examined wet and dry heathlands, our results show that disturbance effects on diversity can be ecosystem dependent and that taxonomic diversity does not always respond in a similar manner to disturbance as FD.

2.5.2. Drivers of FD

The relationship between disturbance and diversity has been the focus of much attention in the previous decades. The Intermediate Disturbance Hypothesis (IDH) postulates that diversity in a system peaks at moderate disturbance intensities. Any particular population is unable to reach competitive equilibrium due to periodic environmental perturbations (Connell 1978; Huston 1979). Although still contested, the IDH has been shown to apply to terrestrial boreal systems in terms of taxonomic diversity (reviewed by Kershaw and Mallik 2012) and to a lesser extent in terms of FD (Biswas and Mallik 2010). Specifically, for fire, there is a consensus in the literature that fire provides a positive benefit to diversity by releasing soil nutrient trapped in recalcitrant forms (Neary et al. 1999; DeLuca et al. 2002)) and opening new niche space for species to colonize (Nilsson and Wardle 2005; Bansal et al. 2014; Li and Waller 2014). No study to date, in my knowledge, has shown how fire of a certain nature can have a negative impact on the FD of multiple functional groups simultaneously. When in place, the ROM filter generated by low-severity fires, leads a homogeneous seedbed suitable for only a portion of the species pool with high vegetative sprouting. The immediate filtering of seed obligate species drastically limits the range of functional traits possible for a post-fire community. I have shown that the principles described in diversity-disturbance relationships such as the IDH that lead to high diversity (e.g. a period of overlap between early and late successional communitites) cannot be observed in post-fire heaths because the environmental heterogeneity required for high diversity is absent immediately following low severity fires. High ROM creates homogeneity in regeneration conditions and allows for competitive equilibrium (i.e. dominance of ericaceous species) to be reached in as little as 13 years.

Separating species into functional groups and then calculating community-weighted mean trait values helped identify the suites of traits that are favored by post-fire conditions. This important finding would have remained hidden had the species set not been subdivided. Here I observe that the group with the highest dispersion in its suite of traits is also the dominant life-form in its respective community: shrub traits are most dispersed in heaths, and trees in forests. In heaths the dispersion of shrubs is more than twice that of the other two groups whereas tree dispersion in forests, while highest, does not reach the order of magnitude seen by shrubs in heath communities. Shrub species displayed high SRL, an ideal trait to be successful in soils of low fertility (Ordonez et al. 2009; Holdaway et al. 2011), which is a characteristic often found in ericaceous heaths. A high SRL means that shrub species are investing more biomass per unit length of belowground resource absorptive surface, increasing nutrient and water uptake ability in areas of low resource availability and high competition (Cornelissen et al. 2003). Since *Kalmia* heaths are more nutrient deficient than forests (Bloom and Mallik 2006) and they have high abundance of ericaceous plants with very high root mass in organic soils (Damman 1971; Mallik et al. 2016), a higher SRL would provide greater success in the capture of nutrients in this nutrient deficient system. This suggests that low-severity fires, which facilitate vigorous shrub regeneration by keeping a significant portion of the organic layer intact, also create ideal habitat for species with high SRL. High severity fires on the other hand, create a patchwork mosaic of regeneration conditions, opening niche space to a greater range of functional groups (Dzwonko et al. 2015).

These results also provide insight into advantages possessed by shrubs over other life forms in areas where they are dominant (i.e. heaths). The phylogenetic similarity and therefore, trait similarity among the members of Ericaceae would not necessarily imply strong competitive interactions between members of the group (Cavender-Bares *et al.* 2009). Funk and Wolf (2016) reported that possessing traits which increase fitness is a much stronger predictor of competitive outcomes than phylogenetic relatedness. Additionally, it has been reported that competition can lead to communities that are more similar to one another, in contrast to the principle of limiting similarity (Price et al. 2014; Kumordzi et al. 2015). I speculate that facilitation within the shrub group overcomes any limitations that may be imposed by a higher degree of niche overlap and subsequent stronger competitive interactions. Once established as a dominant species, *Kalmia* can generate a positive soil feedback by releasing tannins that sequester soil N in forms more readily available to its ericoid mycorrhiza than arbuscular and ectomycorrhizae. This positive feedback would extend to other members of Ericaceae that also form associations with ericoid fungi, and this would contribute to the overall success of these dwarf shrubs in heaths (Montesinos-Navarro et al. 2016). Another competitive advantage inferred to all shrub species in heaths is the suppression of black spruce by *Kalmia* phenolics. Conifer regeneration in heaths is very poor and the inhibition of strong competitors (from a shrubs perspective) eases the light limitation on low stature shrubs in early stages of succession (Gavinet et al. 2016). While both *Kalmia* and *R. groenlandicum* have been shown to exhibit significant morphological plasticity to light availability (Hébert et al. 2011), shrubs less adapted to shade would be free to allocate resources to areas other than vertical growth, such as belowground resource collection and reproduction (Chapin et al. 1987; Fazlioglu et al. 2016). The abiotic filtering (soil conditions favouring high root mass) and biotic filtering (driven by the competitive ability to exploit soil resources) following low severity fires leads to the low functional dispersion observed in heaths. In contrast, high severity fires remove much of the organic matter and allow a wider range of species to establish (Siegwart-Collier and Mallik 2010; Dzwonko et al. 2015). This results in forest communities that are less subject to abiotic and/or biotic filters and therefore experience a greater degree of niche differentiation and functional heterogeneity.

Habitat filtering and niche differentiation are not mutually exclusive mechanisms but one may be more influential than the other in determining community composition (Mason et al. 2011). The mechanism(s) can be detected by comparing functional trait diversity of the communities vs. reference communities, in this case the adjacent unburned stands. My results show that FD experienced no negative impact following high severity fires (forest communities) and was even enhanced in some cases. In contrast, low severity fires (resulting in heath formation) caused a significant loss of overall FD with the majority of life form groups showing a loss. The lower FD in heath could indicate that either habitat filters are restricting the entry of particular functional groups or the particular functional groups are competitively excluded. Only shrub diversity was enhanced in heath communities, suggesting that they possess the set of traits that are best suited to conditions created by low severity fires. Tree and herb functional diversity on the other hand was favoured by high severity fires, which created favourable seedbeds (Mallik et al. 2010) and limit the regeneration potential of shrubs, thereby increasing seed regeneration niche space and limiting the magnitude of belowground competition seen in heaths. This study did not take into account all environmental variables that could be acting as habitat filters however the nature of *Kalmia*'s impact on soil properties has been well documented (Damman 1971; Mallik 2003; Joanisse et al. 2009; Mallik et al. 2016) and if they are considered alongside the functional composition of *Kalmia* heaths, potential mechanisms can be identified, as shown in the following chapter.

The biotic filter imposed by high ericaceous abundance is absent in forest sites, and community assembly therein is likely influenced by species dispersal ability and niche complementarity. Hence, in heaths maximum site productivity cannot be achieved as available niche space (suitable seedbeds, belowground resources) for tree species remains inaccessible (Cardinale et al. 2007). This results in a loss of structural diversity, rendering heath much less of a multi-layered system compared to forests. Community assembly mechanisms in forest succession leads to greater FD compared to heath succession; the overall result is that more trait space is occupied (higher FDis) and individual sites are functionally more heterogeneous, as indicated by greater D_{PW} and D_{NN}.

2.6. Conclusions

The heath succession results in lower FD than forest succession, but only for specific life forms. I showed that overall homogenization of functional trait diversity is associated with heaths and this can be used to describe retrogressive succession. The decreased FD and trait homogenization in heaths can have negative impacts on the functioning of ecosystems and the services they provide. In recent decades, ericaceous heaths has been expanding in closed canopy boreal forests following canopy removing disturbance such as large-scale insect defoliation, forest harvesting and low severity fires (Meades 1983; Payette and Delwaide 2003; Mallik 2003; Côté et al. 2013). In addition, climate projections for eastern Canada indicate an increase in precipitation (Mladjic et al. 2011), which would favour further heath formation by increasing low-severity fires. While this imparts benefits to certain life forms, they do not represent the majority of plants in the area. Land management decisions that remove large areas of closed canopy forest while leaving organic matter relatively undisturbed (i.e., fire suppression and clearcutting) would impose strong abiotic and biotic filters and favour a narrow range of response traits affecting biodiversity, structural integrity and stability of regional plant communities.

2.7 References

Bansal, S., Jochum, T., Wardle, D.A., Nilsson, M.-C. 2014. The interactive effects of surface-burn severity and canopy cover on conifer and broadleaf tree seedling ecophysiology. *Canadian Journal of Forest Research*, **44**, 1032–1041

Biswas, S.R., Mallik, A.U. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. *Ecology*, **91**, 28–35.

Bloom, R. G., Mallik, A. U. 2004. Indirect effects of black spruce (*Picea mariana*) cover on community structure and function in sheep laurel (*Kalmia angustifolia*) dominated heath of eastern Canada. *Plant and Soil*, **265**, 279-293.

Bloom, R. G., Mallik, A. U. 2006. Relationships between ericaceous vegetation and soil nutrient status in a post-fire *Kalmia angustifolia*-black spruce chronosequence. *Plant and Soil*, **289**, 211-226.

Bonner, F. T., Karrfalt, R. P. (eds). 2008. *The Woody Plant Seed Manual*. USDA Forest Service, Agriculture Handbook 727, USA.

Britton, A. J., Fisher, J. M. 2007. Interactive effects of nitrogen deposition, fire and grazing on diversity and composition of low-alpine prostrate *Calluna vulgaris* heathland. *Journal of Applied Ecology*, **44**, 125-135

Cadotte, M. W., Carscadden, K., Mirotchnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079-1087.

Calo, L., Alonso, I., Marcos, E., DeLuis, E. 2007. Effects of cutting and nitrogen deposition on biodiversity in Cantabrian heathlands. *Applied Vegetation Science*, **10**, 43-52.

Canadensys. 2015. Vascan: Database of Vascular Plants in Canada. Accessed December 10, 2015.< >

Cardinale, B. J., Wright, J. P., Cadotte, M. W., Carroll, I. T., Hector, A., Srivastava, D. S., Loreau, M., Weis, J. J. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *PNAS*, **104**, 18123–18128.

Cavender-Bares, J., Kozak, K .H., Fine, P. V. A., Kembel, S. W. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.

Chapin, F. S., Bloom, A. J., Field, C. B., Waring, R. H. 1987. Plant responses to multiple environmental factors. *BioScience*, **37**, 49-57.

Chillo, V., Anand, M., Ojeda, R. A. 2011. Assessing the use of functional diversity as a measure of ecological resilience in arid rangelands. *Ecosystems*, **14**, 1168-1177.

Connell, J. H. 1978. Diversity in tropical rainforest and coral reefs. *Science*, **199**, 1302-1310.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G., Pooter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335-380.

Cornwell, W. K., Schwilk, D. W., Ackerly, D. D. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology*, **87**, 1465-1471.

Damman, A. W. H. 1964. Some forest types of central Newfoundland and their relationship to environmental factors. *Forest Science Monographs*, **8**, 1-62.

Damman, A. W. H. 1971. Effect of vegetation changes on the fertility of a Newfoundland forest site. *Ecological Monographs*, **41**, 253-270.

Damman, A. W. H. An ecological subdivision of the island of Newfoundland. In South, R. (ed.) 1983. *Biogeography and Ecology of the Island of Newfoundland*. Dr. W. Junk Publishers, The Netherlands, pp. 163-206.

de Bello, F., Lepš, J., Sebastià, M.-T. 2006. Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography*, **29**, 801–810.

DeLuca, T., Nilsson, M.-C., Zackrisson, O. 2002. Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. *Oecologia*, **133**, 206–214.

Díaz, S., Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646-655.

Dzwonko, Z., Loster, S., Gawroński, S. 2015. Impact of fire severity on soil properties and the development of tree and shrub species in a Scots pine moist forest site in southern Poland. *Forest Ecology and Management*, **342**, 56–63.

Environment Canada. 2017. Canadian Climate Normals, Gambo, NL. 1981-2010. Available online <http://climate.weather.gc.ca/>.

Fazlioglu, F., Al-Namazi, A., Bonser, S.P. 2016. Reproductive efficiency and shade avoidance plasticity under simulated competition. *Ecology and Evolution*, **6**, 4947–4957.

Gavinet, J., Prévosto, B., Fernandez, C. 2016. Introducing resprouters to enhance Mediterranean forest resilience: importance of functional traits to select species according to a gradient of pine density. *Journal of Applied Ecology*, **53**, 1735–1745.

Gimingham, C. H. 1972. *Ecology of heathlands*. Chapman and Hall, London, p. 39.

Girard, F., Payette, S., Gagnon, R. 2009. Origin of the lichen-spruce woodland in the closed-crown forest zone of astern Canada. *Global Ecology and Biogeography*, **18**, 291–303.

Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.

Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science*, **17**, 255-260.

Hébert, F., Thiffault, N., Munson, A. D. 2011. Does trait plasticity of three boreal nutrient-conserving species relate to their competitive ability? *Écoscience*, **18**, 382–393.

Holdaway, R. J., Richardson, S. J., Dickie, I. A., Peltzer, D. A., Coomes, D. A. 2011. Species- and community-level patterns in fine root traits along a 120 000-year soil chronosequence in temperate rain forest. *Journal of Ecology*, **99**, 954-963.

Huston, M. 1979. A general hypothesis of species diversity. *The American Naturalist*, **113**, 81-101.

Jasinski, J. P. P., Payette, S. 2005. The creation of alternative stable states in the southern boreal forest, Québec, Canada. *Ecological Monographs*, **75**, 561-583.

Joanisse, G. D., Bradley, R. L., Preston, C. M., Bending, G. D. 2009. Sequestration of soil nitrogen as tannin–protein complexes may improve the competitive ability of sheep laurel (*Kalmia angustifolia*) relative to black spruce (*Picea mariana*). *New Phytologist*, **181**, 187-198.

Johnstone, J. F., Hollingsworth, T. N., Chapin III, F. S., Mack, M. C. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, **16**, 1281-1295.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, **3**, 157-164.

Kershaw, H.M., Mallik, A.U. 2013. Predicting plant diversity response to disturbance: Applicability of the Intermediate Disturbance Hypothesis and Mass Ratio Hypothesis. *Critical Reviews in Plant Sciences*, **32**, 383–395.

Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J. Laughlin, D.C. 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology*, **104**, 1299–1310.

Kumordzi, B. B., de Bello, F., Freschet, G. T., Le Bagousse-Pinguet, Y., Lepš, J., Wardle, D. A. 2015. Linkage of plant trait space to successional age and species richness in boreal forest understorey vegetation. *Journal of Ecology*, **103**, 1610–1620.

Laliberté, E., Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299-305.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A., Mayfield, M.M. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, **13**, 76–86.

Laliberté, E., Shipley, B. 2013. Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology – R package ‘FD’, version 1.0-11.

Li, D., Waller, D. 2014. Drivers of observed biotic homogenization in pine barrens of central Wisconsin. *Ecology*, **96**, 1030–1041.

Li, W., Cheng, J.-M., Yu, K.-L., Epstein, H.E., Guo, L., Jing, G.-H., Zhao, J., Du, G.-Z. 2015. Plant Functional Diversity Can Be Independent of Species Diversity: Observations Based on the Impact of 4-Yrs of Nitrogen and Phosphorus Additions in an Alpine Meadow. *PLoS ONE* **10.**

MacArthur, R. H., Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturali*Mallik, A. U. 2003. Conifer regeneration problems in boreal and temperate forests with ericaceous understory: Role of disturbance, seedbed limitation, and keystone species change. *Critical Reviews in Plant Sciences*, **22**, 341-366.

Mallik, A.U. 2003. Conifer Regeneration Problems in Boreal and Temperate Forests with Ericaceous Understory: Role of Disturbance, Seedbed Limitation, and Keytsone Species Change. *Critical Reviews in Plant Sciences*, **22**, 341–366.

Mallik, A. U., Inderjit 2001. *Kalmia angustifolia*: Ecology and management. *Weed Technology*, **15**, 858-866.

Mallik, A. U., Bloom, R. G., Whisenant, S. G. 2010. Seedbed filter controls post-fire succession. *Basic and Applied Ecology*, **11**, 170-181.

Mallik, A. U., Biswas, S.R., Siegwart-Collier L. C. 2016. Belowground interactions between *Kalmia angustifolia* and *Picea mariana*: roles of competition, root exudates and ectomycorrhizal association. *Plant and Soil*, **403**, 471-483.

Mason, N. W. H., de Bello, F., Dolezal, J., Leps, J. 2011. Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology*, **99**, 788–796.

Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S., Vesk, P.A. 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, **19**, 423–431.

Meades, W. J. 1983. Origin and successional status of anthropogenic dwarf shrub heath in Newfoundland. *Advances in Space Research*, **2**, 97-101.

Mladjic, B., Sushama, L., Khaliq, M. N., Laprise, R., Caya, D., Roy, R. 2011. Canadian RCM projected changes to extreme precipitation characteristics over Canada. *Journal of Climate*, **24**, 2565-2584.

Mokany, K., Ash J., Roxburgh, S. 2008. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893.

Mokany, K., Thomson, J.J., Lynch, A.J.J., Jordan, G.J., Ferrier, S. 2015. Linking changes in community composition and function under climate change. *Ecological Applications*, **25**, 2132–2141.

Montesinos-Navarro, A., Segarra-Moragues, J.G., Valiente-Banuet, A., Verdú, M. 2016. Fungal phylogenetic diversity drives plant facilitation. *Oecologia*, **181**, 533–541.

Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management*, **122**, 51–71.

Nilsson, M.-C., Wardle, D.A. 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, 3, 421–428.

Olden, J. D., Rooney, T. P. 2006. On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, **15,** 113–120.

Ordoñez, J. C., Van Bodegom, P. M., Witte, J.-P. M., Wright, I. J., Reich, P. B., Aerts, R. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, **18**, 137–149.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Wagner, H. 2013. vegan: Community Ecology Package. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>

Paquette A., Messier, C. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography,* **20**, 170-180.

Payette, S., Delwaide, A. 2003. Shift of conifer boreal forest to lichen–heath parkland caused by successive stand disturbances. *Ecosystems*, **6**, 540-550,

Petchey, O. L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos*, **101**, 323-330.

Power, R. 2000. *Vegetation Management Plan for Terra Nova National Park 2000-2004.* Parks Canada, Terra Nova National Park.

Price, J.N., Gazol, A., Tamme, R., Hiiesalu, I., Pärtel, M. 2014. The functional assembly of experimental grasslands in relation to fertility and resource heterogeneity. *Functional Ecology*, **28**, 509–519.

R Core Team. 2013. *R: A language and environment for statistical computing.* R

Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Read. D. J. 1996. The structure and function of the ericoid mycorrhizal root. *Annals of Botany*, **77**, 365-374

Reiss, J., Bridle, J. R., Montoya, J. M., Woodward, G. 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution*, **24**, 505–514.

Ricotta, C., Burrascano, S. 2009. Testing for differences in beta diversity with asymmetric dissimilarities. *Ecological Indicators*, **9**, 719–724.

Roem, W. J., Berendse, F. 2000. Soil acidity and nutrient supply ratio as possible factors determining changes in plant species diversity in grassland and heathland communities. *Biological Conservation*, **92**, 151-161.

Sankaran, M., McNaughton, S. J. 1999. Determinants of biodiversity regulate compositional stability of communities. *Nature,* **401,** 691–693.

Siegwart Collier, L. C., Mallik, A. U. 2010. Does post-fire abiotic habitat filtering create divergent plant communities in black spruce forests of eastern Canada? *Oecologia*, **164**, 465-477.

Shenoy, A., Johnstone, J. F., Kasischke, E. S., Kielland, K. 2011. Persistent effects of fire severity on early successional forests in interior Alaska. *Forest Ecology and Management*, **261**, 381-390.

Soil Classification Working Group. 1998. Canadian Soil Classification System, 3rd ed. Agriculture and Agri-Food Canada Publication 1646, NRC Press, Canada.

Sonnier, G., Johnson, S. E., Amatangelo, K. L., Rogers, D. A., Waller, D. M. 2014. Is taxonomic homogenization linked to functional homogenization in temperate forests? *Global Ecology and Biogeography*, **23**, 894–902.

St. Martin, P., Mallik, A. U. 2017. The status of non-vascular plants in ecosystem function studies. *Perspectives in Plant Ecology, Evolution, and Systematics*, **27**, 1-8.

Staples, T. L., Dwyer, J. M., Loy, X., Mayfield, M. M. 2016. Potential mechanisms of coexistence in closely related forbs. *Oikos*, **125**, 1812–1823.

Stubbs, W. J. & Wilson, J.B. 2004. Evidence for limiting similarity in a sand dune community. *Journal of Ecology*, **92**, 557–567.

Suding, K. N., Lavorel, S., Chapin III, F. S., Cornelissen, J. H. C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D., Jackson, S. T., Navas, M. -L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125-1140.

Swenson, N. G., Erickson, D. L., Mi, X., Bourg, N. A., Forero-Montaña, J., Ge, X., Howe, R., Lake, J. K., Liu, X., Ma, K., Pei, N., Thompson, J., Uriarte, M., Wolf, A., Wright, S. J., Ye, W., Zhang, J., Zimmerman, J. K., Kress, W. J. 2012. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. *Ecology*, **93**, S112–S125.

Thiffault, N., Picher, G., Auger, I. 2012. Initial distance to *Kalmia angustifolia* as a predictor of planted conifer growth. *New Forests*, **43**, 849-868.

Urza, A. K., Sibold, J. S. 2017. Climate and seed availability initiate alternate post-fire trajectories in a lower subalpine forest. *Journal of Vegetation Science*, **28**, 43–56.

Velle, L.G., Nilsen, L.S., Nordenhaug, A. Vandvik, V. 2014. Does prescribed burning result in biotic homogenization of coastal heathlands? *Global Change Biology*, **20**, 1429–1440.

Vítová, A., Macek, P., Lepš, J. 2017. Disentangling the interplay of generative and vegetative propagation among different functional groups during gap colonization in meadows. *Functional Ecology*, **31**, 458–468.

Wardle, D. A., Zackrisson, O. 2005. Effects of species and functional group loss on island ecosystem properties. *Nature*, **435**, 806–810.

Wirth, C., Lichstein, J. W., Dushoff, J., Chen, A., Chapin, F. S. 2008. White spruce meets black spruce: dispersal, post-fire establishment, and growth in a warming climate. *Ecological Monographs*, **78**, 489–505.

Chapter 3

Soil chemistry drives above- and belowground plant traits in alternative successional pathway

3.1. Abstract

Understanding how the environment drives functional trait composition is important to understand what drives the functioning of ecosystems. Ecosystem functioning includes its properties such as biodiversity and I questioned whether soil parameters were selecting for a specific suite of traits and a previously observed decrease in functional diversity. Using selected soil parameters, plant traits and species abundances in nine heath and four forest sites in Eastern Canada, I conducted a combined analysis using RLQ and fourth corner methods to examine links between a plant trait matrix and plot level soil parameters, mediated by species abundances. Both above- and belowground traits in heaths were negatively linked with heath soil chemistry. Leaf dry matter content was negatively linked to available NH_4^+ and ericoid mycorrhizal association was negatively linked to soil pH, total phenols, and available NH_4^+, NO_3, and P. The formation of post-fire heaths results in soil conditions that favour a specific suite of traits. Members of Ericaceae, through formation of associations with ericoid mycorrhizae are best suited to the nutrient poor conditions present in heaths. It is not known if they are directly responsible for generating the nutrient poor conditions through soil feedbacks but possible links are suggested.

Keywords: Soil nutrients; RLQ; fourth-corner; mycorrhizae; LDMC; soil feedback

3.2. Introduction

Understanding how plant communities assemble has long been a topic of interest among ecologists, and the processes that govern community assembly have been categorized by Keddy (1992) into assembly and response rules. Assembly rules are those which determine what genotypes can establish and eventually reproduce in a given area; response rules are those that determine what set of traits will allow the established genotypes to persist should habitat factors change. Therefore, finding the link between environmental parameters and plant traits can allow ecologists to determine the assembly and responses rules of a given ecosystem. These two sets of rules essentially describe what habitat filters may exist in an area and how they act to filter out species lacking the necessary traits; the result is a community composed of members all possessing a set of pre-determined traits, as defined by the habitat. Many examples of habitat filters can be found in the literature, ranging from disturbance mediated abiotic filters to biotic filters imposed by dominant species. For example, Jung et al. (2010) showed that in high flooding conditions, maximum plant height above flood levels and high specific leaf area (SLA) are selected by the abiotic filter as successful traits and only species possessing those traits are able to establish in that area. Fire severity, defined in part by the amount of residual organic matter (ROM) remaining after fire, has been shown to impose an abiotic filter on plant communities by several authors (Siegwart Collier and Mallik 2010; Shenoy et al. 2011). In these studies, a threshold in the organic layer depth following a fire determined what type of plant community would emerge based on the regenerative traits of potential colonizers. Habitat filtering can also increase depending on disturbance intensity or land use intensity (Johnstone et al. 2010; Pakeman 2011; Lasky et al. 2013).

Habitat filters can arise through impacts that plants have on their surroundings. These feedbacks have large implications for biodiversity. Generally, negative feedbacks limit the productivity of the species generating the feedback and are thought to promote diversity and species coexistence, whereas positive feedbacks inhibit potential competitors and result in lower diversity (Revilla et al. 2013). Dominant members of a plant community can also generate positive feedbacks, through their physical or chemical traits, which act as biotic filters. The ericaceous shrub *Kalmia angustifolia* (hereafter referred to as *Kalmia*) can regenerate vegetatively and quickly dominate post-fire seedbeds and interfere with black spruce regeneration within the first four years following a fire (Mallik 1995), essentially filtering out species that regenerate primarily by seed. Filters may also be imposed by dominant species as they condition the surrounding soil and generate plant-soil feedbacks (PSF), regulating microbial populations or limiting essential nutrients (Adamczyk et al. 2013). PSF may arise through litter quality (Miki and Kondoh 2002; Carbognani et al. 2014; Eichenberg et al. 2015), alteration of soil nutrient status (Suding et al. 2004; Bloom and Mallik 2006; Joanisse et al. 2009) or through the (in)activity of soil microbial community (Zeng and Mallik 2006; Perkins and Nowak 2013; St. Martin and Mallik 2016).

I studied the effects of soil parameters on community assembly and composition in *Kalmia* heaths in Eastern Canada. Low severity fires often lead to heath succession over forest succession (Siegwart Collier and Mallik 2010). Once established as a dominant species, *Kalmia* has certain effect traits that modify its habitat, suppressing the regeneration of a black spruce forest ensuring its continued dominance. *Kalmia* roots compete intensively for soil N and P in nutrient poor acidic soils (Yamasaki et al. 2002, Mallik et al. 2016), and it possesses the ability to sequester nitrogen in tannin-protein complexes that are readily available to their own ericoid mycorrhizae (Joanisse et al. 2008). *Kalmia* may also inhibit black spruce regeneration through allelopathy. Zhu and Mallik (1994) isolated eight phenolic compounds found in *Kalmia* leaf litter, humus and root leachates, all of which were shown to inhibit black spruce germination and primary root growth. In forest ecosystems, effect traits of black spruce which may keep *Kalmia* in check have not been confirmed, although limitation of light in closed canopy forests is thought to be a prominent factor (Mallik et al. 2012). Following low severity fires, an abiotic filter, high residual organic matter filters out seed regenerating species by lowering seedbed quality (Siegwart Collier and Mallik 2010; Mallik et al. 2010). But species with high sprouting potential that should be favoured by this filter exhibit little to no abundance in heaths (e.g. *C. borealis*, *A. nudicaulis*, and others). I asked the question: are soil parameters associated with the dominance of *Kalmia* acting as a secondary abiotic filter, which is responsible for the observed loss of functional diversity in post-fire heath? I hypothesized that low soil nutrient concentrations in heath is a main driver of this loss, in contrast to forest soils which are less limiting and therefore allow for a greater diversity of functional traits.

3.3. Materials and Methods

3.3.1. Study site description

I conducted this study in and around Terra Nova National Park (Lat. 48’33°N, Long. 53’58.8°W) in the Central Newfoundland ecoregion of the Boreal Shield ecozone (Damman 1983). Mean summer and winter temperatures are 13 °C and -5 °C respectively and the area receives average annual precipitation of 801 to 1200 mm, of which approximately 30% is snowfall (Environment Canada 2017). The soils of the area are nutrient poor podzolic gravel-loam (Soil Classification Working Group 1998). Forests are dominated by trees such as *P. mariana, Abies balsamea* (L.) Mill., mixed with *Betula papyrifera* Marsh., *Populus tremuloides* Michx., and to a lesser extent, *Larix laricina* (du Roi), Koc, and *Acer rubrum* L. with understory ericaceous shrubs such as *R. groenlandicum* and *Vaccinium angustifolium* Aiton. Herbaceous plants such as *Gaultheria hispidula* (L.), Muhl. ex Bigelow, *Linnaea borealis* L. *Cornus canadensis* L., *Clintonia borealis* (Aiton) Raf*.,* mosses such as *Pleurozium schreberi* (Brid.) Mitt., *Dicranum* spp. Hedw., *Ptilium crista-castrensis* (Hedw.) De Not., *Hylocomium splendens* (Hedw.) Schimp., and *Cladina* spp. lichens constitute the ground vegetation. A combined effect of active fire suppression and low-severity wildfires created many *Kalmia* dominated heaths in the study area (Mallik 1995; Siegwart-Collier and Mallik 2010). *Kalmia* heaths are interspersed with *P. mariana* and *Larix laricina* Koch seedlings and saplings. *Rhododendron canadense* (L.) Torr, *R. groenlandicum* (Oeder) Kron and Judd, and *Vaccinium angustifolium* (Aiton) are subordinate to *Kalmia*. Ground cover is dominated by fruticose lichens such as *Cladonia cristatella* Tuck*.,* and *Cladina rangiferina* (Aiton) Raf. (Damman 1964).

I selected study sites based on time since fire, dominant vegetation type and residual organic matter depth (*sensu* Siegwart Collier and Mallik 2010). This method of site selection resulted in two types of study systems: naturally regenerating forests and *Kalmia* heaths, both of which were dominated by *P. mariana* before fire. I selected sites representing the two successional pathways (forest and heath): nine heath sites aged 13 to 52 years since fire and four forest sites aged 12 to 80 years since fire. Time since fire was obtained from Power (2000). Due to limited frequency of high severity fires in the area, naturally regenerating forest sites were very resulting in a disproportionate numbers of heath and forest sites.

3.3.3. RLQ Matrices

In each site I placed 10 randomly located 2 x 2 m quadrats. Species cover was estimated visually using the nomenclature of VASCAN (Database of Vascular Plants in Canada; Canadensys 2015) to form a plot by species matrix (L table). Seven soil parameters were selected for this study. In each plot three soil cores were collected from each plot using a Eijkelkamp split tube sampler (Hoskin Scientific, Burlington, Ontario) 40 cm long and 5.5 cm in diameter. Cores were collected throughout the organic layer, any mineral soil composing the Ae layer was removed prior to storage. Mineral soil was not considered in the study design because Inderjit and Mallik (1999) showed that in sites dominated by *Kalmia*, N and P concentrations were 5-10 times higher in the organic layer than mineral soil. Depth of organic matter was measured upon core extraction and then the three cores were combined to form a composite sample for each plot. An additional core was obtained for bulk density. Available NH_4^+ and NO_3 were determined using a KCl extraction followed by continuous-flow auto-analysing. Available P was determined using the Mehlich III method, total phenols by the Folin-Ciocaltreau method, and pH using a 1:10 soil water mixture. Some plots had very little organic matter yielding insufficient soil to perform all tests. These plots were removed from the final analysis (n = 110). Seven soil parameters comprised the environmental parameters by plot matrix (R table). Mean values of soil parameters were compared using a Kruskal-Wallis test. Due to the greater proportion of plots being in heath sites, the data were not normally distributed (skewed left) and therefore a non-parametric test was used. Having said that, the combined RLQ-4th corner method (described below) includes a randomization step with 49 999 permutations, addresses the low statistical power stemming from the unavoidable imbalanced design.

I selected four aboveground traits: specific leaf area (SLA), leaf dry matter content (LDMC), seed mass, and maximum height, and two belowground traits: specific root length (SRL) and type of mycorrhizal association. The selected traits represent nutrient economics and reproductive strategies employed by plants in post-fire community assembly. I measured SLA as the ratio of fresh leaf area to leaf dry mass, and LDMC as the ratio of fresh leaf mass to dry leaf mass; height as distance from the ground to the highest photosynthetic tissue and SRL as the ratio of length of absorptive roots with diameter < 2 mm to dry root mass. A detailed protocol for trait measurement can be found in Cornelissen *et al*. (2003). Seed mass was obtained from Bonner and Karrfalt (2008) and mycorrhizal association from literature. Cryptogam species were not included in the calculations due to the difficulty in incorporating cryptogamic traits analogous to those possessed by vascular plants (St. Martin and Mallik 2017). These six traits were used to compile the trait by species matrix (Q table).

3.3.4. Statistical analysis

Two methods have been developed that aim to link environmental variables to plant traits: the RLQ method (Dolédec et al. 1996) and the fourth-corner method (Legendre et al. 1997). Both have been employed successfully in past studies but each has its limitations. The RLQ is a multivariate ordinal method that places environmental variables and traits along orthogonal axes based on their links to species abundances. In other words, through correspondence analysis, it depicts the links between environment and species abundances (R and L tables), and species abundances and traits (L and Q tables). If either of those scenarios does not show a link, then it cannot be concluded that environment and traits (R and Q tables) are linked. This gives a graphic visualization of how the three parameters are related but does not provide statistical significance to any of the links. The fourth corner method applies a Monte-Carlo permutation test to provide statistical significance, yet it is a bivariate analysis and does so only for single environment-trait pairs. Dray et al. (2014) have developed a technique that links both methods and allow for a graphical representation of the links along with statistical significance. The results of the fourth corner method are plotted on the axes obtained from the RLQ analysis, effectively combining both methods and allowing for a more complete analysis of how plant traits are linked to the environment.

The detailed procedure used to perform the analyses is outlined in the supplemental material contained in Dray et al. (2014). Briefly, first an RLQ analysis was performed on the three tables. Correspondence analysis was performed on the species table to obtain site and species scores to use as weights for analysing the environment and trait data respectively. Using these weights, correspondence analysis was also applied to the environment and trait tables; as variables in each consisted of continuous and categorical traits, the method employed by Hill and Smith (1976) was used. The RLQ analysis maximized the covariance between the environmental variables and species traits based on species abundances. Secondly, associations between environment and traits were tested using two permutation models, one permutes sites (columns in L table) and another permutes species (rows in L table). Permutations were repeated 49 999 times to reduce likelihood of Type 1 error and p-values were adjusted for multiple comparisons. Finally, RLQ scores were used as traits and environmental variables and the significant associations of the fourth corner method were represented in a colour coded table. The permutation tests also served to partially account for the unbalanced experimental design and low sample sizes of forest sites.

3.4 Results

All five chemical parameters (NH_4^+, NO_3, P, pH, and total phenols) were significantly higher in forest sites whereas the two physical parameters (OM depth and bulk density) showed no significant difference between sites (Kruskal-Wallis test, α = 0.05; Fig.3.1).

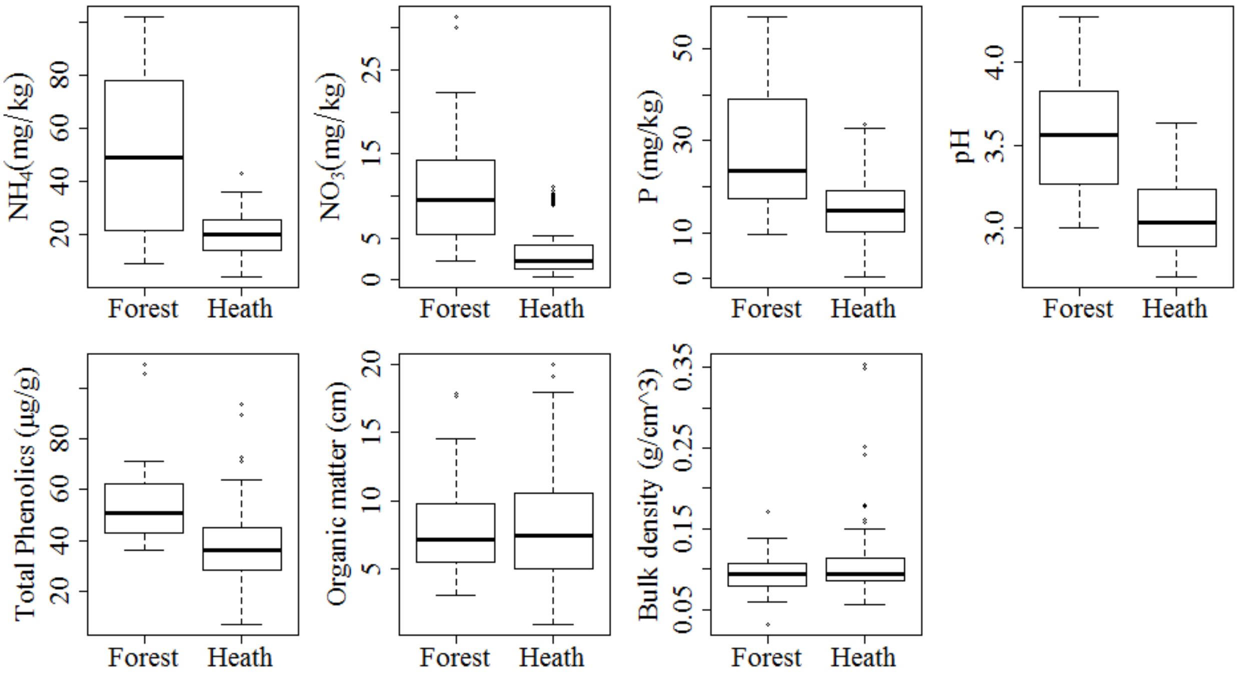


Figure 3.1. Measured soil parameters for forest and heath sites (n = 109).

The RLQ analysis yielded two axes, axis one having an eigenvalue of 1.63 and being strongly correlated with the L table (r = 0.53). Axis two depicted no significant pattern and low correlation (eigenvalue 0.03, r =0.13). The majority of environment parameters are positioned on the right hand side of axis 1 (Fig 3.2b.) and the traits positioned in this area include SLA, Height and all mycorrhizal associations with the exception of ericoid mycorrhizae (Myco.ERM). Traits positioned on the lefts of axis one include LDMC, SRL and Myco.ERM (Fig. 3.2b). The positions of the species show strong clustering. All ericaceous species are positioned on the left of the axis and all other species are on the right of the axis (Fig. 3.2c).

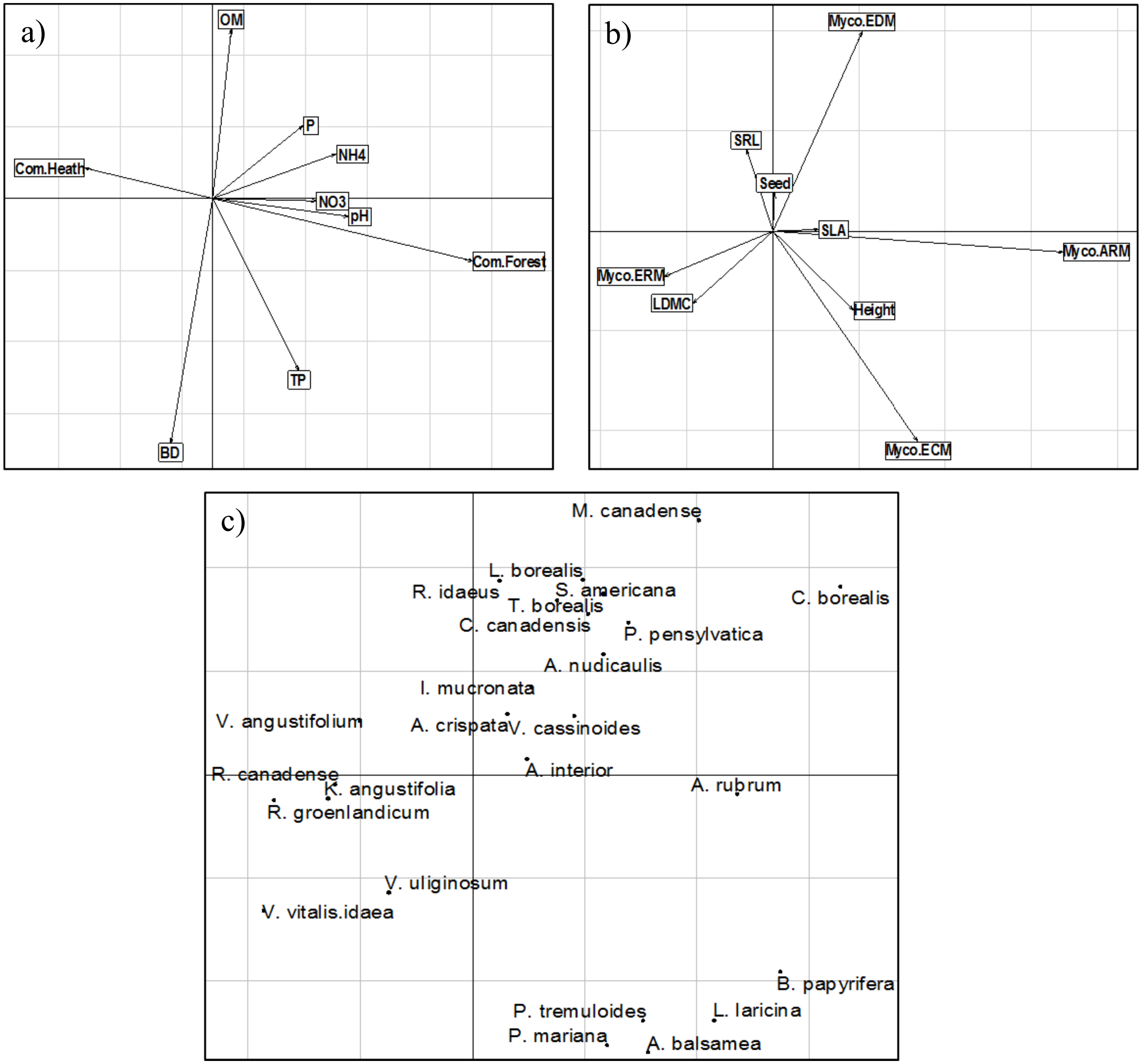
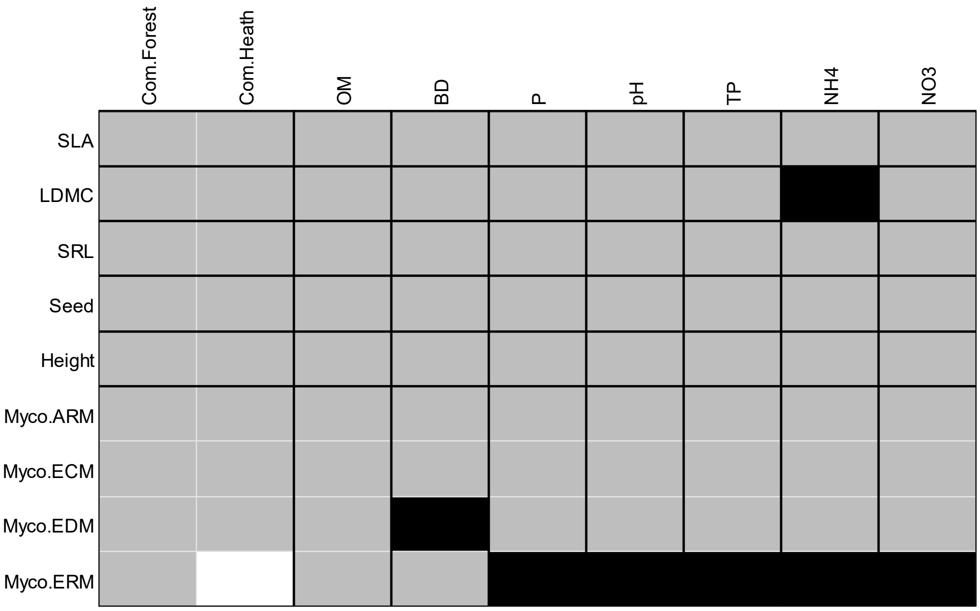


Figure 3.2. Results of RLQ analysis depicting the position of (a) environmental variables, (b) plant traits, and (c) species along the same two orthogonal axes. See Appendix II for full species names**.**

After adjusting the p-value for multiple comparisons, the fourth corner test revealed eight significant links between plant traits and environmental variables (Fig. 3.4). Endomycorrhizal (MYCO.EDM) associations were negatively linked to soil bulk density (BD) and LDMC was negatively associated with soil NH_4^+. Ericoid mycorrhizal associations were positively linked to heath communities and negatively linked to all five chemical soil parameters: NH_4^+, NO_3, P, pH, and total phenols (TP).

When the RLQ analysis was combined with the fourth corner analysis (Fig 3.3), a graphical representation of statistically significant and multivariate links between environment and traits was revealed. Axis 2 had low explanatory power (Fig. 3.2) and therefore did not show any links in the combined analysis depicted in Fig. 3.4. Height is positively associated with environment (AxcR1); traits negatively linked to environment are LDMC and ericoid mycorrhizal associations (Fig. 3.4). Plant traits (AxcQ1) were positively linked with forest succession and all chemical variables tested (N, P, pH, and TP); heath succession and soil bulk density were negatively linked. Organic matter depth was not linked with plant traits.



	Com.Forest	Com.Heath	OM	BD	P	pH	TP	NH4	NO3
SLA	▒	▒	▒	▒	▒	▒	▒	▒	▒
LDMC	▒	▒	▒	▒	▒	▒	▒	■	▒
SRL	▒	▒	▒	▒	▒	▒	▒	▒	▒
Seed	▒	▒	▒	▒	▒	▒	▒	▒	▒
Height	▒	▒	▒	▒	▒	▒	▒	▒	▒
Myco.ARM	▒	▒	▒	▒	▒	▒	▒	▒	▒
Myco.ECM	▒	▒	▒	▒	▒	▒	▒	▒	▒
Myco.EDM	▒	▒	▒	■	▒	▒	▒	▒	▒
Myco.ERM	▒	□	▒	▒	■	■	■	■	■

Figure 3.3. Results of fourth corner analysis depicting significant links between pairs of environmental parameters and plant traits. White cells denote significant positive link, black cells denote significant negative link, and grey cells depict no significant link.

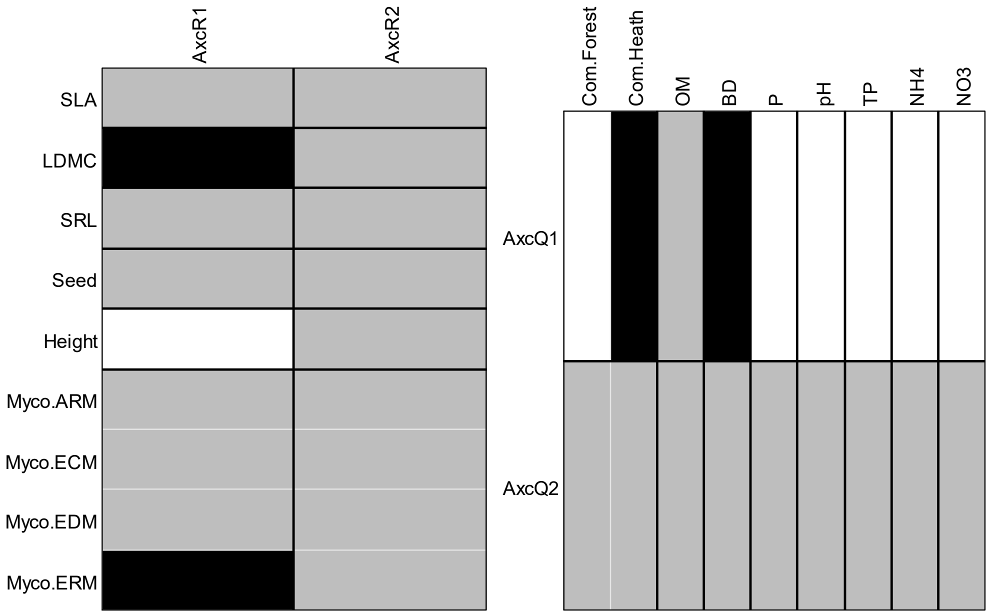


Figure 3.4. Combined RLQ and fourth corner analysis results. RLQ axes scores for environmental parameters (AxcR1 and AxcR2) and plant traits (AxcQ1 and AxcQ2) are used to show significant links. White cells denote significant positive link, black cells denote significant negative link, and grey cells depict no significant link.

3.5. Discussion

I found strong support of my hypothesis that soil nutrient status drives the functional composition of post-fire plant communities. Heath soils dominated by *Kalmia* have low pH and are low in available nutrients (Siegwart Collier and Mallik 2010). This agrees with the findings of other studies conducted in the area (Inderjit and Mallik 1996; Bloom and Mallik 2006) and confirms that post-fire ericaceous heaths are nutrient-limited habitats. In this study I have identified which plant traits allow stress-tolerant ericaceous species the ability to flourish in post-fire heaths. I showed that species with high LDMC and those capable of forming mutualistic associations with ericoid mycorrhizae are likely to be successful in heath soils.

The RLQ analysis revealed a strong clustering of species along the main axis: all ericaceous species were separated from species forming associations with all other types of mycorrhizae. When combined with the fourth corner analysis, the results show that association with ericoid mycorrhizae is negatively linked with inorganic soil N as well as soil P. Often in ericaceous heaths, nitrogen is sequestered in forms unavailable to non-ericoid species (Joanisse et al. 2009) and locked up into organic complexes. Arbuscular mycorrhizal plants have limited access to organic N (Cornelissen et al. 2001; Smith and Read 2008), and only selected ectomycorrhizal fungal species have a limited ability to supply their hosts with required nutrients (Nilsson et al. 1993; Zeng and Mallik 2006; St. Martin and Mallik 2016). The results of this analysis also suggest a potential cause of this nutrient limitation. Lower pH in heath soils compared to forest soils would also decrease N and P mobility, exasperating the nutrient acquisition limitation of non-ericoid species in heath communities. Results also showed that LDMC is negatively linked to soil NH_4^+; in N limiting systems, a conservative use of N is an ideal strategy. High LDMC is not only an ideal resource use strategy in nutrient poor soils but it also drives the nutrient levels even lower (Laughlin et al. 2015). Plant litter with high LDMC has been repeatedly shown to decompose slowly (Carbognani et al. 2014; Eichenberg et al. 2015), decreasing the rates of nutrient cycling where litter inputs containing high LDMC are prevalent. Plants with traits ill-suited to these sites fail to thrive, driving a loss of functional diversity as shown in Chapter 2.

LDMC being positively linked with heath succession and negatively linked with forest succession suggests other mechanisms at play that were not anticipated. Recently, it has been suggested that high LDMC is a trait favorable to tolerate photoinhibition in open plots (Gavinet et al. 2016). Heaths possess very little tree cover and species therein are continually exposed to high light; species requiring moderate to high shade would experience less success in these conditions due to photoinhibition. *Kalmia* has been shown to possess maximum photosynthetic rates under full light (Mallik et al. 2012). Also, high LDMC renders foliage less palatable to herbivores (Westboy et al. 2002) and species that establish in a heath with low LDMC may be preferentially selected by herbivores than the majority of other heath species with low LDMC, resulting in their continued suppression. The high density of moose (*Alces alces*) in the study area leads to high herbivory, which may also be a significant factor behind its species-poor composition (Ellis and Leroux 2017).

The results of this study cannot confirm that the nutrient poor conditions linked with the identified traits are a direct result of a positive feedback generated by *Kalmia* and other ericads but it may be the case. The composition of adjacent unburned stands is typical of mature black spruce boreal forest, dominated by black spruce intermixed with *Abies balsamea, Populus tremuloides,* and *Betula papyrifera*. This would indicate that pre-fire soil conditions were once favourable to the type of plant community seen in forest succession and that the soils have changed after heath formation following the fires. While low to moderate severity fires have a neutral to positive effect on soil nutrient status (Brais *et al.* 2000; Smithwick *et al.* 2005), with nutrient concentrations generally decreasing over time. This is not typically the case observed in post-fire heaths. Bloom and Mallik (2006) reported no change in the concentration of soil nutrients over time in post-fire *Kalmia* heaths. The N and P concentrations reported in this study are consistently lower in *Kalmia* heaths than in post-fire forests, even though the sites span the same time since disturbance (13-80 yrs). The most significant change following the fire is the widespread dominance of *Kalmia* in all heath sites. It is very likely that the decrease in pH and nutrient availability observed in heaths is due to the shift in community composition, from black spruce dominated forests to *Kalmia* dominated heath. Since *Kalmia* dominates post-fire sites through vegetative sprouting in a period as short as five years (Mallik 1995), it is quite possible that the input of its low quality litter and associated beneficial biota (ericoid mycorrhiza), may generate a positive feedback for itself as well as other ericads which thrive in similar low nutrient conditions. Previous studies concerning ericaceous species were predominantly lab or greenhouse based, focusing on growth, metabolic activity, and distribution (Smith and Read 2008; Bueno et al 2017; Martino et al. 2018). Competition-based field studies typically involved only one ericad and a single competing species (Thiffault et al 2012; Wang et al 2017). This study is the first of its kind to employ a community based approach and successfully shows how ericoid mycorrhizal roots are superior to all other mycorrhizal types when nutrient levels are limiting. I have shown that four species of Ericaceae are all able to maintain higher abundance than their taller, or faster growing, non-ericoid neighbours. This contributes to the growing body of literature contradicting the principle of limiting similarity whereby closely related species are thought to be incapable of significant co-existence (Funk and Wolf 2016; Li et al. 2017)

3.6. Conclusions

Post-fire ericaceous heaths arising from low severity fires are habitats with very low soil nutrient concentrations, and this acts as a strong environmental filter. The low nutrient levels may be a result of ericaceous dominance and species that do not form associations with ericoid mycorrhizae perform poorly in these areas. What is seen in post-fire heaths is a clear segregation of a plant community along the lines of strategies described by Grime (1977). R-type species are rare as the post-disturbance soil is readily covered by the rapid spread of *Kalmia* and other ericaceous shrubs; C-type plants such as trees are unable to flourish due to the low nutrient levels. This leaves the S-type plants, able to tolerate the stressful soil conditions, and persist despite their slower growth rates. Being free of competition from many of the species in the regional species pool, slower growth is not a hindrance and ericaceous dwarf shrubs are allowed to exist as the upper canopy and experience full light conditions. Since they possess leaves with high LDMC, this enforces a feedback loop, as the majority of litter contributing to soil is of low quality and decomposes slowly, keeping soil nutrient at limiting levels. The ability of non-ericoid plants to establish in heaths, and potentially modify the soil through their own litter and soil biota, has been poorly studied (with the exception of a few) and should be a focus of ongoing study.

3.7 References

Adamczyk, S., Kiikkila, Kitunen, V., Smolander, A. 2013. Potential response of soil processes to diterpenes, triterpenes and tannins: Nitrification, growth of microorganisms and precipitation of proteins. *Applied Soil Ecology*, **67**, 47-52.

Bever, J. D., Westover, K. M., Antonovics, J. 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology*, **85**: 561-573.

Bloom, R. G., Mallik, A. U. 2006. Relationships between ericaceous vegetation and soil nutrient status in a post-fire *Kalmia angustifolia*-black spruce chronosequence. *Plant and Soil*, **289**: 211-226.

Brais, S., David, P., Ouimet, R. 2000. Impacts of wild fire severity and salvage harvesting on the nutrient balance of jack pine and black spruce boreal stands. *Forest Ecology and Management*, **137**, 231–243.

Bueno, C.G., Moora, M., Gerz, M., Davison, J., Öpik, M., Pärtel, M., Helm, A., Ronk, A., Kühn, I., Zobel, M., 2017. Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. *Global Ecology and Biogeography*, **26**, 690–699.

Carbognani, M., Petraglia, A., Tomaselli, M. 2014. Warming effects and plant trait control on the early-decomposition in alpine snowbeds. *Plant and Soil*, **376**, 277–290.

Cornelissen, J., Aerts, R., Cerabolini, B., Werger, M., Heijden, M. van der,. 2001. Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia*, **129**, 611–619.

Dakora, F. D., Phillips, D. A. 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant and Soil*, **245**: 35-47.

Damman, A. W. H. 1964. Some forest types of central Newfoundland and their relationship to environmental factors. *Forest Science Monographs*, **8**, 1-62.

Damman, A. W. H. An ecological subdivision of the island of Newfoundland. In South, R. (ed.) 1983. *Biogeography and Ecology of the Island of Newfoundland*. Dr. W. Junk Publishers, The Netherlands, pp. 163-206.

Dolédec, S., Chessel, D., ter Braak, C. J .F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environtal and Ecological Statistics*, **3**, 143–166.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., ter Braak, C .J. F. 2013. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, **95**, 14–21.

Eichenberg, D. 2015. Shifts in community leaf functional traits are related to litter decomposition along a secondary forest succession series in subtropical China 8, 401–410. *Journal of Plant Ecology*, **8**: 401-410.

Elgersma, K. J., Yu, S., Vor, T., Ehrenfeld, J. C. 2012. Microbial-mediated feedbacks of leaf litter on invasive plant growth and interspecific competition. *Plant and Soil*, **356**: 341-355.

Ellis, N. M., Leroux, S. J. 2017. Moose directly slow plant regeneration but have limited indirect effects on soil stoichiometry and litter decomposition rates in disturbed maritime boreal forests. *Functional Ecology*, **31**: 190-801

Funk, J.L., Wolf, A.A. 2016. Testing the trait-based community framework: Do functional traits predict competitive outcomes? *Ecology*, **97**, 2206–2211.

Gavinet, J., Prévosto, B., Fernandez, C. 2016. Introducing resprouters to enhance Mediterranean forest resilience: importance of functional traits to select species according to a gradient of pine density. *Journal of Applied Ecology*, **53**, 1735–1745.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**: 902-910.

Hill, M. O., and Smith, A. J. E. 1976. Principal component analysis of taxonomic data with multi-state discrete characters. *Taxon*, **25**, 249-255.

Inderjit, Mallik, A. U. 1999. Nutrient status of black spruce (*Picea mariana* [Mill.] BSP) forest soils dominated by *Kalmia angustifolia* L. *Acta Oecologia*, **20**, 87-92.

Joanisse, G. D, Bradley, R. L, Preston, C. M., Bending, G. D. 2009. Sequestration of soil nitrogen as tannin–protein complexes may improve the competitive ability of sheep laurel (*Kalmia angustifolia*) relative to black spruce (*Picea mariana*). *New Phytologist*, **181**: 187-198.

Johnstone, J. F., Hollingsworth, T. N., Chapin III, F. S., Mack, M. C. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, **16**: 1281-1295.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, **3**, 157-164.

Laughlin, D. C., Richardson, S. J., Wright, E. F., Bellingham, P. J. 2015. Environmental filtering and positive plant litter feedback simultaneously explain correlations between leaf traits and soil fertility. *Ecosystems*, **18**, 1269–1280.

Lasky, J. R., Sun, I-F., Su, S.-H., Chen, Z.-S., Keitt, T. H. 2013. Trait-mediated effects of environmental filtering on tree community dynamics. *Journal of Ecology*, **101**: 722-733.

Li Y., Shipley B., Price J. N., Dantas V. de L., Tamme R., Westoby M., Siefert A., Schamp B. S., Spasojevic M. J., Jung V., Laughlin D. C., Richardson S. J., Bagousse-Pinguet Y. L., Schöb C., Gazol A., Prentice H. C., Gross N., Overton J., Cianciaruso M. V., Louault F., Kamiyama C., Nakashizuka T., Hikosaka K., Sasaki T., Katabuchi M., Frenette Dussault C., Gaucherand S., Chen N., Vandewalle M., Batalha M. A., Vesk P. 2017. Habitat filtering determines the functional niche occupancy of plant communities worldwide. *Journal of Ecology*, 106, 1001–1009.

Legendre, P., Galzin, R., Harmelin-Vivien, M.L., 1997. Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology*, **78**, 547–562.

Mallik, A. U. 1995. Conversion of temperate forests into heaths: role of eco-system disturbance and ericaceous plants. *Environmental Management.*, **19**, 675-684.

Mallik, A. U., Wang, J. R., Siegwart-Collier, L. S., Roberts, B. A. 2012. Morphological and ecophysiological responses of sheep laurel (*Kalmia angustifolia*) to shade. *Forestry*, **85**, 513-522.

Mallik, A. U., Bloom, R. G., Whisenant, S. G. 2010. Seedbed filter controls post-fire succession. *Basic and Applied Ecology*, **11**, 170–181.

Mallik, A. U., Biswas, S. R., Sieqwart Collier, L. C. 2016. Belowground interactions between *Kalmia angustifolia* and *Picea mariana*: roles of competition, root exudates and ectomycorrhizal association. *Plant and Soil*, **403**, 471–483.

Miki, T., and Kondoh, M. 2002. Feedbacks between nutrient cycling and vegetation predict plant species coexistence and invasion. *Ecological Letters*, **5**: 624-633.

Nilsson, M.- C., Högberg, P., Zackrisson, O., and Fengyou, W. 1993. Allelopathic effects by *Empetrum hermaphroditum* on development and nitrogen uptake by roots and mycorrhizae of *Pinus silvestris*. *Canadian Journal of Botany*, **71**: 620-628.

Pakeman, R. J. 2011. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. *Journal of Ecology*, **99**: 1143-1151.

Perkins, L. B., and Nowak, R. S. 2013. Native and non-native grasses generate common types of plant–soil feedbacks by altering soil nutrients and microbial communities. *Oikos***, 122**: 199-208.

Shenoy, A., Johnstone, J. F., Kasischke, E. S., Kielland, K. 2011. Persistent effects of fire severity on early successional forests in interior Alaska. *Forest Ecology and Management*, **261**: 381-390.

Siegwart Collier, L. C., Mallik, A. U. 2010. Does post-fire abiotic habitat filter create divergent plant communities in black spruce forests of eastern Canada? *Oecologia*, **164**: 465-477.

Smith, S. E., Read, D. J. 2008. *Mycorrhizal Symbiosis* 3rd ed. Academic Press, New York, 814 pp.

Smithwick, E.A.H., Turner, M.G., Mack, M.C., Chapin, F.S. 2005. Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. *Ecosystems*, **8**, 163–181.

St. Martin, P., Mallik, A.U. 2016. Growth release of stunted black spruce (*Picea mariana*) in *Kalmia* heath: the role of ectomycorrhizal fungi and near-ground microclimate. *Canadian Journal of Forest Research*, **46**, 666–673.

Suding, K. N., Larson, J. R., Thorsos, E., Stelzer, H., Bowman, W. D. 2004. Species effects on resource supply rates: do they influence competitive interactions? *Plant Ecology*, **175**: 47-58.

Thiffault, N., Picher, G., Auger, I. 2012. Initial distance to *Kalmia angustifolia* as a predictor of planted conifer growth. *New Forests*, **43**, 849–868.

Wang, L., Otgonsuren, B., Godbold, D.L. 2017. Mycorrhizas and soil ecosystem function of co-existing woody vegetation islands at the alpine tree line. *Plant and Soil*, **411**, 467–481.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.

Zeng, R. S., Mallik, A. U. 2006. Selected ectomycorrhizal fungi of black spruce (*Picea mariana*) can detoxify phenolic compounds of *Kalmia angustifolia. Journal of Chemical Ecology*, **32**: 1473-1489.

Zhu, H., Mallik, A. U. 1994. Interactions between *Kalmia* and black spruce: isolation and identification of allelopathic compounds. *Journal of Chemical Ecology*, **20**: 407-421.

Chapter 4

Predicting successional states using dominant species response and effect traits by fuzzy logic modeling

4.1. Abstract

Natural ecosystems may undergo state shifts following changes in disturbance regime. Pre-disturbance dominant species lacking the necessary response traits to deal with the new disturbance regime may be replaced by new dominant species. Previous research identified a link between response and effect traits that are responsible for state shifts in order to predict succession. However, it mostly focused on a single life form and rarely considered the effects of pre-disturbance communities on post-disturbance community assembly. Here I present evidence suggesting that one can accurately predict the establishment of either vegetatively sprouting shrubs or seed regenerating trees by employing a fuzzy logic modeling approach. I combined community flammability, fire weather indices, organic matter thickness, and pre-fire propagule density to predict post-fire community assembly. A Mamdani-type fuzzy inference system based on 141 antecedent-consequence rules correctly identified pre-fire conditions where a forest may lose ecological resilience and risk being replaced by ericaceous heath. In general, sites having moderate to high organic matter depth, composed of less flammable species, and with moderate to high ericaceous shrub cover are likely to experience a state shift after fire. This model can benefit ecologists studying community assembly and land managers to predict successional change after fire.

Keywords: Mamdani; fire; black spruce; state shift; flammability

4.2. Introduction

State shifts in plant communities are a natural occurrence in many ecosystems. State shifts can be initiated when disturbance regimes are altered through changes in climate or anthropogenic disturbance. A shift in disturbance regime can create conditions in which species other than the typical dominants are favoured; the new species possess a set of traits better suited to regenerate and/or better suited to resisting the new disturbance regime. For example, if flooding levels were to increase past normal heights, taller plants with high specific leaf area would be selected over shorter ones (Jung et al. 2010). Or if fires burned more severely due to drier climates, this favours trees with smaller seeds over trees with larger seeds (Johnstone and Chapin III 2006; Johnstone et al. 2010). State shifts can also occur if disturbances are compounded (Bergeron and Dansereau 1993; Jasinski and Payette 2005). All the above examples are cases where a dominant species is replaced by one in a similar life form group, i.e. a grass replacing a grass or a tree replacing a tree. Since the new dominant possesses a similar trait syndrome to the one it replaced (i.e. both are from the same functional group), a state shift should have a minimal impact on the overall diversity of functional traits and general functioning of the ecosystem (Naeem 1998; Laliberté et al. 2010). What would be the implications if the new dominant life form was significantly different from the one it replaced? It would present a possibility that the overall functional diversity of a system could change, potentially in a negative way (Suding et al. 2008; Girard et al. 2009). A significant shift in functional composition could in turn impact disturbance regimes. Pyrogenic communities are those composed of plants whose traits promote high severity fires, and thereby benefit from frequent or severe fires, or both (Odion et al. 2010). The debate concerning whether plant traits have evolved to promote fires is ongoing and beyond the scope of this paper. Nevertheless, the composition of a plant community can influence the severity of a fire through biomass, morphology, and litter of its constituent species. The severity of a fire in turn can promote certain response traits over others.

Cases where disturbances cause one functional group to be replaced by another have been reported in a variety of systems. Grazing by reindeer and caribou in tundra ecosystems can lead to a shift in vegetation states dominated by lichens, mosses, or dwarf shrubs (Van der Wal 2006). Another example is the succession of ericaceous dwarf shrubs over tree species in many areas of the boreal forest. Following low severity fires or clear cut harvesting, areas that previously existed as forests are converted to heaths with well documented negative impacts on soil nutrients (Bloom and Mallik, 2004) and conifer regeneration (Mallik et al. 2010). It has been established that post-fire habitat filters create divergent communities in eastern Canada (Siegwart Collier and Mallik 2010). Other studies have found similar cases where response and effect traits of plant communities play a central role in succession (Lavorel and Garnier 2002). Effect traits of pre-disturbance communities impose legacy effects that select for certain response traits and influence post-fire community assembly, sometimes leading to alternate stable states (Johnstone et al. 2010; Jasinski and Payette 2005).

It is unknown to what degree legacies of pre-fire communities in the black spruce (*Picea mariana* (black spruce) - *Kalmia angustifolia* (hereafter *Kalmia*) ecosystems of Newfoundland play in determining post-fire community assembly. Both black spruce and *Kalmia* are fire adapted species but their regeneration strategies differ considerably: black spruce possess semi-serotinous cones with many seeds that are able to germinate immediately after fire provided suitable seedbeds, whereas *Kalmia* has underground rhizomes that, if undamaged by the fire, may sprout quickly and dominate a site within four to five years (Mallik 1993). This dichotomy of response traits is the reason that the post-fire conditions of the habitat can act as a strong filter:

high levels of residual organic matter (ROM) impede the germination of seeds because of unfavourable seedbeds (Mallik et al. 2010) which harbour *Kalmia* rhizomes. Conversely, low levels of ROM make suitable seedbeds for black spruce seedling regeneration and contain very few *Kalmia* rhizomes, restricting recolonization by vegetative growth. The importance of ROM as a filter is dependent not only on the severity of fire, which will determine the amount of organic matter consumed, but also on the pre-fire abundance of *Kalmia* that controls the abundance of post-fire rhizomes, a source of its vegetative propagation. Thus, pre-fire community composition may influence post-fire assembly in two ways: community flammability acting on fire severity (effect trait) and pre-fire *Kalmia* abundance acting as the potential for post-fire vegetative sprouting (response trait) depending on fire severity. The importance of both abiotic and biotic factors to post-fire community assembly was noted by Boiffin et al. (2015), where the authors concluded that abiotic and biotic processes operate at broad and fine scales respectively.

Heath formation may occur naturally however it has increased concomitantly with an increase of anthropogenic influence on the landscape, namely fire suppression and prescribed burns. It is important to determine the susceptibility of an area to state shift from forest to heath as shown in that it is associated with a loss in functional diversity (Chapter 2). It is also necessary to determine whether the state shift results in an alternate stable state or simply a period of delayed succession. Evidence for alternate stable states has been provided by multiple studies (Jasinski and Payette 2005; Wirth 2008; Johnstone et al. 2010) where shifts in disturbance regimes favour new types of response traits, yielding new plant communities that are self-replacing through plant-soil feedbacks. Dominant species possess effect traits that influence post-disturbance habitat conditions, generating a positive feedback that favours their own response traits. However, should the disturbance regime shift or the local climate change, the feedback cycle can be disrupted, potentially allowing for a new dominant species. This new dominant may start to generate its own feedbacks that favour its own regeneration over that of the previous dominant. Very few studies reported on state shifts from closed canopy forest system to an open system such as when shrub species replace tree species as the dominant vegetation type (Mallik 2004; Girard et al. 2009). One may question if it is an artefact of limited investigation or the fact that shrub species cannot maintain dominance over tree species in a time scale of centuries (Mallik and Kravchenko 2018). Should the latter be correct, it would imply that the observed shrub dominance after disturbance, as in the case of conifer forests with ericaceous understories (Mallik 1993), is but a matter of delayed succession.

Many models have been developed to predict plant community succession yet to our knowledge none considered incorporating key plant response and effect traits in predicting post-fire succession. It remains unclear as to how the effect traits (flammability on fire severity) and response traits (seed vs. vegetative regeneration) of pre-disturbance communities directs the successional outcome. I used a fuzzy logic approach to explore the link between functional traits and post-disturbance community assembly; fuzzy logic is employed for decision making and risk assessment in cases where uncertainty about the system exists. My objective was to construct a model based on fuzzy logic by incorporating plant traits in a fashion that can be employed by researchers and land managers.

4.3. Methods

4.3.1. Fuzzy logic modelling

Fuzzy logic is a concept based on classical set theory developed by Zadeh (1965) as a means of analysing and predicting complex systems. This approach was readily embraced by various disciplines including engineering and computer science (Zadeh 2015). It has been successfully applied to support decision making in ecosystem management (Adriaenssens et al. 2004; Prato 2007), and modelling dynamics in terrestrial (Roberts 1996; Svoray et al. 2007; Glenz et al. 2008) and aquatic (Gutiérrez-Estrada et al. 2013; de Andrade et al. 2016) ecosystems. Fuzzy logic seems to be an ideal method in ecosystem management as it is able to compensate for uncertainties often associated with ecology such as incomplete data sets, microsite heterogeneity, and scale dependent temporal and spatial variations. It can also accommodate uncertainties inherent in human interactions: decisions often must be made by individuals who lack mathematical backgrounds, or lack the capability to develop and communicate the model to a broad audience (Marchini 2011).

Contrary to Boolean logic which applies a binary assignment to a variable (e.g. cold or hot), fuzzy logic considers a variable having a degree of truthfulness in the form of a membership function which ranges between 0 - 1. Consider for example temperature as an environmental gradient. In the traditional approach a temperature of 10 °C would be considered cold and 30 °C hot; the classification of input data is defined by sharp boundaries and crossing one to another requires passing some threshold value. It would assign a temperature of 10 °C and 30° C as having a 0.8 and 0.2 membership respectively to the cold category. The memberships would be opposite in the hot category. By softening the boundaries that define variables, fuzzy logic allows for variables to belong to two categories at once, and the transition from one state to another occurs along a gradient. This allows a model to be constructed using linguistic variables and rules rather than numerical variables and data, increasing its accessibility and transparency (Marchini 2011).

4.3.2. Model parameters

Pérez-Harguindeguy et al. (2013) developed a protocol for assigning the flammability of individual plant species based on their functional traits. The traits include twig dry matter content (TDMC), orders of ramifications (degree of branching along stems), standing fine litter (dead plant matter still attached to the plant), and presence of volatiles (strong aromas or tacky substances). These traits contribute to different aspects of fire behaviour, including the ease with which a fire begins, spreads, and how long it is sustained (Blackhall et al. 2017). All traits were categorical with a range of 1-5 with the exception of TDMC. TDMC was determined by dividing the oven-dry mass of a terminal twig by its fresh mass. TDMC was then converted to a categorical value by referencing Table 1 in Pérez-Harguindeguy et al. (2013). All other traits were assessed qualitatively. A modification was made to the protocol to account for the relative biomass of a species. This is important because biomass represents the amount of available fuel, which determines how long it can burn. Therefore, a categorical trait 'biomass' was added to the traits; ranging from 1-5 representing the gradient from herb to tree. Measuring these traits allows for species to be assigned a flammability class by averaging the five categorical traits of each species. For example, a species such as *Clintonia borealis.* which has little stem branching, low dry matter content in its stem, little to no standing litter, and low relative biomass receives a value of 1 in all categories and thus is assigned a flammability value of 1. *Picea mariana,* having twigs with high dry matter content, many orders of ramification, high standing litter, high levels of volatiles, and a large relative biomass receives values of 5, 3, 4, 3, 5 for each category respectively and thus is assigned a flammability value of 4. I determined flammability of the 25 most abundant species in the study area (Table 4.1).

Table 4.1. Species flammability measured using categorical functional traits: ramification order, standing dead litter, presence of volatiles, twig dry matter content (TDMC) and relative biomass.

Species	**Ramification**	**Litter**	**Volatiles**	**TDMC**	**Biomass**	**Flammability**
Picea mariana	5	3	4	3	5	4
Abies balsamea	5	3	4	2	5	3.8
Betula papyrifera	4	3	3	2	5	3.4
Acer rubrum	4	2	2	2	5	3
Prunus pensylvatica	4	2	2	3	4	3
Alnus crispata	4	3	1	3	3	2.8
Larix laricina	3	2	2	2	5	2.8
Populous tremuloides	4	2	1	2	5	2.8
Ilex mucronata	4	2	1	3	3	2.6
Vaccinium angustifolium	5	2	1	3	2	2.6
Rhododendron groenlandicum	4	2	1	3	2	2.4
Sorbus americana	3	2	1	2	4	2.4
Viburnum cassinoides	2	2	1	3	4	2.4
Amelanchier canadensis	3	2	1	2	3	2.2
Kalmia angustifolia	2	3	1	3	2	2.2

Table 4.1 (continued)

Species	Ramification	Litter	Volatiles	TDMC	Biomass	Flammability
Rhododendron canadense	3	2	1	3	2	2.2
Vaccinium uliginosum	4	2	1	3	1	2.2
Rubus idaeus	3	1	1	2	2	1.8
Linnaea borealis	2	2	1	2	1	1.6
Vaccinium vitalis-idaea	1	2	1	3	1	1.6
Aralia nudicaulis	1	1	1	2	1	1.2
Cornus canadensis	1	1	1	3	1	1.2
Maianthemum canadenses	1	1	1	2	1	1.2
Trientalis borealis	1	1	1	2	1	1.2
Clintonia borealis	1	1	1	1	1	1

Site flammability was calculated for nine heath and four forest sites of varying stages of succession. It was determined as the community-weighted mean flammability of all species in a site, weighted by their abundance. These data produced the input variable Community Flammability (CF) ranging from 0-5 and was assigned to three classes with the membership functions shown in Figure 4.1a. The second input variable, Fire Weather Index (FWI) was based on data obtained from the Parks Canada Newman Sound Fire Weather Index. The FWI was a rating system used to describe fire intensity and also used as an index of fire danger in forested areas of Canada. The FWI was determined using several climate and environmental parameters including fine fuel moisture code, duff moisture content, precipitation, and wind speed (Natural Resources Canada, 2017). The index ranges from 0-30 across four levels designated by Parks Canada and membership functions were assigned to each (Figure 4.1b). Together, these parameters model the severity of a fire such as how hot and how long a fire would burn given the amount of fuel available and the climatic conditions when fire is initiated.

The third model parameter, Pre-fire Organic Matter Depth (OM), is linked to fire severity in two ways: moisture content increases with depth and therefore combustibility decreases; fires of higher severity will consume a greater portion of the organic layer (Miyanishi and Johnson 2002). This is an important part of all fires as the amount of organic matter remaining largely determines which regeneration strategy will be favoured after fire (Siegwart Collier and Mallik 2010). OM depth ranged from 0-20 cm based on the mean OM depths measured in all plots of all sites as the possible range of OM depth prior to fire (Appendix IV). Membership functions were assigned for four categories (Figure 4.1c). The final input variable was Pre-fire *Kalmia* cover (PreK). This was selected as an input variable for two reasons. First, it indicates the regeneration potential for vegetatively regenerating plants. Even if conditions were such that vegetative sprouting could be promoted (low severity fire, high post-fire OM depth), if there are few rhizomes present before the fire, sprouting would be low simply due to low propagule density. Second, vegetative sprouting (or lack thereof) was used to represent the success of either regeneration strategy. The successful establishment of seed regenerating plants is dependent on the density of resprouting plants in the initial few years after a fire (Mallik and Kravchenko 2018). If sprouting plants regenerate in high densities, they effectively outcompete seedlings by their higher growth rate, attributed to carbohydrate reserves in surviving underground rhizomes.

This measure was based on the observed aboveground abundance of *Kalmia* in regenerating heaths and forests, as well as mature unburned stands (Chapter 2). It ranged from 0-100 and had three levels each with an associated membership function (Figure 4.1d).

The only output variable of the model was Post-fire *Kalmia* cover (PostK). Based on the extensive work of A.U. Mallik in post-fire landscapes in eastern Canada (Mallik 1993, 1994, 1995; Inderjit and Mallik 1999; Mallik and Inderjit 2001; Bloom and Mallik 2004, 2006; Siegwart Collier and Mallik 2010; Mallik et al. 2016; St. Martin and Mallik 2016; Mallik and Kravchenko 2018; and others) three categories of post-fire *Kalmia* cover were established. It was determined that *Kalmia* abundance four years following fire is a critical point (Bloom and Mallik 2004); if *Kalmia* exists at a relatively high abundance by that time (> 20% cover), progression of post-fire succession will most certainly lead to an ericaceous heath. PostK ranged from 0-100 consisting of three levels each with a respective membership function (Figure 4.1e).

4.3.3. Fuzzy inference system

Input and output variables were assigned membership functions based on both overall understanding and inference (Fig 4.1). A combination of field data and experience working in post-fire heaths spanning over 30 years were used to assign membership functions and 'If-Then' rules. A total of 141 rules encompassing the possible combinations of the four antecedent input variables were created. Rules were aggregated using the AND operator, which yields a fuzzy output set through the intersection of all fuzzy input sets, defining it as a Mamdani-type inference system (Mamdani and Assilian 1975). An example of a rule is as follows:

IF CF is medium AND FWI is high AND OM is high AND PreK is low THEN PostK is low

The fuzzy output set was then defuzzified using the ‘centroid’ method, which calculates the center of mass of the fuzzy output set and returns a single crisp output (Fig 4.2). The fuzzy inference system was built using MATLAB R2017b (The MathWorks, Inc. USA).

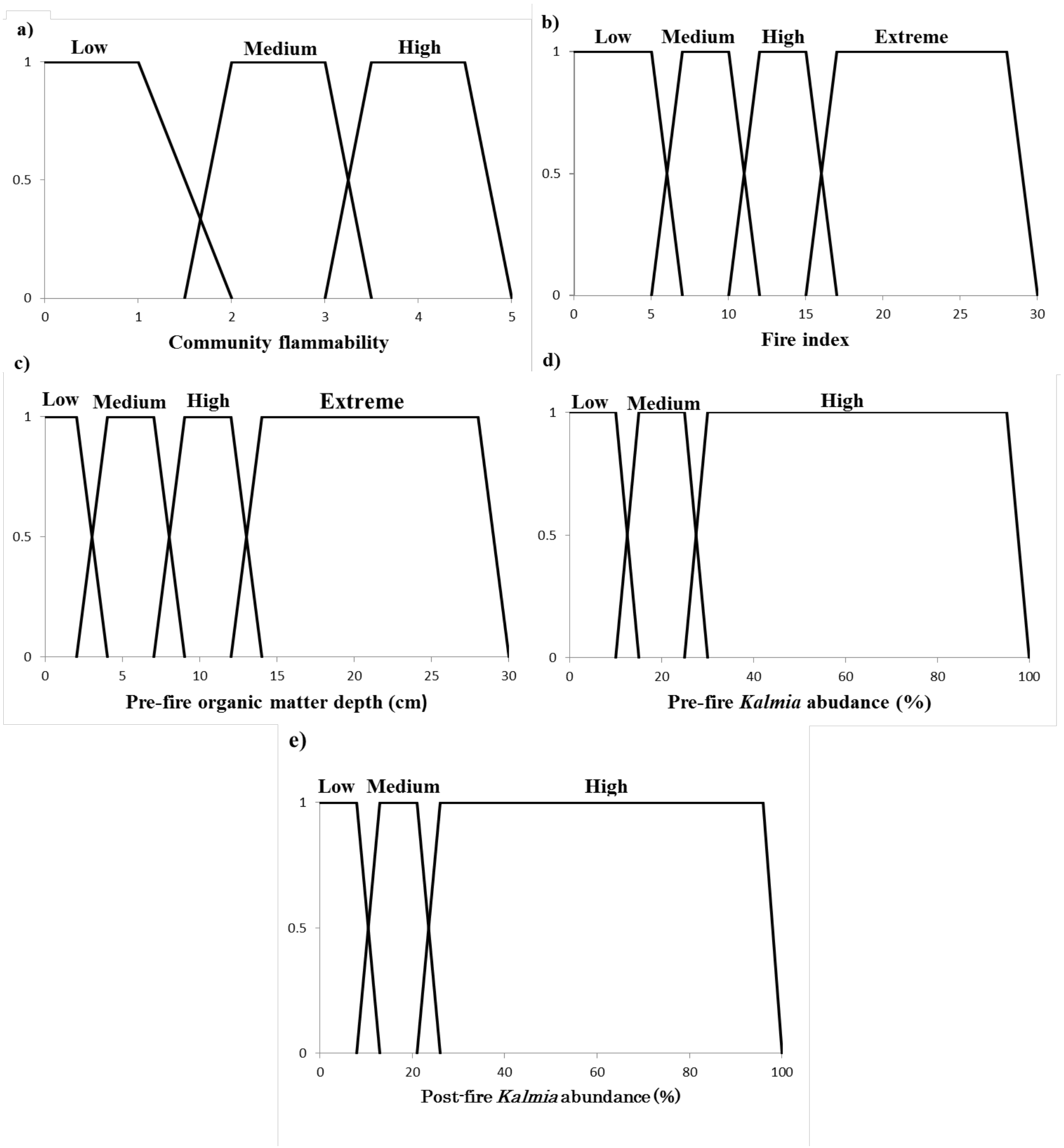


Figure 4.1. Membership functions of the four input variables (a-d) and the output variable (e). Set ranges for each category and corresponding membership functions were assigned using expert knowledge. Variables were standardized for use in the model but are shown here prior to standardization.

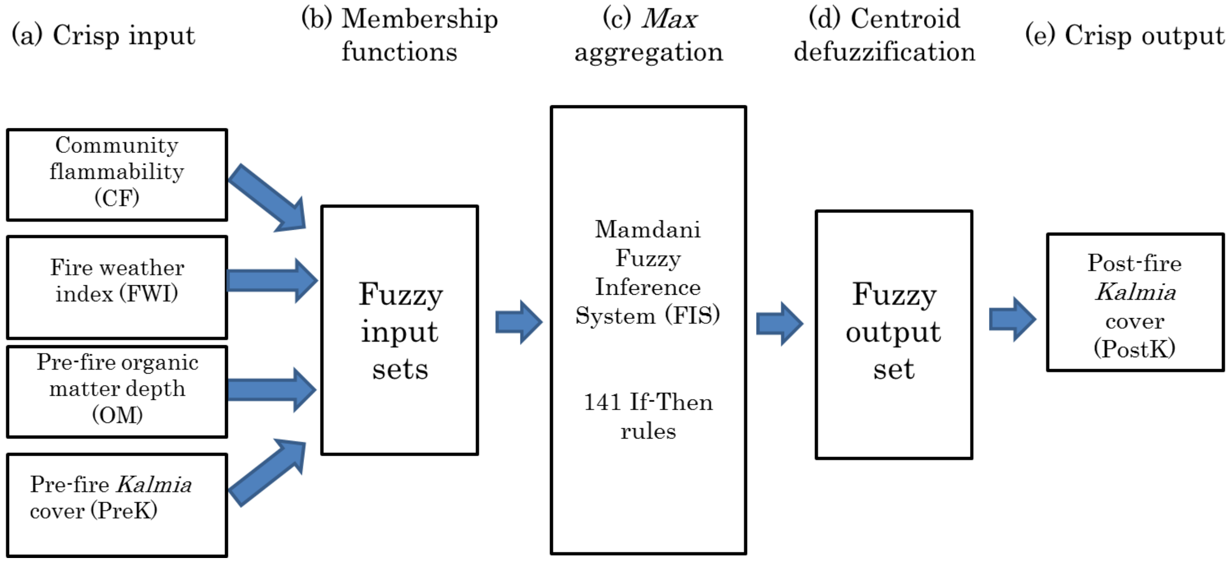


Figure 4.2. Visual representation of the fuzzy model used to predict post-fire *Kalmia* abundance. (a) Crisp values are obtained from a null set generated from data collected in heath and forest sites of Eastern Newfoundland; (b) crisp values are converted to fuzzy sets based on their assigned membership functions; (c) fuzzy sets are aggregated according to If-Then rules using the *max* method, generating a fuzzy output set; (d) fuzzy output set is defuzzified using the centroid method; (e) a single crisp output value is returned by the model.

Input data used for model simulations were obtained by randomly drawing 1000 normally distributed numbers from within the ranges of each variable in the data set. Random combinations were drawn from the ranges and distribution of field data obtained from forest and heath sites measured in the summers of 2015 and 2016, as well as the Parks Canada Newman Sound Fire Weather Index data for the summer of 2015. Data in the simulated set were standardized to a mean of zero and unit variance prior to model input to give each variable equal weight.

4.3.4. Model behaviour and validation

The crisp output returned from the model was sorted based on the three major pre-fire characteristics: Fire severity (based on CF and FWI), pre-fire OM depth (OM), and pre-fire *Kalmia* cover (PreK). Model behaviour was checked by inputting the entire range of OM while keeping all other input variables within a range that simulates one of four scenarios. For example, the entire range for OM (Low to High) was entered into the model while inputs for CF, FWI, and PreK were kept constant within the Low range. The model output, PostK, was then plotted against OM. This process was repeated for PreK, entering its entire range while keeping OM within one range at a time. For each of the eight scenarios, post-fire *Kalmia* abundance predicted by the model was validated by assessing correctly classified instances (CCI), or the proportion of simulations that agreed with the expert knowledge.

4.4. Results

4.4.1. Model behaviour

Model behaviour based on four scenarios consisting of various combinations of fire severity and organic matter depth (OM), and fire severity and pre-fire *Kalmia* abundance (preK) is shown in Figures 4.3 and 4.4, respectively. When all variables were kept constant with the exception of pre-fire OM, the model yielded two distinct phases for post-fire *Kalmia* cover (PostK): one indicating PostK as being below 20% and another showing it to be above 20% (Fig. 4.3a-d). This boundary marks the point where heath formation becomes very likely. All four scenarios show this sharp transition between phases to occur as OM increases, the only difference being at what point the transition takes place. Simulations suggest that low severity fires will lead to > 20% PostK if OM is > 8 cm, regardless of PreK being either low or high (Fig. 4.3a,b). High severity fires allow for a larger amount of OM, and that the transition to high PostK occurs at 13.5 cm OM irrespective of PreK levels (Fig. 4.3c,d). Simulations also suggest a greater range in PostK for scenarios with low PreK: some simulations returned PostK as potentially being 1-5% when OM is within the first phase described above. For high PreK conditions, the majority of simulations returned a PostK value near the transition point (Fig. 4.3b,d).

Similar results were obtained when OM was kept constant in lieu of PreK showing four combinations of low and high fire severity and OM (Fig. 4.4). All simulations performed with low OM conditions returned PostK values below the 20% threshold along the entire PreK gradient, indicating that if OM is low at the time of fire, PostK will always be low (Fig. 4.4a,c). The separation of two distinct phases by the PostK transition line was only apparent in scenarios with high OM. Phase transition from low to high PostK occurs at approximately 10-15% PreK for both low and high severity fires (Fig. 4.4b,c).

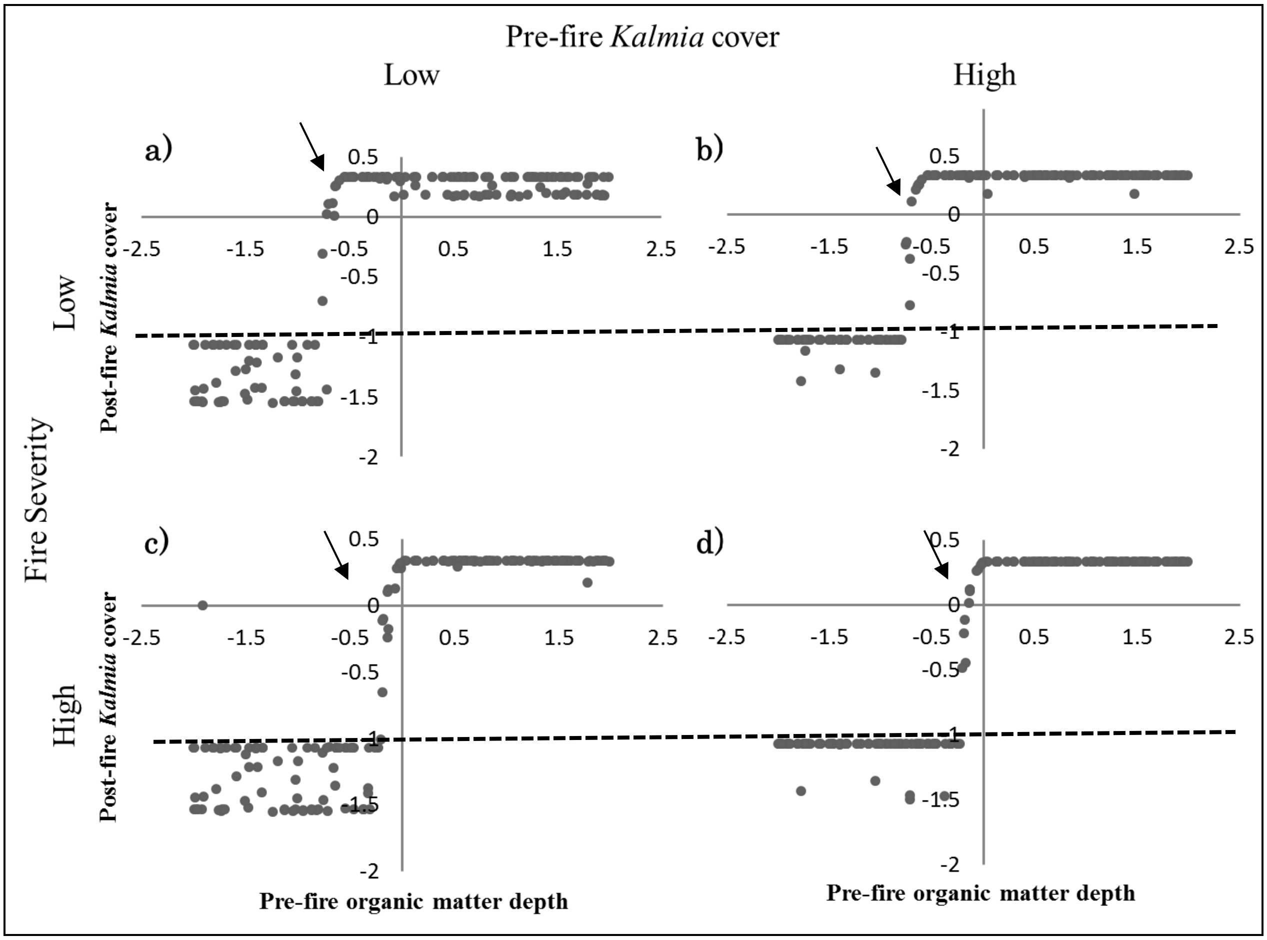


Figure 4.3. Model behavior showing post-fire *Kalmia* cover (PostK; output) as a function of pre-fire OM depth (OM; input). Shown are four different pre-fire scenarios depicting different levels of fire severity and pre-fire *Kalmia* cover: (a) Low fire severity and low *Kalmia* cover, (b) Low severity fire and high *Kalmia* cover, (c) High severity fire and low *Kalmia* cover, (d) High severity fire and high *Kalmia* cover. Dashed line represents the critical threshold where post-fire *Kalmia* abundance is such that heath formation is inevitable (~ 20% cover). Note that in Fig.4.3a & b the threshold point is crossed between -0.85 & -0.78 on the standardised axis 1 (see the arrow) and in Fig.4.3c & d the threshold point is crossed between -0.22 & -0.17 on the standardised axis 1 (see the arrow).

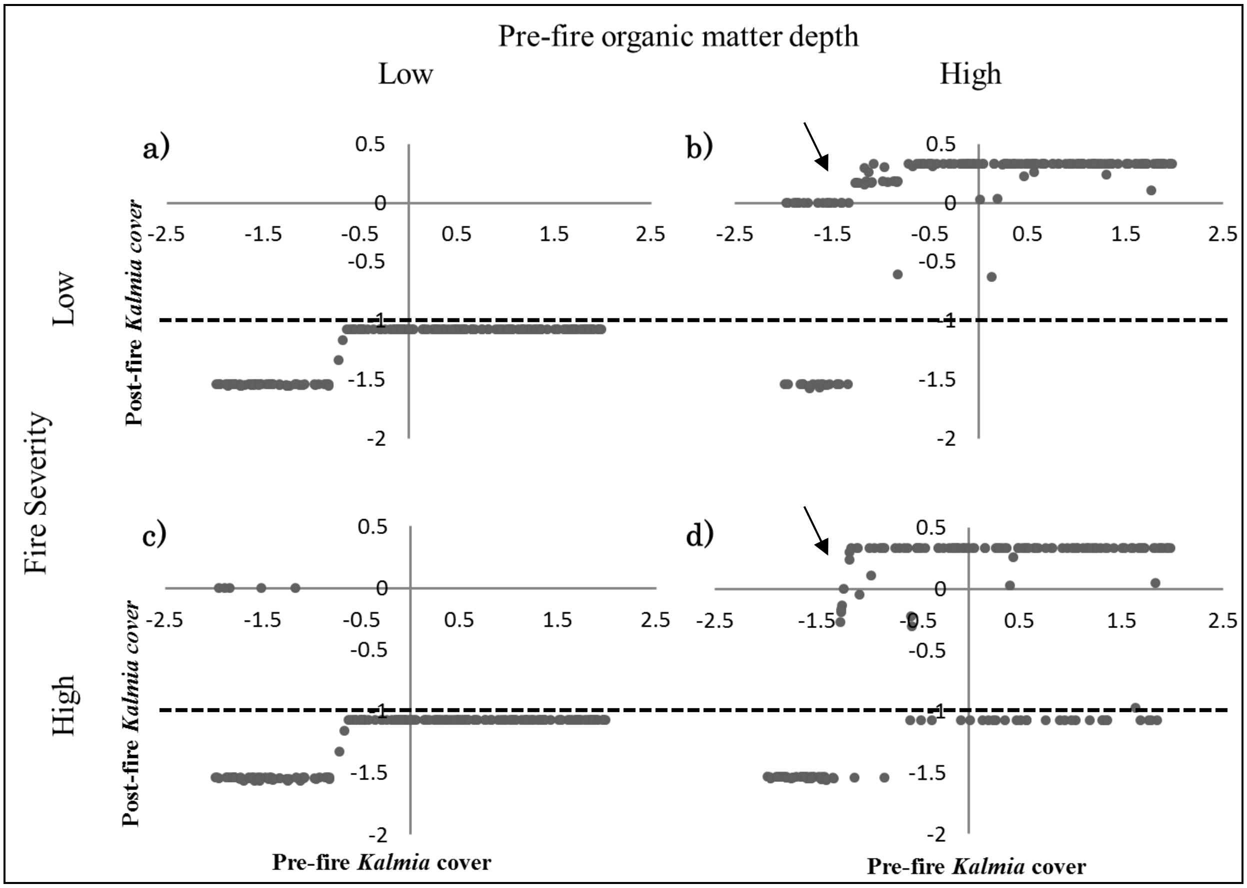


Figure 4.4. Model behaviour showing post-fire *Kalmia* cover (PosK; output) as a function of pre-fire *Kalmia* (PreK; input) cover. Four different pre-fire scenarios depicting different levels of fire severity and pre-fire organic matter depth: (a) low fire severity and low organic matter, (b) low severity fire and high organic matter, (c) high severity fire and low organic matter, (d) high severity fire and high organic matter. Dashed line represents the critical threshold where post-fire *Kalmia* abundance is such that heath formation is inevitable (~ 20% cover). Note that in Fig.4.4a & c the threshold point is never crossed and in Fig.4.3 b & d the threshold point is crossed between -1.32 & -1.15 on the standardised axis 1 (see the arrow).

Model validation was performed for each scenario (Table 4.2) individually as well as a whole. Correctly classified instances (CCI) are the percentage of simulations that agree with the expert knowledge (obtained from A.U. Mallik, myself, and literature) relative to the total number of simulations (Adriaenssens et al. 2004). The model was more accurate when OM was not a fixed variable (99-100% CCI) than when PreK was not fixed (88.3-100% CCI). Accuracy of the model overall was 93.8% CCI (Table 4.2)

Table 4.2. Pre-fire scenario conditions (Fire severity, Pre-fire OM/*Kalmia* cover) for the eight scenarios simulated. Scenarios correspond to panels in Figs. 4.3 and 4.4. Pre-fire threshold represents the maximum value a parameter can take before the model predicts post-fire *Kalmia* cover to be > 20%. Correctly classified instances (CCI) are listed for each scenario as well as for the total value of all simulations combined.

Scenario	Fire severity	Pre-fire OM/*Kalmia* cover	Pre-fire threshold	CCI (%)
4.3a	Low	Low PreK	7.5 - 8.0 cm OM	100
4.3b	Low	High PreK	7.5 - 8 cm OM	100
4.3c	High	Low PreK	13-13.5 cm OM	99
4.3d	High	High PreK	13-13.5 cm OM	100
4.4a	Low	Low OM	Any PreK% cover	100
4.4b	Low	High OM	10-15% PreK cover	90
4.4c	High	Low OM	Any PreK % cover	97.2
4.4d	High	High OM	10-15% PreK cover	88.3
Total				93.8

4.5. Discussion

By employing fuzzy logic, I developed a model that simulated post-fire regeneration of a dominant ericaceous shrub in agreement with expert knowledge on regeneration dynamics of dominant plants in secondary succession. Understanding of plant functional traits and how they influence disturbance regimes and dictate species response to disturbances has continued to rise; this increase in knowledge has been applied to predict community reassembly following fires but only in limited scope. Many models consider only one type of regeneration trait such as seeding (Pausas 2006; Splawinski et al. 2014). In cases where different response traits are integrated in the model, the species modelled belong to a single life-form group such as trees (He and Mladendoff 1999; Lasky et al. 2013). The current model incorporates the response traits (seeding and sprouting) and effect traits (flammability) of two distinct life forms (tree and shrub) to predict when a heathland dominated by dwarf shrubs can replace a forest dominated by trees after fire. The benefit of a model based on fuzzy logic is that, unlike other models that require extensive temporal and spatial data sets, here data requirements are relatively light. With data on forest inventory, species composition, flammability, and OM depth, land managers can easily determine the risk of a forested area to be replaced by a heath after a fire. The fuzzy logic model can be a useful tool to assist decisions on wildfire suppression and prescribed burning. It is easy to use because MATLAB software is user friendly but it does require knowledge of computer coding.

The model has identified situations when a forest loses resilience to fires and is replaced by *Kalmia* heath. In general, forests with little *Kalmia* cover and flammable overstory species such as *Abies balsamea* and *Picea mariana* and moderate OM depth (~10-13 cm) have low risk of being replaced by a heath after fire. An area loses resilience when it is composed of less flammable species, for example a *P. tremuloides* over story with *Kalmia* and *C. borealis* in the understory. Such a forest is identified by the model as having a high probability of being replaced by a heath should it burn, even if pre-fire OM depth is low (~8 cm). Organic matter depth (Johnstone and Chapin 2006; Siegwart Collier and Mallik 2010; Bansal et al. 2014) and propagule density (Hubble 2006) have long been known to be key elements in post-disturbance community assembly and the model simulations agree with the literature. The model accurately simulated these two key parameters at once and identified what ranges those parameters must simultaneously take for a threshold point to be reached. Once this threshold is crossed, a state shift occurs and a different plant community succeeds (Suding and Hobbs 2009).

The model also provides insight into mechanisms that could lead to an alternative stable state. An alternative stable state is characterized as an assemblage of species that differs from the one typically observed in an area, which is also self-replacing (Connell and Sousa 1983; Suding et al. 2004). The three most flammable species in the area are all trees (*Picea mariana*, *Abies balsamea*, *Betula papyrifera*), which have low abundance in heaths (Mallik 1995; Mallik and Kravchenko 2018; Chapter 2). A greater amount of trees naturally leads to a large difference in aboveground biomass between forest and heath, a forest provide much more fuel to a fire. Trees also have a distinct effect on fire behaviour in that more organic matter is consumed near tree stems and large roots, a result of sustained smouldering combustion (Green et al. 2007). Altogether this suggests that forests have a functional composition such that a fire would burn for a longer time, removing significant amounts of organic matter through surface fires and smouldering. A fire in a heath would have considerably less fuel and would therefore burn much faster, having little impact on OM levels unless it makes a smoldering fire. Because of the high vegetative propagule density in a heath (PreK > 30%), only a high severity fire could destroy vegetative propagules and open the seedbed for obligate seeders; the low flammability of heath species ensures that high severity fires are rare. Unless flammable tree species successfully invade, a heath could potentially self-replace over multiple disturbance cycles and establish an alternate stable state. The mechanism that would drive the establishment of this alternative stable state is similar to that identified in other studies where two distinct communities are able to co-exist on the landscape because one community excludes fire due to its regeneration traits (Odion et al. 2010; O'Connor et al. 2017). A *Kalmia* heath would not exclude fire but its low flammability and low fuel load would limit the damage to underground rhizomes. A low severity fire where the majority of underground rhizomes survive would ultimately have a similar effect on post-fire assembly as would excluding fire altogether.

The main benefit of this model is that it can be used in areas where fires of varying severity favour one response trait over another leading to communities dominated by distinct life forms (trees vs. shrubs). Models such as the LANDIS model (Mladendoff 1996) consider different response traits, but only within a forest community. The model presented here incorporates the effect traits of the pre-fire community and how they influence fire events. The data requirements for the model are light and the operating language can be easily grasped by individuals with limited modeling background. This eliminates the uncertainties in obtaining large and detailed data sets and incorporating them into complex mathematical models, and lack of background knowledge in computing. Fire weather index levels are monitored by government agencies and available to the public and species traits that determine flammability can be found in the literature (including this document) or from databases such as TOPIC (Traits Of Plants in Canada, Aubin et al. (2012)). The fuzzy inference system used by the model is easily navigable through the MATLAB software (The MathWorks, Inc. USA) and the FIS is available upon request. Further calibration of the model will be made possible from the input of experienced users who may provide their own expert knowledge. Collecting post-fire data in a site where pre-fire conditions have been recorded will be of great benefit to the refinement of this model. Even without further refinement, the model currently allows for the assessment of community resilience to disturbance or the anticipation of community response, which can reduce the need for restoration efforts (Larios et al. 2017). The model has high applicability to decision making and management, features that have been identified as key attributes of threshold models (Suding and Hobbs 2009).

4.6. References

Adriaenssens, V., Baets, B.D., Goethals, P.L.M., Pauw, N.D., 2004. Fuzzy rule-based models for decision support in ecosystem management. *Science of the Total Environment*, **319**, 1–12.

Aubin, I., Messier, C., Gachet, S., Lawrence, K., McKenney, D., Arseneault, A., Bell, W., De Grandpré, L., Shipley, B., Ricard, J.-P. & Munson, A.D. 2012. TOPIC - Traits of Plants in Canada. Natural Resources Canada, Canadian Forest Service, Sault Ste. Marie, Ontario, Canada. Available online: http://www.nrcan.gc.ca/forests/research-centres/glfc/20303

Bansal, S., Jochum, T., Wardle, D.A., Nilsson, M.-C., 2014. The interactive effects of surface-burn severity and canopy cover on conifer and broadleaf tree seedling ecophysiology. *Canadian Journal of Forest Research*, **44**, 1032–1041.

Bergeron, Y., Dansereau, P.-R., 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. *Journal of Vegetation Science*, **4**: 827–832.

Blackhall, M., Raffaele, E., Paritsis, J., Tiribelli, F., Morales, J.M., Kitzberger, T., Gowda, J.H., Veblen, T.T., 2017. Effects of biological legacies and herbivory on fuels and flammability traits: A long-term experimental study of alternative stable states. *Journal of Ecology*, **105**, 1309–1322.

Bloom, R. G., Mallik, A. U. 2004. Indirect effects of black spruce (*Picea mariana*) cover on community structure and function in sheep laurel (*Kalmia angustifolia*) dominated heath of eastern Canada. *Plant and Soil*, **265**, 279-293.

Bloom, R. G., and Mallik, A. U. 2006. Relationships between ericaceous vegetation and soil nutrient status in a post-fire *Kalmia angustifolia*-black spruce chronosequence. *Plant and Soil*, **289**: 211-226.

Boiffin J., Aubin I., Munson A. D., Roxburgh S. 2015. Ecological controls on post-fire vegetation assembly at multiple spatial scales in eastern North American boreal forests. *Journal of Vegetation Science*, **26**, 360–372.

Connell, J.H., Sousa, W.P., 1983. On the evidence needed to judge ecological stability or persistence. *The American Naturalist*, **121**, 789–824.

de Andrade, L.P., Espíndola, R.P., Pereira, G.C., Ebecken, N.F.F. 2016. Fuzzy modeling of plankton networks. *Ecological Modelling*, **337**, 149–155.

Glenz, C., Iorgulescu, I., Kienast, F., Schlaepfer, R. 2008. Modelling the impact of flooding stress on the growth performance of woody species using fuzzy logic. *Ecological Modelling*, **218**, 18–28.

Gutiérrez-Estrada, J.C., Pulido-Calvo, I., Bilton, D.T. 2013. Consistency of fuzzy rules in an ecological context. *Ecological Modelling*, **251**, 187–198.

He, H.S., Mladenoff, D.J. 1999. Spatially Explicit and Stochastic Simulation of Forest-Landscape Fire Disturbance and Succession. *Ecology*, **80**, 81–99.

Hubbell, S.P. 2006. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, **19**, 166–172.

Inderjit, Mallik, A.U. 1999. Nutrient status of black spruce (*Picea mariana* [Mill.] BSP) forest soils dominated by *Kalmia angustifolia*. *Acta Oecologia*, **2**, 87-92.

Jasinski, J.P.P, and Payette, S. 2005. The creation of alternate stable states in the southern boreal forest , Québec, Canada. *Ecological Monographs*, **75**: 561-583.

Johnstone, J.F., and Chapin III, F.S. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems* **9**: 14–31.

Johnstone, J.F., Chapin III, F.S., Hollingsworth, T.N., Mack, M.C., Romanovsky, V., and Turetsky, M. 2010. Fire, climate change, and forest resilience in interior Alaska. *Canadian Journal of Forest Research*, **40**: 1302-1312.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., and Muller, S. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology*, **98**: 1134–1140.

Lasky, J.R., Sun, I.-F., Su, S.-H., Chen, Z.-S., Keitt, T.H. 2013. Trait-mediated effects of environmental filtering on tree community dynamics. *Journal of Ecology*, **101**, 722–733.

Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A. & Mayfield, M.M. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, **13**: 76–86.

Larios, L., Hallett, L.M., Suding, K.N. 2017. Where and how to restore in a changing world: a demographic-based assessment of resilience. *Journal of Applied Ecology*, **54**, 1040–1050.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**: 545–556.

Mallik, A.U. 1993. Ecology of a forest weed of Newfoundland: vegetative regeneration strategy of *Kalmia angustifolia*. *Canadian Journal of Botany*. **71**, 161–166.

Mallik, A.U. 1994. Autecological response of *Kalmia angustifolia* to forest types and disturbance regimes. *Forest Ecology and Management*, **65**, 231–249.

Mallik, A.U., 1995. Conversion of temperate forests into heaths: Role of ecosystem disturbance and ericaceous plants. *Environmental Management*, **19**, 675–684.

Mallik, A.U., Biswas, S.R., Siegwart-Collier, L.C. 2016. Belowground interactions between *Kalmia angustifolia* and *Picea mariana*: roles of competition, root exudates and ectomycorrhizal association. *Plant and Soil*, **403**, 471–483.

Mallik, A.U., Bloom, R.G., Whisenant, S.G. 2010. Seedbed filter controls post-fire succession. *Basic and Applied Ecology*, **11**, 170–181.

Mallik, A., Kravchenko, D. 2018. Recruitment and ontogenic patterns of stunting and growth release of black spruce (*Picea mariana*) in post-fire *Kalmia* heaths. *Forest Ecology and Management*, **407**, 135–144.

Mallik, A.U., Inderjit. 2001. *Kalmia angustifolia*: Ecology and Management. *Weed Technology*, **15**, 858-866.

Mamdani, E.H., Assilian, S. 1975. An experiment in linguistic synthesis with a fuzzy logic controller. *International Journal of Man-Machine Studies*, **7,** 1-13.

Marchini, A. 2011. Modelling ecological processes with fuzzy logic approaches. In: Jopp, F., Reuter, H., Breckling, B. (eds) *Modelling Complex Ecological Dynamics,* Springer-Verlag, Berlin, pp. 133-145.

Mladenoff, D.J., O.E. Host, J.E. Boeder, T.R. Crow. 1996. LANDIS: a spatial model of forest landscape disturbance, succession, and management. In (M.E Ooodchild, L.T. Steyaert, and B.O. Parks, eds.) *GIS and Environmental Modeling: Progress and Research Ideas*. GIS World Books. p. 175-179.

Naeem, S., 1998. Species redundancy and ecosystem reliability. *Conservation Biology*, **12**: 39–45.

Natural Resources Canada. 2018. Canadian wildland fire information system: Canadian forest fire weather index (FWI) system. Available online http://cwfis.cfs.nrcan.gc.ca/background/summary/fwi

O'Connor, C. D., Falk, D. A., Lynch, A. M., Swetnam, T. W., Wilcox, C. P. 2017. Disturbance and productivity interactions mediate stability of forest composition and structure. *Ecological Applications*, **27**, 900–915.

Odion, D.C., Moritz, M.A., DellaSala, D.A. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology*, **98**, 96–105.

Pausas, J.G. 2006. Simulating Mediterranean landscape pattern and vegetation dynamics under different fire regimes. *Plant Ecology*, **187**, 249–259.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J. G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M. G. A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*. **61**, 167–234.

Prato, T. 2007. Assessing ecosystem sustainability and management using fuzzy logic. *Ecological Economics*, **61**, 171–177.

Roberts, D. W., 1996. Modelling forest dynamics with vital attributes and fuzzy systems theory. *Ecological Modelling*, **90**, 161–173.

Siegwart-Collier, L., Mallik, A. U. 2010. Does post-fire abiotic habitat filtering create divergent plant communities in black spruce forests of eastern Canada? *Oecologia*, **164**, 465–477.

Splawinski, T. B., Greene, D. F., Gauthier, S. 2014. A model of the post-fire recruitment of *Picea mariana* and *Pinus banksiana* as a function of salvage timing and intensity. *Ecological Modelling*, **282**, 35–43.

St. Martin, P., Mallik, A.U. 2016. Growth release of stunted black spruce (*Picea mariana*) in *Kalmia* heath: the role of ectomycorrhizal fungi and near-ground microclimate. *Canadian Journal of Forest Research*, **46**, 666–673.

Suding, K. N., Gross, K. L., Houseman, G. R. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, **19**, 46–53.

Suding, K. N., Hobbs, R. J. 2009. Threshold models in restoration and conservation: a developing framework. *Trends in Ecology & Evolution*, **24**, 271–279.

Suding, K. N., Lavorel, S., Chapin III, F. S., Cornelissen, J. H. C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D., Jackson, S. T., & Navas, M. -L. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**: 1125-1140.

Svoray, T., Mazor, S., Bar (Kutiel), P. 2007. How is shrub cover related to soil moisture and patch geometry in the fragmented landscape of the northern Negev desert? *Landscape Ecology*, **22**, 105–116.

Van der Wal, R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, **114**, 177–186.

Wirth, C., Lichstein, J.W., Dushoff, J., Chen, A., and Chapin, F.S., 2008. White spruce meets black spruce: dispersal, postfire establishment, and growth in a warming climate. *Ecological Monographs*, **78**: 489–505.

Zadeh, L. A. 1965. Fuzzy sets. *Information and Control*, **8**, 338-353.

Zadeh , L. A. 2015. Fuzzy sets – A personal perspective. *Fuzzy Sets and Systems*, **281**, 4-20.

Chapter 5

Conclusion

5.1 Summary

The study of community re-assembly following disturbances is not a novel concept in plant ecology. Even viewing succession through an additional functional lens rather than an exclusively taxonomic one is an approach that has been applied often in the past two decades. But the focus of previous research on successional dynamics centered mostly within a single life-form group, along a single successional pathway. The post-fire black spruce-*Kalmia* communities undergoing two distinct successional pathways in Terra Nova National Park, provided an ideal system to study the effects, causes, and implications of post-fire community re-assembly, and through their functional composition, elucidate properties of ecosystems and the mechanisms that drive them. I can make the following general conclusions from the study.

First, if the post-fire community follows a heath succession there will be a loss in FD. In heaths I found a constriction of the functional trait space of trees and herbs, but not shrubs. This shrinking of the utilized niche space in heaths suggests that the post-fire communities do not reach their potential in terms of productivity because available niche space was not filled. Tree and herb species that normally fill this space (as in forest succession) are not able to enter the communities, which I directly attribute to habitat filters. The restriction of a subset of species present in the area is also indicated by the lower beta FD observed in heaths. Low beta FD within heath sites shows that each site, and even each plot within the sites, is composed of species that all possess similar functional composition; in other words, heaths are functionally homogeneous. Forest sites are by comparison functionally heterogeneous; the reason is that here was a greater range of trait values in forests, resulting in less functional similarity between plots and sites. This lower dispersion of traits for the majority of species (trees and herbs) and higher similarity in the functional composition of those present resulted in lower overall alpha and beta diversity in heath succession, an effect not observed in black spruce forest succession. This shows that fire (typically thought to be beneficial to boreal ecosystems) is not always linked to high diversity. Low severity fires create homogeneous seedbeds as opposed to the heterogeneous mosaic of seedbeds created by fires of high severity. This lack of variety in post-fire regeneration conditions leads to homogenization of the community's functional diversity.

Second, the constriction of the functional trait space and subsequent functional homogenization observed in Chapter 2 are often a signs that habitat filters are in place. Soil nutrient concentrations are lower in heaths and I identified the traits that were linked with the poor concentrations of N and P. Forming associations with ericoid mycorrhizae is the optimal strategy in nutrient poor acidic soils. Ericoid species experience an advantage over others that form associations with other kinds of mycorrhizae. Some experience poor growth, or even fail to establish because they do not possess the competitively ability to capture soil nutrients in soils dominated by ericaceous species. In addition, heath soil N is kept at highly limiting levels by species with high LDMC. Litter input by these species is low in N and this creates a feedback loop where the reintroduction of already limiting N is kept at low levels and those species that incorporate relatively low levels of N in their leaves have an additional advantage of not experiencing high levels of N limitation. Therefore, limiting soil nutrients, especially N, are acting as a habitat filter in heath succession, effectively impeding the growth and even establishment of a significant proportion of the species pool. The novelty of this study is its use of community-based approach to examine response and effect traits related to resource economics and how they relate the competitive abilities of species in post-fire heath. The findings identified traits related to both resource acquisition (ericoid mycorrhizae) and use (high LDMC) that provide the highest competitive advantage in nutrient limiting habitats, and also provide further evidence that the principle of limiting similarity is not as ubiquitous as once thought.

Third, I showed how the undesirable effects of heath formation (Chapter 2) caused by the dominance of ericaceous species (Chapter 3) can easily come about if certain conditions are in place immediately before and after a fire. Community flammability and weather act on fire severity, which plays a deciding role in the amount of residual organic matter. If ROM is low and ericaceous propagule density is low, then risk of heath formation is low. The model presented in Chapter 4 identifies conditions whereby a forest could easily undergo a state shift and be replaced by a heath. Furthermore, the model can predict biophysical conditions that can help perpetuate heath through disturbance cycles and establishing as an alternate stable state.

The results of this dissertation contribute to the continued understanding of succession in how distinct life forms, characterized by distinct suites of functional traits, respond in opposing manners to fire. This varying response has serious implications for the integrity and stability of the landscape as a whole. From a conservation standpoint, the loss of diversity in the first decades following disturbance should be seen as a cause for alarm, especially when the loss is exasperated by anthropogenic activities. From a land management perspective, the results presented here can be used to make well informed decisions when balancing the protection human interests with the maintenance of the integrity of our natural landscapes.

5.2 Future directions

The functional trait approach applied in this dissertation has been useful in identifying mechanisms driving the composition of post-fire communities in eastern Newfoundland. These findings could be reinforced with a more detailed and intensive sampling protocol. The existence of intraspecific trait variability has been recognized as important when considering interspecific interactions. The plasticity exhibited in a single species' traits could allow it to adapt to heterogeneity at the microhabitat scale, heterogeneity including abiotic gradients and the density of neighbouring species. This approach would be extremely useful in identifying a particular species competitive ability compared to other members of the community, being able to adjust trait values (exhibit plasticity) to its immediate surroundings would give an individual an advantage in terms of maximizing the efficiency with which it captures and utilizes nutrients. The results of Chapter 2 identified that shrub diversity was the only metric to respond positively to heath formation, due in part to the success of non-ericaceous shrubs alongside their ericaceous counterparts. Future work could be done to examine why these non-ericaceous shrubs thrive in heath, despite not possessing the ideal trait syndrome identified in Chapter 3 (High LDMC and ericoid mycorrhizae). Further investigation could identify whether non-ericaceous shrubs possess alternate trait syndromes that also impart effective resource acquisition and use in heaths, or that non-ericaceous shrubs receive facilitative effects from ericaceous dominance, such as competitive release from light-competing tree species.

Much work has been done on the aboveground response of *Kalmia* and black spruce to shade levels, such as plasticity in leaf traits as they relate to photosynthetic ability. Also, the four ericaceous shrubs present in heaths exhibit altering flowering times and blossom colours: *R. canadensis* (pink flowers) and *R. groenladicum* (white flowers) flower in early summer, then

Kalmia (pink flowers) and *V. angustifolia* (white flowers) bloom later in the summer. Yet little has been done in this system for belowground traits and how trait values may shift alongside gradients representing nutrient availability and root density of neighbouring species. Khan (2016) showed how two *Vaccinium* spp. shift reproductive trait values when growing together in clearcuts and forests of northern Ontario thereby reducing niche overlap and allowing for enhanced coexistence. It is likely that a similar mechanism exists that allows four ericads to coexist at relatively high abundances in post-fire heath and is a worth examining.

The ability of a heath to persist and resist tree invasion is also worthy of future research efforts. This dissertation showed that heath species are well adapted to the low soil nutrients and are able to maintain dominance over tree species, Bloom and Mallik (2004) projected that tree abundance would not increase until approximately 80 years following a fire although this has not been confirmed. The mechanisms whereby trees may eventually invade a heath have not been clearly identified, without a fire to remove the organic layer the seedbed remains unfavourable to tree colonization. Mechanisms allowing for tree invasion may be elucidated by combined field and greenhouse experiments. Establishing permanent plots immediately following fire and monitoring tree colonization and establishment over the long term would allow one to determine how the suitability of the seedbed changes overtime. In the greenhouse, plant-soil feedback experiments could show how tree species respond to soil conditioned by *Kalmia*. Monitoring the growth rate of trees in soil conditioned by (i) *Kalmia* alone and (ii) *Kalmia* and its associated soil microbial community could identify if *Kalmia* is directly responsible for the poor soil conditions of post-fire heath and the continued suppression of tree species. In short, *Kalmia* is an aggressive species, able to significantly modify its habitat. It would make an ideal model species to study a wide range of important ecological topics such as mechanisms of co-existence, ecosystem engineering, and invasion ecology.

Appendix I. Traits used to calculate functional diversity indices. Selection was based on using traits which incorporated a variety of competitive strategies of plants and the effects those strategies may have on ecosystem functioning.

Trait	**Measurement and units**	**Relevance to ecosystem function**
Specific leaf area (SLA)	Fresh leaf area/dry leaf mass – $m^{2\cdot}kg^{-1}$	Potential growth rate; photosynthetic rate
Leaf dry matter content (LDMC)	Fresh leaf mass/dry leaf mass – $mg^{\cdot}g^{-1}$	Leaf life span; defense from herbivory; litter decomposability
Seed mass	Mass - mg	Dispersal, germination and establishment success.
Specific root length (SRL)	Length of absorptive root/dry mass – $m^{\cdot}g^{-1}$	Nutrient and water uptake; drought tolerance
Maximum height	Height - cm	Light capture
Mycorrhizal association (MYCO)	Categorical	Nutrient uptake, defense from pathogens

Appendix II. Functional trait matrix of the 25 forest and heath species used for functional diversity calculations.

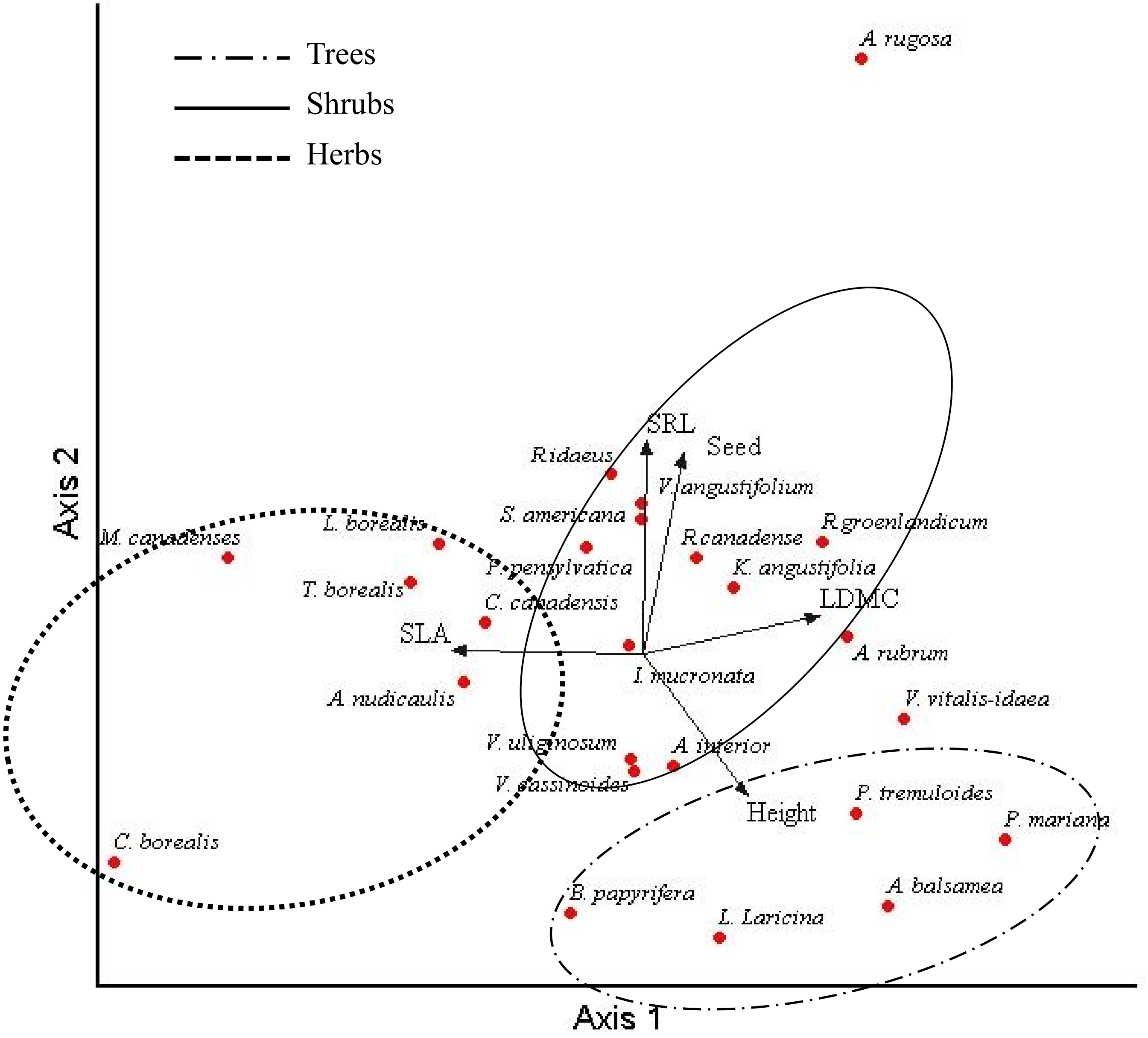
Plant species	**SLA ($m^2 \cdot kg^{-1}$)**	**LDMC ($mg \cdot g^{-1}$)**	**SRL ($m \cdot g^{-1}$)**	**Seed mass (mg)**	**Height (m)**	**MYCO**
Trees						
Abies balsamea (L.), Mill.	97.9	388	17.9	7.6	23	ECM
Acer rubrum L.	103.3	344	74.2	13.8	25	ARM
Betula papyrifera Marsh.	205.7	277	19.3	0.3	20	ECM
Larix laricina (Du Roi), K. Koch	148.2	328	12.1	0.2	20	ECM
Picea mariana (Mill.), BSP.	63.7	422	38.7	0.9	27.5	ECM
Populus tremuloides Mich.	139.9	409	40.6	0.2	25	ECM
Prunus pensylvatica L.	215.2	321	57.7	70.4	12	EDM
Sorbus americana Marsh.	172.3	336	79.6	3.13	10	EDM

Shrubs						
Alnus rugosa (DuRoi) Sprengel	114.4	394	53.7	355.1	3.0	ECM
Amelanchier interior Nielsen	167.2	397	14.6	5.56	2.5	EDM
Ilex mucronata (L.), PSA.	183.6	375	39.3	108.4	3	EDM
Kalmia angustifolia L.	127.4	401	50.0	0.005	1	ERM
Rhododendron canadense (L.), Torr.	152.4	402	55.8	0.018	1	ERM
Rhododendron groenlandicum (Oeder), K. & J.	96.8	436	57.7	0.006	1	ERM
Rubus idaeus L.	172.0	351	75.7	1.29	1.5	EDM
Vaccinium angustifolium Aiton	147.2	349	68.7	0.256	0.6	ERM
Viburnum cassinoides L.	144.9	327	14.8	16.4	3	EDM
Herbs						
Aralia nudicaulis L.	229.9	309	33.0	4.58	0.6	EDM

Clintonia borealis (Aiton), Raf.	288.9	89	7.39	4.7	0.4	EDM
Cornus canadensis L.	204.2	293	44.7	6.78	0.2	EDM
Linnaea borealis L.	240.2	303	61.4	1.2	0.15	EDM
Maianthemum canadenses Des.	305.6	206	61.1	0.45	0.22	EDM
Trientalis borealis Raf.	253.0	296	54.2	0.4	0.2	EDM
Vaccinium uliginosum L.	198.6	414	12.7	0.26	0.1	ERM
Vaccinium vitis-idaea L.	65.1	469	18.7	0.965	0.07	ERM

ARM: Arbuscular mycorrhiza; ECM: Ectomycorrhiza; EDM: Endomycorrhiza; ERM: Ericoid mycorrhiza

Appendix III. Principal component analysis of 25 species used based on their functional traits. Cumulatively, the two axes account for 85.4% of the variation in the data. Circles indicate clusters of groups representing the subdivision of the species set (with a few exceptions).



Appendix IV. Soil variables measured in post-fire forest and heaths sites (n=110)

Community type	Organic matter depth (cm)	Bulk density (g/cm^3)	Available P (mg/kg)	pH	Total phenolics (µg/g)	NH_4 (mg/kg)	NO_3 (mg/kg)
Heath	2.8	0.18	15.4	2.9	56.5	30.2	0.97
	4.0	0.07	20.1	2.78	43.8	16.1	0.71
	3.8	0.10	12.7	2.77	36.5	14.4	0.40
	7.0	0.07	22.2	2.84	41.9	31.8	1.16
	2.0	0.14	17.5	2.76	89.3	19.4	1.34
	5.2	0.09	24.3	2.72	71.1	28.2	0.82
	2.5	0.35	15.5	2.93	43.8	20.4	0.53
	4.5	0.06	10.9	2.81	93.5	43.2	1.16
	8.0	0.09	5.8	2.84	27.7	18.3	2.97
	9.3	0.10	9.6	3.03	34.6	32.6	3.88
	19.2	0.09	15.1	3.04	34.6	20.0	3.30
	3.8	0.11	16.3	3.07	24.2	16.9	2.90
	7.8	0.07	29.7	3.08	34.6	16.2	4.31
	2.5	0.18	6.9	3.23	62.3	21.0	3.26
	12.3	0.10	11.3	3.16	36.4	22.6	3.22
	5.3	0.09	10.6	3.54	22.5	25.6	5.23
	8.0	0.09	18.8	3.14	50.2	18.5	3.68
	4.0	0.06	15.4	3.2	29.2	18.4	3.88
	8.3	0.08	14.2	2.81	23.7	21.2	1.27
	1.5	0.25	18.8	3.29	29.2	20.4	1.56
	5.3	0.24	11.5	3.18	18.2	12.7	0.50
	9.5	0.11	11.4	3.01	32.8	22.0	2.17
	3.0	0.12	15.8	3.15	27.4	29.1	1.65
	5.5	0.09	25.6	2.85	34.6	21.6	1.57
	7.2	0.12	11.4	3.35	40.1	22.7	1.80
	1.8	0.09	9.8	3.45	38.3	14.1	1.51
	6.0	0.08	17.8	2.98	32.9	16.4	0.58
	9.8	0.08	21.2	2.82	46.7	18.0	0.88
	7.0	0.08	22.1	2.9	43.3	19.4	1.27
	6.8	0.09	22.9	2.94	43.3	23.5	0.92
	5.3	0.11	21.4	2.98	26.0	20.3	0.90
	13.7	0.08	11.3	2.96	32.9	21.2	1.13

(continued)

Community type	**Organic matter depth (cm)**	**Bulk density (g/cm^3)**	**Available P (mg/kg)**	**pH**	**Total phenolics (µg/g)**	**NH$_4$ (mg/kg)**	**NO$_3$ (mg/kg)**
Heath	8.2	0.09	21.3	3.26	36.4	19.5	1.11
	10.7	0.09	19.2	3.02	53.7	15.0	1.03
	7.5	0.10	18.5	3.06	64.1	19.2	1.45
	12.0	0.09	33.5	3.16	36.5	17.7	1.19
	14.3	0.06	24.5	3	29.2	28.8	2.13
	7.5	0.13	16.4	3.31	23.7	33.4	1.95
	6.8	0.09	20.8	3.63	27.4	19.5	0.83
	5.8	0.09	21.0	3.28	60.2	21.1	1.22
	6.2	0.11	20.1	3.05	23.7	25.6	1.39
	6.8	0.08	18.7	3.02	38.3	24.5	1.86
	9.3	0.09	14.1	3.18	52.9	27.7	1.63
	11.8	0.10	4.9	3.23	89.3	31.4	4.01
	10.2	0.10	0.7	2.81	47.4	23.4	3.90
	13.5	0.06	0.5	3.08	27.4	22.6	3.25
	10.5	0.10	1.1	3.32	72.9	27.3	3.18
	10.7	0.09	0.4	2.86	32.8	20.0	2.85
	10.8	0.09	7.4	2.79	20.1	20.9	2.48
	10.5	0.08	3.4	3.01	18.2	20.0	3.00
	10.2	0.10	4.4	2.94	25.5	23.2	3.23
	10.0	0.10	7.7	2.96	62.0	26.3	2.83
	8.2	0.07	32.7	3.35	34.6	29.6	2.22
	9.3	0.11	18.5	2.78	27.4	30.3	1.84
	4.3	0.12	14.0	2.93	47.4	25.5	2.64
	7.3	0.09	18.8	2.96	40.1	23.2	2.19
	9.2	0.09	16.6	2.94	32.8	24.1	2.01
	9.3	0.10	19.8	3.25	41.9	32.3	2.48
	6.7	0.08	19.1	2.93	51.1	29.8	2.08
	6.3	0.16	19.1	2.96	38.3	31.6	1.77
	3.5	0.35	11.0	3.11	43.3	35.6	2.41
	0.8	0.12	8.0	3.12	57.1	36.3	1.83
	5.8	0.13	15.9	3.29	39.8	4.7	9.08
	2.8	0.15	9.1	3.14	39.8	5.2	9.95

(continued)

Community type	Organic matter depth (cm)	Bulk density (g/cm^3)	Available P (mg/kg)	pH	Total phenolics (µg/g)	NH$_4$ (mg/kg)	NO$_3$ (mg/kg)
	4.0	0.08	13.7	3.47	27.7	4.3	10.62
	4.3	0.13	11.2	3.63	50.2	4.4	9.88
	3.1	0.16	13.6	3.4	38.1	5.0	9.78
	5.5	0.13	12.5	3.33	27.7	5.3	11.17
	4.8	0.13	13.5	3.35	34.6	5.1	9.68
	6.5	0.10	16.2	3.32	32.9	5.2	10.37
	16.7	0.10	5.3	2.7	32.9	6.9	9.51
	11.7	0.10	6.8	2.81	38.1	9.6	9.29
	12.0	0.09	7.2	3.11	51.9	7.5	8.93
	16.0	0.06	7.7	3.49	36.4	6.0	10.23
	12.3	0.09	11.9	3.17	36.4	6.8	9.38
	10.3	0.09	4.3	2.89	24.2	6.2	9.35
	18.0	0.14	10.4	2.86	41.5	6.2	9.25
	11.7	0.10	11.1	2.87	32.9	5.7	8.89
	11.0	0.09	18.5	2.87	6.9	6.3	9.94
	20.0	0.09	23.5	2.81	22.5	5.9	9.96
Forest	5.5	0.07	13.3	3.42	46.7	11.8	9.30
	6.8	0.03	9.5	4.04	69.2	16.4	8.53
	3.0	0.11	22.9	4.23	60.6	26.3	9.61
	3.5	0.07	16.7	3.56	50.2	12.6	11.09
	5.5	0.08	22.6	3.68	67.5	44.1	16.88
	4.5	0.08	20.5	3.83	62.3	13.1	14.27
	5.0	0.11	12.6	4.02	39.8	10.9	16.12
	17.7	0.11	10.8	3.36	50.2	8.9	12.16
	4.8	0.10	23.6	3.83	40.1	102.2	8.60
	7.8	0.12	42.4	3	63.8	25.5	8.56
	6.0	0.11	24.6	3.26	36.5	49.2	9.29
	6.8	0.09	40.6	3.27	36.5	46.5	8.15
	9.5	0.11	40.7	3.39	60.2	21.5	14.55
	5.5	0.09	54.4	3.32	51.1	82.2	12.00
	5.7	0.10	57.0	3.48	41.9	56.5	11.99
	9.7	0.11	26.2	3.13	71.0	87.0	9.69
	10.0	0.17	24.8	3.19	62.3	75.7	22.33

(continued)

Community type	**Organic matter depth (cm)**	**Bulk density (g/cm^3)**	**Available P (mg/kg)**	**pH**	**Total phenolics (µg/g)**	**NH_4 (mg/kg)**	**NO_3 (mg/kg)**
Forest	5.5	0.11	22.1	4.28	55.4	79.0	30.11
	9.2	0.09	17.3	4.24	57.1	42.1	15.54
	7.2	0.09	18.8	4.28	50.2	12.1	31.39
	7.5	0.14	24.1	3.67	38.1	73.1	2.36
	5.8	0.10	39.2	3.83	105.6	78.1	3.78
	9.8	0.06	28.0	3.6	109.1	63.4	2.24
	14.5	0.08	44.2	3.08	64.1	79.3	3.09
	14.5	0.10	44.7	3.03	43.3	78.7	2.86
	17.8	0.08	16.5	3.24	41.5	72.2	5.47
	10.5	0.08	23.5	3.22	46.7	51.9	11.26
	9.2	0.07	18.3	3.96	62.3	96.2	3.37
	14.0	0.08	9.4	3.78	43.3	43.9	4.39