PATTERNS AND MECHANISMS OF EPIPHYTIC MACROLICHEN ABUNDANCE, DIVERSITY AND COMPOSITION IN BOREAL FOREST

BY

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ABSTRACT

Epiphytes are important components of the forest ecosystem, but the mechanisms that control epiphyte diversity are not clear. Epiphytes are sensitive to disturbance, but their responses to stand-replacing fire are poorly understood. Furthermore, despite increasing rates of logging in boreal forests, there is lack of understanding of the potential effects of logging relative to wildfire on epiphytic lichen abundance, diversity, and composition. The focus of this thesis was to: (*1*) identify the mechanisms that regulate epiphytic species diversity; (*2*) examine the responses of epiphytic macrolichen abundance, diversity, and composition to stand-replacing fire and multiple successional pathways of the canopy tree layer; (*3*) examine the temporal dynamics of epiphytic macrolichen cover, richness, and composition as affected by disturbance origin, time since disturbance, and forest type; and (*4*) examine the influence of time since disturbance and host tree species on the species dynamics of epiphytic macrolichens in the central boreal forest of Canada.

A comprehensive literature review was conducted to explore possible mechanisms that regulate epiphytic species diversity and to develop a mechanistic framework to guide investigations of epiphyte assemblages. Six putative mechanisms of epiphyte species diversity were identified, and the extent to which the mechanisms interact was evaluated in a conceptual model. The mechanisms include constrained dispersal, slow growth rate, substrate availability, host tree mortality, disturbance, and global climate change. They are identified as inherent, local- and stand-level, and landscape-level mechanisms. The mechanisms are interrelated and the linkages between

them were elaborated. Future studies should test these mechanisms over broad spatial and temporal scales.

The effects of time since wildfire and overstory composition on the dynamics of epiphytic lichens were examined in a retrospective study of 51 stands of conifer, mixed-wood, and broadleaf overstory boreal forest stands ranging from 7 to 209 years since fire. Total lichen cover continuously increased with stand age for all overstory types, and mixed-wood and conifer stands had higher total lichen cover than broadleaf stands in all age classes except similarly low cover in stands ≤ 15 years old for all overstory types. Lichen species richness reached peaks in 98- or 146-year-old stands, and mixed-wood stands had higher lichen richness than broadleaf and conifer stands at 98 years old, but not at other age classes. Multivariate analysis indicated that lichen communities were compositionally distinct for all age classes and overstory types. The results demonstrate that epiphytic lichen communities show continued changes with time since disturbance that may span decades to centuries. Also, epiphytic lichens show a strong association with overstory composition with higher diversity in mixed-woods than conifer and broadleaf stands at canopy transition stage.

The temporal dynamics of epiphytic macrolichen cover, richness, and composition as affected by disturbance origin, time since disturbance, and forest type was compared for logging vs. wildfire over 33-year chronosequences in Ontario, Canada. Epiphytic macrolichens had not recovered 7 years after fire or logging, but their cover and richness thereafter increased with stand age for all overstory types. Within the same age and overstory, post-logged stands had lower or similar macrolichen cover and richness than post-fire stands, except for 33-year-old mixed-wood stands. More pronounced was the compositional difference of epiphytic lichens among overstory types, stand ages, and disturbance origins. The results demonstrate that epiphytic macrolichen abundance and diversity increase with stand age and lichen species composition is strongly influenced by overstory tree species composition. Furthermore, logging produces epiphytic macrolichen communities different from fire. The different effects of logging *vs*. fire could be a result of different regeneration density, genetic diversity of trees, and soil nutrient availability and stoichiometry.

Epiphytic macrolichen species in post-fire successional stands were examined in relation to forest stand age (7 to 209 years since last fire disturbance) and host tree species (jack pine *Pinus banksiana*, trembling aspen *Populus tremuloides*, paper birch *Betula papyrifera*, black spruce *Picea mariana*, and balsam fir *Abies balsamea*) in the central boreal forest. Recruitment of epiphytic lichen species after fire increased with time since fire, with new recruits at every stage. The occurrence of individual epiphytic macrolichen species was strongly influenced by time since fire and host tree species. Some lichen species, most of which reproduce asexually, colonized early on in the stand initiation stage whereas others appeared to establish only in the mature and old-growth stands. Frequency of occurrence of some epiphytic lichen species on the host trees increased with time since fire, whereas others decreased. Multivariate analyses indicated significantly different epiphytic lichen species composition on host trees at each stand age. The majority of epiphytic lichen species appeared to be generalist species with occurrence on all tree species, except for a few species that were found exclusively on aspen.

In summary, epiphyte species diversity is regulated by multiple, interacting mechanisms that operate at local, stand-level, and landscape level. Epiphytic macrolichen abundance and diversity increase with stand age and lichen species composition is strongly influenced by overstory tree species composition. Epiphytic macrolichen communities in logged stands differ from in post-fire stands. Epiphytic lichens show habitat preferences, but the majority of species are rarely host-specific.

Key words: boreal forest, conceptual framework, epiphyte diversity, logging, macrolichens, overstory composition, stand-replacing fire, time since disturbance.

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NOTE

This is a manuscript-based thesis. The various chapters were written to suit the submission requirements of the peer-reviewed journals; therefore, formatting and reference styles may differ.

Chapters:

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CHAPTER ONE: GENERAL INTRODUCTION

Epiphytes are specialized species that grow on long-lived woody plants. They constitute an important component of the forest ecosystem as they contribute to nutrient and mineral cycling, provide shelter and nesting materials for some insect and bird species, and are important sources of food for some foraging animals (Pike 1978, Knops et al. 1991, Coxson and Nadkarni 1995, Knops et al. 1996, Matzek and Vitousek 2003). Epiphytes are also useful indicators of environmental quality and forest health (McCune 2000, Jovan and McCune 2005). Despite their ecological importance, many aspects of their development, persistence, and growth are poorly understood. This is in part attributable to the lack of a conceptual framework to guide epiphytic studies. Specifically, the mechanisms that regulate epiphyte species diversity are not fully known because the present literature is typically descriptive rather than analytical and contains few references to causal mechanisms.

Epiphytes are susceptible to disturbance because of their attachment to trees and are eliminated when their host trees are cut down or killed by fire. Wildfire is the principal natural disturbance factor that shapes the structure and function of North American boreal forests (Johnson 1996, Weber and Flannigan 1997). But, the responses of epiphytes to stand-replacing fire and the multiple successional pathways of the canopy tree layer are poorly understood. Furthermore, clear-cut harvesting (logging) in recent years has emerged as an important stand-replacing disturbance in boreal forests as a result of increased demand for forest resources in the 21st century. However, few studies have examined the conservation potential of logging relative to the natural wildfire disturbance.

This thesis was compiled to address the following: (*1*) to identify the mechanisms that regulate epiphytic species diversity; (*2*) to examine the influence of stand-replacing fire and multiple successional pathways of the canopy tree layer on epiphytic macrolichen abundance, diversity, and composition to; (*3*) to examine the temporal dynamics of epiphytic macrolichen cover, richness, and composition as affected by disturbance origin, time since disturbance, and forest type; and (*4*) to examine the influence of forest stand age and host tree species on epiphytic macrolichen species in the central boreal forest of Canada.

Chapter two of this thesis presents a literature review of the mechanisms that regulate epiphyte species diversity. Chapter three presents an empirical study of the dynamics of epiphytic macrolichen abundance, diversity, and composition in the central boreal forests of Canada. The study examines the dynamics of epiphytic macrolichens following wildfire and tests the independent and interactive effects of time since fire and overstory composition on epiphytic macrolichen abundance, diversity, and composition. Chapter four also presents an empirical study of the temporal dynamics of epiphytic macrolichen cover, richness, and composition as affected by disturbance origin, time since disturbance, and overstory composition. This study specifically compares epiphytic lichen cover, richness, and composition between logging and wildfire in young successional forest. Chapter five presents an empirical study of the species dynamics of epiphytic lichen species in relation to forest stand age and host tree species. This examines the successional statuses and habitat preferences of individual lichen species as well as the epiphytic species occurrence and compositions on individual host trees.

CHAPTER TWO: MECHANISMS REGULATING EPIPHYTIC PLANT DIVERSITY

I. INTRODUCTION

Epiphytes, commonly referred to as “air-plants,” are specialist plants that grow on another plant (usually trees and shrubs). They derive their nourishment from atmospheric sources. In forest ecosystem, epiphytes play useful roles in nutrient cycles, provide shelter and nesting materials for some insects and bird species, and are important sources of food for some foraging animals (Pike, 1978; Coxson and Nadkarni, 1995; Knops et al., 1996; Stuntz et al., 2002). Epiphytes constitute an important bioindicator group of species that can be monitored to provide useful information on overall ecosystem health and productivity, because of their arboreal lifestyle and sensitivity to environmental stress (McCune, 2000; Jovan and McCune, 2006). However, unlike their terrestrial counterparts, little is known about the ecology of epiphytes; largely due to the logistical constraints associated with sampling epiphytes and the lack of robust generalizations or conceptual framework to guide epiphyte community studies (Barker and Pinard, 2001; Burns and Zotz, 2010).

The literature on epiphytes is typically descriptive rather than analytical, and contains few references to causal mechanisms. Therefore, the present understanding of epiphyte species assemblages is based on accounts of descriptive patterns and not towards causality. Furthermore, the mechanisms underlying epiphyte species diversity have not been explicitly recognized in many studies primarily due to the lack of a clear synthesis linking observations to theory. Accounting for the factors controlling local and regional variation in diversity, distribution, and abundance is regarded as one of the challenges in ecology (Ricklefs, 1977; Huston, 1979; Hubbell, 2001). For epiphytes, this may be even more challenging due to the lack of theoretical framework to assess the patterns in epiphyte assemblages.

Epiphyte species diversity are influenced by various factors including (1) host tree and stand structural characteristics (Esseen et al., 1996; Price and Hochachka, 2001; Callaway et al., 2002), (2) dispersal limitation (Dettki et al., 2000; Sillett et al., 2000; Werth et al., 2006), (3) resource availability (Benzing, 1990; Zotz and Hietz, 2001; Laube and Zotz, 2003), (4) disturbance (Wolf, 2005; Hietz et al., 2006; Werner and Gradstein, 2009), and (5) global climate change (Ellis and Coppins, 2007). Collectively, these factors explain the patterns of epiphyte species diversity at broad temporal and spatial scales. However, there have been fewer attempts to critically assess the extent of their observational or experimental support, and the prospective mechanisms of epiphyte species diversity remain sparse in literature and have not been sufficiently tested. Moreover, we do not yet know the extent to which the various mechanisms might interact.

The desire to forge a more integrative approach in the study of epiphytes based on sound knowledge of the mechanisms involved motivated the present synthesis. Here, the published studies are reviewed in an attempt to identify the important mechanisms of epiphyte diversity in light of what is known today on important aspects of epiphyte assemblages. The role of each of the putative mechanisms in epiphyte species diversity is discussed based on evidence from experimental and observation studies, and the extent to which the mechanisms interact is also highlighted. The mechanisms are identified as inherent, and local-, stand-, and landscape-level mechanisms.

II. PATTERNS OF EPIPHYTE SPECIES DIVERSITY

For the purpose of this review, both vascular and nonvascular epiphyte species are considered. Distinctions are made, when necessary, to differentiate between the epiphytic plant life forms. Epiphytes diversity is used here in a broad sense to include species richness, evenness, and composition. For epiphytes, individual host trees are habitat units. The state of the host tree in consideration, e.g., its species, size or age, is influenced by stand structural attributes. Hence, we briefly discuss epiphyte species diversity in relation to the influence of individual host tree and stand structural characteristics.

Host tree characteristics: Epiphytes depend on their host tree mainly for support, whereby individual host trees provide the substrate for epiphyte species establishment. Successful establishment of epiphytes on their hosts depends on several host tree traits such as size, age, branch quality, and bark texture (Esseen et al., 1996; Callaway et al., 2002; Lie et al., 2009). Trees generally increase in size as they grow old, corresponding to an increase in area for epiphyte species establishment. Trees with larger trunks provide wider surface area and heterogeneous microsites to be colonized by epiphytes, supporting higher epiphyte diversity (Nieder, 2001; Zotz and Vollrath, 2003; Burns and Dawson, 2005; Laube and Zotz, 2006a). Age of the host tree is also an import determinant because epiphytes species biomass accumulates slowly over time (Sillett et al., 2000). Ultimately, old and large trees often support high epiphyte diversity and abundance than young and small trees because both physical and chemical qualities of host trees change through time (Hietz and Hietzseifert, 1995; Flores-Palacios and Garcia-Franco, 2006; Lie et al., 2009). Likewise, older trees might have had longer periods to intercept and accumulate greater numbers of dispersing epiphyte propagules (Burns and Dawson, 2005). Some epiphyte species show preference for particular host and host traits (Callaway et al., 2002; Hirata et al., 2009)The linkage between epiphyte species and tree species suggests that the loss of a preferred host species could translate into the loss of diversity (Hietz, 1998; Gonzalez-Mancebo et al., 2003; Laube and Zotz, 2006b).

Stand structural characteristics: Epiphytes are sensitive to stand structural changes, and stand structural attributes such as stand age and tree species composition are important factors contributing to epiphyte species establishment and diversity (Hyvarinen et al., 1992; Neitlich and McCune, 1997; Price and Hochachka, 2001; Cleavitt et al., 2009). Generally, epiphytes are abundant in old-growth forests than young forests, owing to their slow growth rate and inefficient dispersal (Lesica et al., 1991; McCune, 1993; Esseen et al., 1996). Old-growth stands are structurally heterogeneous, usually with large trees, i.e., greater substrate area for epiphyte colonization and establishment, compared with young stands. Areas made heterogeneous by the presence of canopy gaps, trees with large diameter lower branches, and old-growth remnant trees are considered hotspots of epiphytes diversity (Neitlich and McCune, 1997). Structural changes and altered microclimate associated with gaps have potential for promoting epiphytes species diversity. Stand composition affects epiphytes diversity through substrate characteristics (bark physical and chemical quality) provided by each individual host tree species. Epiphytes differ in their substrate preferences which likely result in differences in frequency of occurrence between stands of different tree species composition. Mixed composition of tree species in a stand is often thought to harbour higher epiphyte diversity because the various tree species provide diverse substrates for colonization (Cleavitt et al., 2009).

Below are six putative mechanisms that explain epiphyte species diversity. They are classified into inherent, local- and stand-level, and landscape-level mechanisms (Fig. 1). These mechanisms, derived from both observation and experimental studies (Table 1), are typically inductive inferences due to inadequate manipulative studies.

III. INHERENT MECHANISMS

A. Constrained Dispersal

The successful establishment of epiphytes is typically dispersal-limited (Sillett et al., 2000; Werth et al., 2006; Cascante-Marin et al., 2009). Thus, sufficient and efficient dispersal is critical for epiphyte species diversity. Whether an epiphyte species can be present on the host species depends on whether it can disperse and establish there, as well as its growth rate and reproductive success. Dispersal limitation is directly linked with whether sexually or asexually dispersed. Asexually dispersed species are more likely to be dispersal limited than sexually dispersed species (Hedenas et al., 2003; Lobel et al., 2006).

Dispersal in epiphytes is typically localized and restricted to within-tree propagation, usually over short distances, by already established species (Laube and Zotz, 2006a; Cascante-Marin et al., 2009; Koster et al., 2009). Dispersal limitation is an important factor explaining the low abundance of epiphytes in young stands. Old-growth stands and remnant trees presumably function as propagule sources for epiphyte species colonization in young stands, whereby distance to source populations or propagule sources is important for efficient dispersal (Sillett and Goslin, 1999; Dettki et al., 2000; Sillett et al., 2000). For example, epiphytic lichens on *Nothofagus solandri* var. *cliffortioides* trees are limited in their ability to colonize new substrate, even over distances of less than 1 km, due to dispersal and establishment limitation (Buckley, 2011).

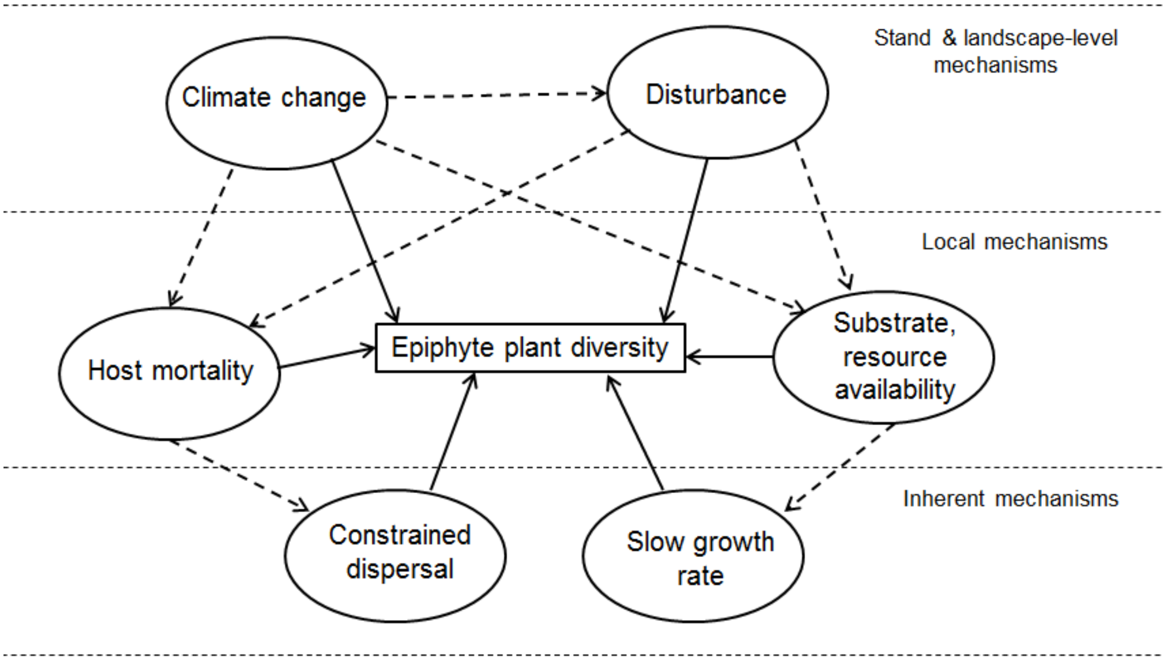


FIGURE 2-1. Conceptual model of possible interactions between the mechanisms of epiphyte species diversity. The mechanisms are grouped into inherent mechanisms, local mechanisms, and stand and landscape-level mechanisms. Solid arrows indicate direct effects, and dashed arrows indicate indirect effects.

B. Slow Growth Rate and Establishment Limitation

Epiphytes are inherently slow growing organisms and usually take a long period of time to fully reach maturity and colonize their hosts (Zotz, 1998; Schmidt and Zotz, 2002). Their slow growth results in slow biomass accumulation and a slow species turnover, which likely explains the lower epiphyte biomass and diversity in young stands compared with old-growth stands (McCune, 1993; Esseen et al., 1996; Price and Hochachka, 2001). The slow growth of epiphytes is assumed to be a result of the intermittent supply of water and nutrients in the habitats they occupy (Benzing, 1990; Laube and Zotz, 2003).

Growth rates and habitat suitability determine epiphyte establishment process. The inability of epiphytes to colonize or establish in a new stand can be referred to as establishment limitation. Establishment limitation in epiphytes could be related to biotic factors like competition and host specificity (Sillett et al., 2000; Callaway et al., 2002; Antoine and McCune, 2004). For example, Werth et al. (2006) demonstrated that dispersal limitation is not the only important mechanism that hinders colonization of the epiphytic lichen *Lobaria pulmonaria*, but competition by other fast-growing lichens and bryophytes reduces the availability of favourable microsites for *L. pulmonaria*.

TABLE 2-1. Examples of some representative studies that illustrate evidence or inferences supporting the mechanisms explaining epiphytic species diversity

Mechanism	Biome	Plant form	Examples of studies
Constrained dispersal	Boreal	Lichen	Dettki et al. (2000); Hilmo and Sastad (2001); Ockinger et al. (2005)
	Temperate	Lichen	Sillett et al. (2000); Werth et al. (2006)
	Tropical	Vascular	Cascante-Marin et al. (2009)
Slow growth	Temperate	Lichen	Snelgar and Green (1982);
		Vascular	Jarman and Kantvilas (1995)
	Tropical	Vascular	Zotz (1995); Schmidt and Zotz (2002)
Substrate, resource availability and heterogeneity	Boreal	Lichen	Fritz et al. (2008); Ranius et al. (2008) Juriado et al. (2009)
		Bryophyte	Caners et al. (2010)
	Temperate	Lichen	Heylen et al. (2005); Coote et al. (2007); Williams and Sillett (2007)
		Bryophyte	Peck et al. (1995); Coote et al. (2007); Williams and Sillett (2007)
		Vascular	Williams and Sillett (2007)
	Tropical	Lichen	Benner and Vitousek (2007); Normann et al. (2010);
		Bryophyte	Benner and Vitousek (2007); Gonzalez-Mancebo et al. (2004); Sporn et al. (2010)
		Vascular	Callaway et al. (2002); Laube and Zotz (2003) Wolf and Alejandro (2003); Mucunguzi (2007); Obregon et al. (2011); Poltz and Zotz (2011); Wester et al. (2011)
Host mortality	Boreal	Bryophyte	Snall et al. (2003); (Snall et al., 2005)
Disturbance	Boreal	Bryophyte	Caners et al. (2010)
		Lichen	Dettki and Esseen (1998); Peterson and McCune (2001); Root et al. (2010)
	Temperate	Bryophyte	da Costa (1999)
		Lichen	Andersson and Gradstein (2005)
	Tropical	Bryophyte	Zartman (2003); Andersson and Gradstein (2005); Noske et al. (2008); Patino et al. (2009) Werner and Gradstein (2009); Alvarenga et al.

			(2010)
		Vascular	Barthlott et al. (2001); Wolf (2005); Hietz et al. (2006); Noske et al. (2008); Koster et al. (2009); Larrea and Werner (2010); Werner and Gradstein (2009); Werner (2011)
		Lichen	Ellis and Coppins (2007); (Ellis et al., 2007)
Global climate change	Temperate	Vascular	Benzing (1998); Nadkarni and Solano (2002); Zotz et al. (2010)

IV. LOCAL MECHANISMS

C. Substrate, Resource availability and Heterogeneity

Substrate availability is a critical factor in epiphyte species diversity because dispersed seeds or spores, and soredia of lichens require suitable substrates to germinate, grow and colonize. Epiphytes usually establish on the tree bark and branches, and trapped soil or organic matter in crevices on bark surfaces and branches. Their preference for these substrates is related to the roughness, water-holding capacity, bark pH , branch age and branch size (Esseen et al., 1996; Callaway et al., 2002; Hirata et al., 2009).

Individual host trees can contain a diverse community of epiphytes that may, or may not, be similar to those found on other host trees belonging to even the same species, emphasizing host-specific differences in epiphyte community assemblages (Laube and Zotz, 2006b). Individual host trees can therefore be conceptualized as discrete patches or habitat units that are associated with many distinct microhabitats that may be different from that provided by other host trees. If host-specific differences in epiphyte assemblages occur, then epiphyte species diversity may be related to variation in microhabitats within individual host trees, when compared with host trees belonging to the same or different species.

Microhabitat resource availability, particularly water supply and, to a lesser extent, nutrient supply has perhaps the strongest influence on epiphyte diversity, and is a key factor in determining a good host (Zotz and Hietz, 2001; Callaway et al., 2002; Laube and Zotz, 2003; Zotz et al., 2010). Resource heterogeneity resulting in variation in moisture and light availability provide a highly diverse physical environment to which epiphytes show various kinds of adaptations. Studies on the vertical gradients of epiphytes on their hosts suggest that many species prefer, or are adapted to establish at different portions or microhabitats of the host trees (McCune, 1993; Hietz and Briones, 1998; Lyons et al., 2000; Antoine and McCune, 2004), supporting niche theory or the resource heterogeneity concept (Bartels and Chen, 2010). This height-related niche partition of epiphytes reflects growth, physical and physiological responses to gradients in canopy microclimate and ventilation in upper canopy exposures (Campbell and Coxson, 2001; Coxson and Coyle, 2003). Competition, particularly between lichens and bryophytes, also plays a role in the vertical niche partitioning (Antoine and McCune, 2004; Werth et al., 2006).

Many epiphytes show preference for host species and host traits such as age, size, and branch size, bark quality, and also microclimatic conditions associated with the host (Esseen et al., 1996; Zotz and Vollrath, 2003; Hirata et al., 2009). Individual host trees form discrete patches of habitat that can be colonized by many different epiphyte species, according to their preferences (Laube and Zotz, 2006b). Therefore, variation among host trees in terms of species composition, age and size-class, i.e., habitat diversity, can support a diverse community of epiphytes. Heterogeneous substrates and resource environments associated with habitat diversity, in light of the environmental heterogeneity and resource hypotheses (Ricklefs, 1977; Huston, 1979; Bartels and Chen, 2010) would, in theory, support high diversity of epiphytes.

D. Host Tree Mortality

For epiphytes, individual host trees are habitat units; however, the host trees are ecologically dynamic patches that emerge, grow and fall, and therefore offer only a temporarily limited habitat. The death of a host tree through insect outbreak, disease, anthropogenic disturbance, or aging (Chen and Popadiouk, 2002; Liu et al., 2007; Kurz et al., 2008; Luo and Chen, 2011) could lead to the loss or gradual elimination of the distinct epiphyte community it hosts; particularly true for obligate epiphytes that depend solely on the arboreal lifestyle (Benzing, 2004). Tree mortality may therefore result in a loss or decline in establishment substrates for epiphytes and consequently loss of diversity. Old trees, usually large individuals, harbour diverse epiphyte species and greater epiphyte biomass because of their size and the variety of microhabitats they offer (Nieder, 2001). Therefore, the loss of old trees could translate into the loss or declines in epiphyte species that are associated with large and old trees or those that require large branches as establishment substrate or slow-growing epiphytes that require a long period of time to complete their life cycles (Snall et al., 2003; Lie et al., 2009). Hence, the loss of old-growth trees can result in significant declines in epiphyte diversity at the stand or community level.

V. STAND- AND LANDSCAPE-LEVEL MECHANISMS

E. Nature and Severity of Disturbances

Disturbance is an important phenomenon that promotes changes in epiphyte species diversity. Disturbance that causes the loss of preferred host species or suitable substrates can consequently results in the loss of dependent epiphyte species (Hietz, 1999; Hirata et al., 2009). In addition, a disturbance event disrupts the prevailing microclimatic conditions in the habitat, and the resulting changes in the microclimate are key determinants of epiphyte assemblages (Werner and Gradstein, 2009). At the landscape, disturbance can alter forest structure and long-term successional or compositional patterns which can result in a mosaic of forest stands belonging to different successional stages, depending on the nature and severity of the disturbance (Chen and Popadiouk, 2002; Franklin et al., 2002; Chen and Taylor, 2011). Typically, disturbance events can be distinguished into two general categories depending on the nature and severity: (1) stand-replacing disturbance, and (2) intermediate or non-stand-replacing disturbance. Both types of disturbance might affect epiphytes species diversity in the several ways described below.

Stand-replacing disturbances have both short- and long-term effects on epiphyte diversity (Patino et al., 2009). Stand-replacing disturbance such as wildfire potentially consumes all host trees including old, large trees and branches, together with available *in situ* dispersed propagules, resulting in loss of epiphytes in the stand or landscape. Because all trees present are physically consumed including old trees, specialized epiphyte species that require or establish solely on old and large trees and branches are particularly vulnerable. In the event that stand-replacing disturbance initiates a new stand or creates a mosaic of young and old-growth stands at the landscape, epiphyte propagules for colonizing the new, young stands would have to come from a nearby source community, usually an adjacent old-growth stand (Dettki et al., 2000). In this case, insufficient propagule supply and inefficient dispersal from the source community would result in fewer epiphytes arriving in the new stand, and hence less diversity. It may take a long time for epiphytes to fully colonize and become established in the new stand; hence epiphyte diversity would increase slowly over time as the stand develops.

Intermediate or non-stand replacing disturbances such as treefall, blowdown, disease, and insect outbreak cause partial tree mortality, resulting in the loss of habitat or establishment substrates for epiphytes. However, because of their less severe nature, many preferred hosts and habitats are retained, together with *in situ* propagules, and therefore less diversity loss. Such small-scale disturbances typically create space in the canopy with the concomitant release of hitherto scarce resources such as light and moisture. This may enhance epiphyte species diversity since the niche requirements of the different resident epiphytes can be met. Unlike stand-replacing disturbances, epiphytes would require less time to recover, following an intermediate disturbance because both host trees, i.e., suitable habitats and substrates, and propagules are retained (Robertson and Platt, 2001). There is, however, the potential of high insolation and desiccation in the new open environment in the disturbed habitat to which epiphyte species that are not well adapted to it may be affected (Laube and Zotz, 2003).

In disturbed habitats, the key considerations in maintaining epiphyte diversity are structural integrity and taxonomic composition of the tree community. Comparing natural and anthropogenic disturbances, for example, natural disturbances such as windthrow or insect outbreak that have minimal impacts on forest structure and composition would retain most epiphyte species, contrary to anthropogenic disturbances such as deforestation or conversion of the forest into landscapes without trees. The conversion of primary forests into secondary, fragmented forests or agricultural landscapes reduces epiphytic diversity (Esseen and Renhorn, 1998; Zartman, 2003; Werner and Gradstein, 2009). Primary forests typically maintain the structural integrity and tree species composition of the forest unlike secondary forests (Gibson et al., 2011). As such, there is appreciably less epiphyte diversity in secondary forest compared with primary forest (Barthlott et al., 2001; Koster et al., 2009). The impact of anthropogenic disturbance including forest management on epiphyte diversity has received much attention (Hedenas and Ericson, 2003; Wolf, 2005; Werner and Gradstein, 2009), but how the effects of natural disturbance on epiphytes remains largely unstudied. Observational and manipulative studies are, however, needed to contrast the impact of anthropogenic and natural disturbances on epiphyte diversity.

F. Global Climate Change

Climate change is widely considered one of the greatest threats to biodiversity (Bellard *et al.*, 2012). Epiphytes occupy narrow ecological niches because of their existence at the interface of vegetation and atmosphere; therefore, slight changes in atmospheric climate can potentially alter their diversity. Many studies have demonstrated that temporal and spatial variation in climatic conditions including moisture, humidity, temperature, and rainfall patterns influence epiphyte diversity (Gentry and Dodson, 1987; Wolseley and Aguirre-Hudson, 1997; Hietz and Briones, 1998; Zotz and Hietz, 2001; Ellis and Coppins, 2007; Ellis et al., 2007; Zotz et al., 2010). For example, in the Western Amazonia, high rainfall in combination with low seasonality provides suitable conditions necessary to harbour high epiphyte diversity (Kreft et al., 2004). Although the effect of climate change on epiphyte diversity via drought is not currently known, many vascular epiphytes are drought-intolerant, and tend to suffer desiccation leading to mortality and consequent diversity loss, when exposed to prolonged periods of drought. However, how epiphyte species that exist in present climatic conditions will cope with future climates is largely unknown (Benzing, 1998; Nadkarni and Solano, 2002; Zotz et al., 2010).

Epiphyte diversity is not only directly affected by changing climates. Drought and warming-induced tree mortality, fire activity, and insects and pathogens associated with climate change (Logan et al., 2003; Flannigan et al., 2009; Allen et al., 2010) may significantly affect epiphyte diversity. For example, increased tree mortality associated with climate change (van Mantgem et al., 2009; Allen et al., 2010) would be expected to result in the loss of preferred host species, propagules, and suitable substrates, and consequently epiphyte diversity. But, observational and experimental studies are needed to examine the link between climate warming and drought to epiphyte diversity directly or via loss of host species, propagules, and suitable substrates.

VI. LINKING THE MECHANISMS

We propose the interdependence among the mechanisms (Figure 2-1). The model hypothesizes direct and indirect effects of disturbance and global climate change on host mortality, substrate, propagule and resource availability (including substrate and resource heterogeneity), and direct effects of substrate, propagule and resource availability on dispersal and growth rates of epiphytes. The linkages suggest a hierarchical level of influence among the mechanisms whereby stand- and landscape-level mechanisms influence local mechanisms, and local mechanisms also likely influence the inherent mechanisms.

The pathway involves the potential effects of global change on disturbance, and on host mortality and substrate, propagule and resource availability, which in turn can influence dispersal or growth rate (Figure 1). Global climate change may trigger other mechanisms or acts as a precursor. For instance, severe environmental stress caused by global climate change can lead to erratic rainfall patterns and drought, increases tree mortality directly by drought (Klos et al., 2009; van Mantgem et al., 2009) or via more frequent fire occurrences and insect pests or disease outbreaks (Flannigan et al., 2005; Kurz et al., 2008; Allen et al., 2010), and hence loss of epiphyte diversity.

Future efforts of both experimental and observational studies should consider simultaneously testing how these interacting mechanisms affect epiphyte diversity in various ecosystems. Although all mechanisms proposed here are important for epiphyte diversity from a global perspective, their relative strengths may differ with species of interest, ecosystem types, and scale of investigation. Understanding the relative strengths of these mechanisms for a particular species, group of species, and/or ecosystem type will be particularly useful for conservation of epiphytes, a unique group of plants in the plant kingdom.

VII. BIOME-SPECIFIC CONSIDERATIONS

There are both observational and experimental evidence in the published literature for many of the mechanisms of epiphyte diversity identified in this review. Table 2-1 presents some representative studies that illustrate evidence or inferences for the mechanisms. It is noted, however, that the available literature is limited, as the mechanisms have not been studied for all epiphytic plant forms and/or in all biomes, For example, dispersal limitation in epiphytic lichens and vascular epiphytes has been studied in the various biomes, but dispersal limitation in epiphytic bryophytes is rarely investigated, although dispersal in epiphytes is an inherent characteristic that is not restricted to any one taxonomic group of epiphytes or forest ecosystem. Similarly, the few documented evidence of the impact of climate change on epiphytes in the published literature comes from observations in temperate and tropical forests, but not from the boreal forests. Furthermore, few studies have investigated vascular and nonvascular epiphytes diversity simultaneously in the same study system (Williams and Sillett, 2007; Affeld et al., 2008; Werner and Gradstein, 2009), limiting possible comparisons between the different epiphytic life forms.

Epiphytic lichens and bryophytes are widely studied in the boreal forest (Table 2-1), but vascular epiphytes have not been documented in the region. Epiphytic lichens and bryophytes are the dominant epiphytic life forms in the boreal forests, whereas vascular epiphytes including bromeliads, ferns and orchids are diverse and widely distributed in tropical and temperate forests. The limited occurrence or exclusion of vascular epiphytes in the boreal forests could possibly be explained by the fact that many vascular epiphytes are drought-intolerant, and there susceptible to desiccation leading to mortality when exposed to drought conditions or low water availability (Zotz et al., 2010). This likely explains their high diversity in the tropical and temperate rainforests (Kreft et al., 2004; Kromer et al., 2005), and their rareness in biogeographic regions such as boreal forests where rainfall is in limited supply.

VIII. CONCLUSION

The mechanisms presented here correspond to both inherent and external factors, and are pivotal mechanisms that are likely responsible for the observed patterns of epiphyte diversity in all terrestrial ecosystems. Epiphytes are inherently slow growing organisms whose establishment in a given habitat largely depend on efficient dispersal, sufficient propagule supply, and availability of suitable substrates. Once successfully established, epiphytes can persist on their hosts until the death of the host. Mortality of the host, either through aging or disturbance, leads to the death of resident epiphyte species, and loss of epiphyte diversity. Disturbance dictates both long-term and short-term changes in epiphyte diversity by influencing forest structure, substrates, propagule availability, and abiotic resource conditions. The impact of disturbance, however, depends on the nature and severity of the disturbance. Like disturbance, global climate change also impacts epiphyte diversity directly through changes in atmospheric climate conditions, and indirectly through disturbance, tree mortality, and loss of substrate and propagule availability. The interrelationships between the mechanisms probably explain why the mechanisms of epiphyte species diversity have been elusive and not explicitly recognized in many studies.

The mechanisms presented here are typically inductive due to inadequate observational and manipulative studies on epiphyte diversity patterns. The scale of a study may be an important consideration in predictions of the patterns of epiphyte species assemblages. Therefore, efforts to disentangle the mechanisms of epiphyte diversity need to rely on multi-scale approaches. Although the mechanisms proposed here adequately explain epiphyte species diversity patterns, it is likely that the various life forms of epiphytes, i.e., vascular and nonvascular epiphytes, would respond differently to changes in environmental conditions. For example, dispersal limitation may be more pronounced in nonvascular epiphytes than their vascular counterparts. Finally, the individual mechanisms involved are likely interrelated and therefore shall not be studied in isolation. Considering the present limitations in the scope of the published studies, sufficient experimental and observational studies over broad spatial and temporal scales are necessary for future predictions of epiphyte diversity patterns.

CHAPTER THREE: DYNAMICS OF EPIPHYTIC MACROLICHEN ABUNDANCE, DIVERSITY, AND COMPOSITION IN BOREAL FOREST

INTRODUCTION

Epiphytes are specialized species that grow on long-lived woody plants. Epiphytic lichens, particularly macrolichens that are identifiable in the field by non-specialists, are useful indicators of environmental quality and forest health (McCune 2000a; Will-Wolf 2002; Bergamini *et al.* 2005). Some epiphytic lichens fix atmospheric nitrogen and thereby contribute to nutrient cycling of forest ecosystems (Coxson & Nadkarni 1995). More frequently recognized is that epiphytic lichens are sources of food for many foraging animals (Rominger, Robbins & Evans 1996; Ellwood & Foster 2004). Despite their ecological importance, many aspects of epiphytic lichen development including their persistence, growth, and colonization are poorly understood. Moreover, the potential mechanisms that regulate epiphyte diversity have little empirical support (Bartels & Chen 2012; Ellis 2012). Understanding the controls for epiphytic lichen abundance, diversity, and composition is therefore urgent for maintenance of their diversity and services in forest ecosystems.

Wildfire is frequent in boreal forests (Johnson 1996; Senici *et al.* 2013). Epiphytes are susceptible to stand-replacing fire because of their attachment to trees and are eliminated when their host trees are killed by fire. After fire, epiphytic lichen community recovery is limited by their dispersal, growth, and colonization abilities as well as the availability of suitable substrates (Dettki, Klintberg & Esseen 2000; Sillett *et al.* 2000; Bartels & Chen 2012; Ellis 2012), suggesting a long recovery process to the pre-disturbance level (Johansson 2008). Thus, time since stand-replacing disturbance, that is stand age, is an important determinant of the extent of post-disturbance recovery of epiphytic lichen communities (McCune 1993; Boudreault, Gauthier & Bergeron 2000; Price & Hochachka 2001; Johansson 2008; Boudreault, Bergeron & Coxson 2009). Too often, however, stand age effect is determined by comparing young managed stands and fire-origin old-growth stands (e.g., Lesica *et al.* 1991; Hyvärinen, Halonen & Kauppi 1992; Esseen, Renhorn & Petersson 1996; Kuusinen & Siitonen 1998; Sillett *et al.* 2000), leading to coupled effects of stand age and stand origins. Furthermore, existing data on epiphytic lichen communities are scanty and inadequate to allow for a comprehensive evaluation of age-related patterns due to limited stand development stages sampled, seldom including young (< 40 years old) stands. Therefore, long-term dynamics of epiphytic lichen abundance, diversity, and composition change following fire remain unclear.

Overstory tree species diversity and composition affect epiphyte communities because some epiphytic plants may show preference for specific host traits such as bark quality and microclimatic conditions (Bartels & Chen 2012; Ellis 2012). However, evidence for overstory composition effects on epiphytes remains limited (Price & Hochachka 2001; Cleavitt, Dibble & Werier 2009; Kiraly & Odor 2010; Kiraly *et al.* 2013). In North American boreal forests, most tree species can establish and grow on mesic sites. As such, various forest compositional types can occur after stand-replacing fire or logging as a result of the variability of species composition among pre-disturbance stands (Ilisson & Chen 2009). Through stand development with presence of secondary disturbances such as insect outbreaks and wind-throws, multiple successional pathways take place and result in either broadleaf, conifers, or mixed species dominance at any given stage of stand development (Chen & Popadiouk 2002; Taylor & Chen 2011). Yet, the effect of forest composition independent from stand age in post-disturbance stands has not been previously examined.

In this study, we used chronosequences of boreal forest stands that represent the various stages of stand development to examine the independent and interactive influences of time since disturbance and overstory composition on epiphytic lichen abundance, diversity, and composition. We addressed: (*1*) How do epiphytic lichen abundance, diversity, and composition change with stand development after fire? (*2*) Do epiphytic lichen abundance, diversity, and composition vary among overstory types? (*3*) Do stand age-dependent trends in epiphytic lichen abundance and diversity differ with overstory compositional type? Answers to these questions would provide comprehensive insights into lichen diversity in the disturbance-driven boreal forest. We predict that epiphytic lichen abundance increases with stand development because the recovery of epiphytic lichens after stand replacing disturbance is a long process (Johansson 2008). We expect that epiphytic lichen diversity increases with stand development and peaks in the intermediate stand ages since epiphyte communities may undergo succession in conjunction with overstory species dynamics (Brassard *et al.* 2008), as predicted by the intermediate disturbance hypothesis (Connell 1978). We also expect high diversity in mixed-species stands as species that specialize in either conifers or broadleaves can co-occur. Since macrolichen functional groups (foliose and fruticose) may differ in their colonization in regenerating forests (Dettki, Klintberg & Esseen 2000) and have different indicator statuses and conservation values (McCune 2000b; Will-Wolf 2002; Bergamini *et al.* 2005), we examined whether their responses to stand development and overstory composition may differ.

METHODS

Study area and sites

The study was conducted in the mixed-wood boreal forest north of Lake Superior and west of Lake Nipigon in the Black Spruce Forest, located approximately 100 km north of Thunder Bay, Ontario, Canada (49°23'N to 49°36'N, 89°31'W to 89°44'W). The area falls within the Moist Mid-Boreal (MBX) ecoclimatic region (Ecoregions Working Group 1989) and is characterized by warm summers and cold, snowy winters. Mean annual temperature is 2.5°C and mean annual precipitation is 712 mm at the closest meteorological station located in Thunder Bay, Ontario (Environment Canada 2014). Dominant overstory tree species include jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* [Mill] B.S.P.), white spruce (*Picea* glauca [Moench] Voss), and balsam fir (*Abies balsamea* L. Mill). Common understory shrub and herb species in the area as studied by Hart and Chen (2008) include mountain maple (*Acer spicatum* Lam.), dwarf raspberry (*Rubus pubescens* Raf.), alder (*Alnus* spp.), beaked hazel (*Corylus cornuta* Marsh.), bluejoint reedgrass (*Calamagrostis canadensis* Michx.), Canada mayflower (*Maianthemum canadense* Desf.), violet (*Viola* spp.) and large-leaved aster (*Aster macrophyllus* L.). Soils of the upland sites belong to the Brunisolic order (Soil Classification Working Group 1998). Fire is the most common natural disturbance in the study area, with an average fire return interval of approximately 100 years for the past century (Senici et al. 2010). Commercial logging, mainly clear-cut harvesting began in the area in the 1970s.

Sampling design

To determine the effect of time since fire, we selected chronosequences of stands of fire origin that have not been managed. Although the use of the chronosequence method has been criticized because it makes the assumption that sample stands along the temporal sequence have followed the same developmental history (Johnson & Miyanishi 2008), given careful site selection, replication, and demonstration of developmental links, the chronosequence method is well suited for studying successional processes over decadal to centennial time scales (Walker *et al.* 2010). Based on available fire-origin stands in the study area, we sampled six age classes: 7-, 15-, 33-, 98-, 146-, and 209-years since fire, representing stand initiation, early stem exclusion, late stem exclusion, early canopy transition, late canopy transition, and gap dynamic stages of stand development, respectively, modified from Chen and Popadiouk (2002).

At any given stand development stage on mesic sites in the region, stands originating from fire can be dominated by conifer, broadleaf, or the mixture of both group of species in the overstory (Frelich & Reich 1995; Chen & Popadiouk 2002; Ilisson & Chen 2009; Taylor & Chen 2011). Therefore, we made every effort to sample all three overstory stand types for each age class originated from fire. We attempted to have three replicates for each age class and overstory type, resulting in a total of 51 stands sampled (Table 3-1). For the conifer overstory type, however, it was not possible to have three replicates with road or boat access at ages 98 and 146 years old. The infrequency of fire has likely narrowed sampling possibilities. Additionally, stands of conifer overstory at these age ranges are primary candidates for logging in the region.

Every effort was made to avoid sampling stands of the same age in close proximity to one another to minimize the impact of spatial structure (Legendre & Legendre 1998), resulting in distances between stands in the range of 0.5 to 10 km. Interspersion was achieved by selecting stands of the same age class from different road accesses. A true spatially interspersed sample of different stand ages was, however, impossible due to fire history and fire size of the study area. For example, there was only one 33-year-old fire of 120 000 ha and one 209-year-old fire of 2000 ha.

In order to minimize site variability, all selected stands were located on mesic sites on flat-mid-slope positions, with no slope exceeding 5%. All stands were located on well-drained (sandy or silty loams) glacial moraines, >50 cm depth, which is the prevailing soil type in our study area. To ensure that each sample stand met the selection criteria, soil pits were dug in each candidate stand to verify whether the site was mesic, following the procedures described in Taylor *et al.* (2000). The selected stands were > 1 ha in area, visually homogeneous in stem density and composition.

Time since last stand-replacing fire (TSF) for sample stands ≤70 years old was determined from detailed fire records (Senici *et al.* 2010). For stands >70 years old, tree ages were used to estimate TSF following the procedures described by Senici *et al.* (2010). For all the sampled stands, we were able to select either jack pine or trembling aspen trees to determine TSF. No fewer than three canopy stems were sampled for each stand. For each selected tree, a core or disk at breast height (1.3 m above root collar) was taken and brought to the laboratory, where the cores were mounted on constructed core strips and disks were cut transversely and sanded to make rings visible. Rings were then counted using a hand-held magnifier until the same count was obtained three successive times. Based on a locally derived age correction model developed by Vasiliauskas and Chen (2002), we added 7 years to ring counts to determine TSF.

Field measurements

In each selected stand, we established a 400-m^2 circular plot within which all measurements were taken. Plots were randomly located in the selected stands, but were at least 50 m from the forest edge in order to avoid edge effects on epiphytic lichens (Esseen & Renhorn 1998; Hilmo & Holien 2002). We identified all tree species and measured the diameter at breast height (DBH; 1.3 m above the root collar) of all trees of each sample plot for stands ≥ 33 years old. For the younger (7- and 15-year old) stands, tree stems were counted by species. Stand density and basal area by species were summed to plot level and scaled up to level per hectare (Table 3-1). Overstory types were assigned based on the relative density or basal area of broadleaf and conifer tree species in a plot. Broadleaf and conifer stands were defined as having > 65% broadleaf or conifer tree species composition by stand basal area or stem density. Mixed-wood stands were defined as neither broadleaf nor conifer tree species representing > 65% composition by stand basal area or stem density (Table 3-1).

TABLE 3-1. Characteristics of 51 stands of fire origin sampled in the boreal forest of Ontario, Canada

Stand age (years)	Over-story*	*n*	Stand density (stems/ha) or basal area (m^2/ha)*, †	Stand composition (%)†					
				Trembling aspen	White birch	Jack pine	Black spruce	Balsam fir	Others‡
7	B	3	5783 (808)	58 (19)	28 (19)	15 (2)			
7	C	3	5608 (2249)		2 (2)	97 (2)	<1.0		
7	M	3	3275 (290)	38 (10)	15 (7)	43 (15)	4 (3)		
15	B	3	10242 (60)	80 (5)	7 (1)	13 (5)			
15	C	3	4433 (405)	29 (18)	2 (2)	69 (17)			
15	M	3	6383 (736)	57 (8)	<1.0	34 (2)	9 (8)		
33	B	3	33.4 (3.9)	89 (4)	4 (3)	4 (1)	1 (1)		<1.0
33	C	3	32.2 (2.4)	4 (2)	1 (1)	94 (3)	1 (1)		
33	M	3	25.6 (0.5)	36 (7)	<1.0	55 (12)	8 (8)		
98	B	3	56.2 (7.2)	95 (2)	2 (1)		1 (1)	1 (1)	1 (1)
98	C	1	49.1 (5.6)		4	60	29	7	
98	M	3	53.4 (3.5)	44 (12)	16 (12)	11 (7)	13 (7)	16 (3)	
146	B	3	65.2 (8.9)	85 (3)	8 (4)		3 (2)	1 (1)	3 (1)
146	C	2	63.0 (6.4)	<1.0	3 (2)	80 (2)	12 (4)	4 (2)	
146	M	3	45.8 (5.3)	44 (14)	18 (9)		11 (3)	25 (1)	2 (2)
209	B	3	49.0 (4.3)	57 (24)	25 (17)		11 (7)	8 (3)	
209	C	3	46.3 (9.0)	5 (4)	8 (4)		32 (7)	54 (16)	<1.0
209	M	3	48.2 (2.4)	14 (2)	31 (8)	3 (3)	29 (12)	23 (16)	

Notes: *Overstory types: B – broadleaf, C – conifer, and M – mixed-wood.

†Values are means with 1 SE in parentheses. Stand density (stems/ha) was determined for the younger (7- and 15-year-old) stands and basal area (m^2/ha) for older stands.

‡The "Others" category includes (*Picea glauca*), balsam poplar (*Populus balsamifera* L.), and mountain maple (*Acer spicatum*) with DBH > 5 cm.

In each plot, we conducted a thorough reconnaissance of the entire plot and sampled macrolichens using the whole-plot ocular method modified from McCune and Lesica (1992). On each tree of the sample plot, we visually estimated the percent cover of all epiphytic macrolichen species present on stems and branches, similar to the visual estimation method used for ground vegetation (Mueller-Dombois & Ellenberg 1974). We viewed individual trees as habitat units or quadrats and epiphyte communities on the trees as metacommunities or groups of spatially isolated communities connected by dispersal (Laube & Zotz 2006; Burns 2007). Sampling included the surface area of the stem and all branches we could visually see on the tree, but excluded tree trunk <0.5 m above root collar to avoid inclusion of terricolous or saxicolous lichen species. The nomenclature of epiphytic macrolichens follows Brodo, Sharnoff, and Sharnoff (2001).

Data analyses

Epiphytic macrolichen abundance was calculated as the mean percent cover of all macrolichen species on all trees within each plot. Macrolichen diversity assessed as species richness was the total number of macrolichen species recorded in the plot. In addition, we separately analysed cover and richness of the two epiphytic macrolichen functional groups distinguished by their morphology, i.e. the shrubby or pendulous foliose lichens, and the flattened or leafy fruticose lichens (Brodo, Sharnoff & Sharnoff 2001). Similarly, epiphytic macrolichen composition was at the plot level and was derived as the mean percent cover of each macrolichen species on all trees within each plot.

The effects of stand age and overstory type on epiphytic macrolichen cover and richness were examined using the following model:

$$Y_{ijk} = \mu + A_i + T_j + A \times T_{ij} + e_{k(ij)} \qquad (1)$$

where Y_{ijk} is cover or species richness (separately analysed by total macrolichen, foliose lichen, and fruticose lichen), μ is the overall mean, A is stand age class (i = 1, 2, 3…6), T is overstory type (j = 1, 2, 3), and, e is random sampling error from replications (k =1, 2, 3) within stand age and overstory type.

Because macrolichen cover was estimated as percentage, we applied arcsine-square-root transformation, as recommended by Crawley (2007). Since both cover and richness did not confirm the assumptions of normality and homogenous variances for general linear models, we used a generalized linear model (GLM) with the Gaussian family error distribution and an identity link function for cover data and a GLM with a Poisson error distribution and a logarithmic link function for species richness (count data) in R (R Development Core Team 2013). However, the initial models showed evidence of overdispersion; hence, we corrected the standard errors using a quasi-GLM model with the variance given by $ø \times \mu$, where ø is the dispersion parameter (Zuur *et al.* 2009). The significance of the predictors was tested using F tests by means of analysis of deviance, and the deviance explained by each variable in the model was calculated as a percentage of residual deviance explained from the null model. The significance of differences among A and T levels was tested using Tukey's multiple comparison with the *glht* function in the "multcomp" package (Hothorn, Bretz & Westfall 2008). Statistical significance was set at $\alpha = 0.05$.

We used permutational multivariate analysis of variance (PERMANOVA) to test the effects stand age and overstory compositional type on lichen species composition. PERMANOVA, which is a nonparametric, multivariate analysis that uses permutation techniques to test for compositional differences between more than one factor (Anderson 2001), was run using the Bray-Curtis dissimilarity and 1000 permutations of the compositional data. We then examined the trends in the compositional data using nonmetric multidimensional scaling (Kruskal 1964), which is an ordination method suitable for data that are non-normal or on discontinuous scales (McCune & Grace 2002) by specifying the Bray-Curtis dissimilarity index. The PERMANOVA test was conducted without including 7-year-old stands in which no epiphytic macrolichens were found.

Furthermore, we performed indicator species analysis (ISA) using PC-ORD Version 5.0 (McCune & Mefford 2006) to identify epiphytic macrolichen species' affinity for particular stand age class and overstory type (Dufrêne & Legendre 1997). ISA is a multivariate approach used for testing significant differences between priori groups. It calculates indicator values for all species based on species abundance scores and proportional frequency of the species in a particular group (Dufrêne & Legendre 1997; McCune & Grace 2002). The statistical significance of the maximum indicator value (IV) for each species was evaluated using a Monte Carlo procedure based on 1000 random reassignments. The p-value generated through this process represents the probability that the calculated indicator value is greater than that found by chance.

RESULTS

We recorded a total of 22 epiphytic macrolichen species, of which 17 were foliose lichens and 5 were fruticose lichens. The 7-year-old stands consistently lacked epiphytic macrolichen species or only contained traces of undifferentiated lichen thalli mainly on beaked hazel (*Corylus cornuta*). Total macrolichen cover estimated per plot ranged between 2% to 98% (mean ± 1 SE: 29.7 ± 4.3) and the number of species per plot varied between 3 and 14 (9.1 ± 0.5).

Total macrolichen cover was significantly influenced by stand age, overstory type, and their interaction (Table 3-2). Total macrolichen cover increased with stand age for all overstory types (Fig. 3-1A). While it did not differ among overstory types in the 15-year-old stands, total macrolichen cover was lower in broadleaf than conifer overstory types for all stands ≥ 33 years old. Total macrolichen cover did not differ between conifer and mixed-wood overstory types for all stand ages, but it was higher in mixed-wood and conifer than broadleaf overstory types in the older (146- and 209-year old) stands (Fig. 3-1A). When analysed by macrolichen functional groups, both foliose lichen cover and fruticose lichen cover showed similar responses to stand age and overstory type as total cover (Table 3-2 and Figs. 3-1B and 3-1C).

TABLE 3-2. Effects of stand age and overstory composition on epiphytic macrolichen cover, richness, and macrolichen species composition.

Cover or diversity	Source*	df	Deviance or variance explained (%)	*P*
Total lichen cover	*Age*	5	74.8	<0.001
	Overstory composition	2	7.7	<0.001
	Age × Overstory composition	10	7.2	0.036
Foliose lichen cover	*Age*	5	76.3	<0.001
	Overstory composition	2	3.1	0.019
	Age × Overstory composition	10	8.8	0.028
Fruticose lichen cover	*Age*	5	69	<0.001
	Overstory composition	2	12.7	<0.001
	Age × Overstory composition	10	11.4	<0.001
Total lichen richness	*Age*	5	91.2	<0.001
	Overstory composition	2	0.2	0.242
	Age × Overstory composition	10	5.9	<0.001
Foliose lichen richness	*Age*	5	88.1	<0.001
	Overstory composition	2	0.7	0.072
	Age × Overstory composition	10	7.1	<0.001
Fruticose lichen richness	*Age*	5	86.6	<0.001
	Overstory composition	2	0.3	0.472
	Age × Overstory composition	10	6.8	<0.001
Species composition†	*Age*	4	44	<0.001
	Overstory composition	2	14	<0.001
	Age × Overstory composition	8	24	<0.001

†Species composition analysis was analysed by permutational multivariate analysis of variance

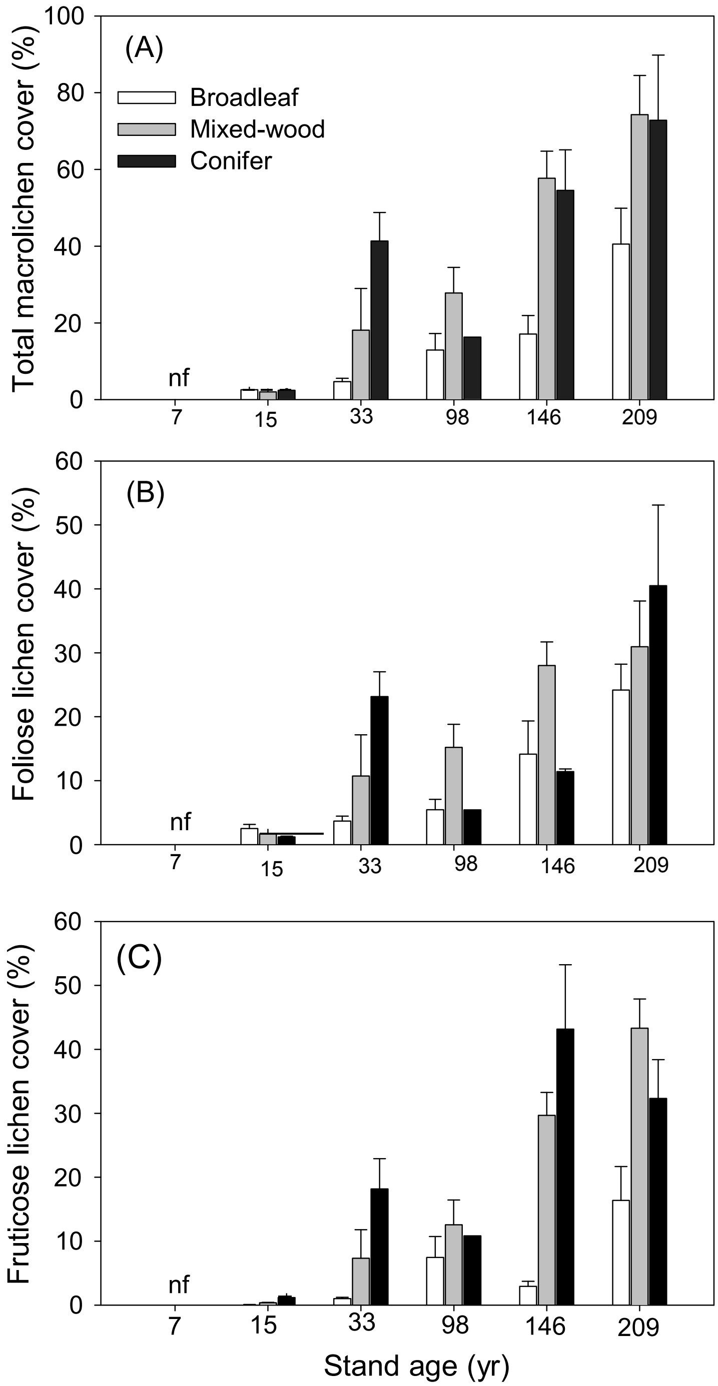


FIGURE 3-1. Epiphytic macrolichen cover (mean + SE) in relation to stand age (7-, 15-, 33-, 98-, 146-, and 209-years) and overstory type (B = broadleaf, M = mixedwood, C = conifer). (A) total macrolichen cover, (B) foliose lichen cover, and (C) fruticose lichen cover in stands of fire origin. The "nf" indicates no epiphytic macrolichen species found in the 7-year-old stands.

Total epiphytic macrolichen richness was strongly influenced by stand age, which accounted for 91.2% of total deviance in species richness, and the interaction between stand age and overstory type was also significant (Table 3-2). It increased with stand age with peak richness in broadleaf and mixed-wood overstory types in 146- and 98-year-old stands, respectively. Total macrolichen richness was higher in mixed-wood than broadleaf and conifer types in the intermediate-aged (98-year-old) stands, but not in other age classes (Fig. 3-2A). Like macrolichen cover, the trends of foliose lichen richness and fruticose lichen richness were similar to that of total macrolichen richness (Table 3-2, Figs. 3-2B and 3-2C).

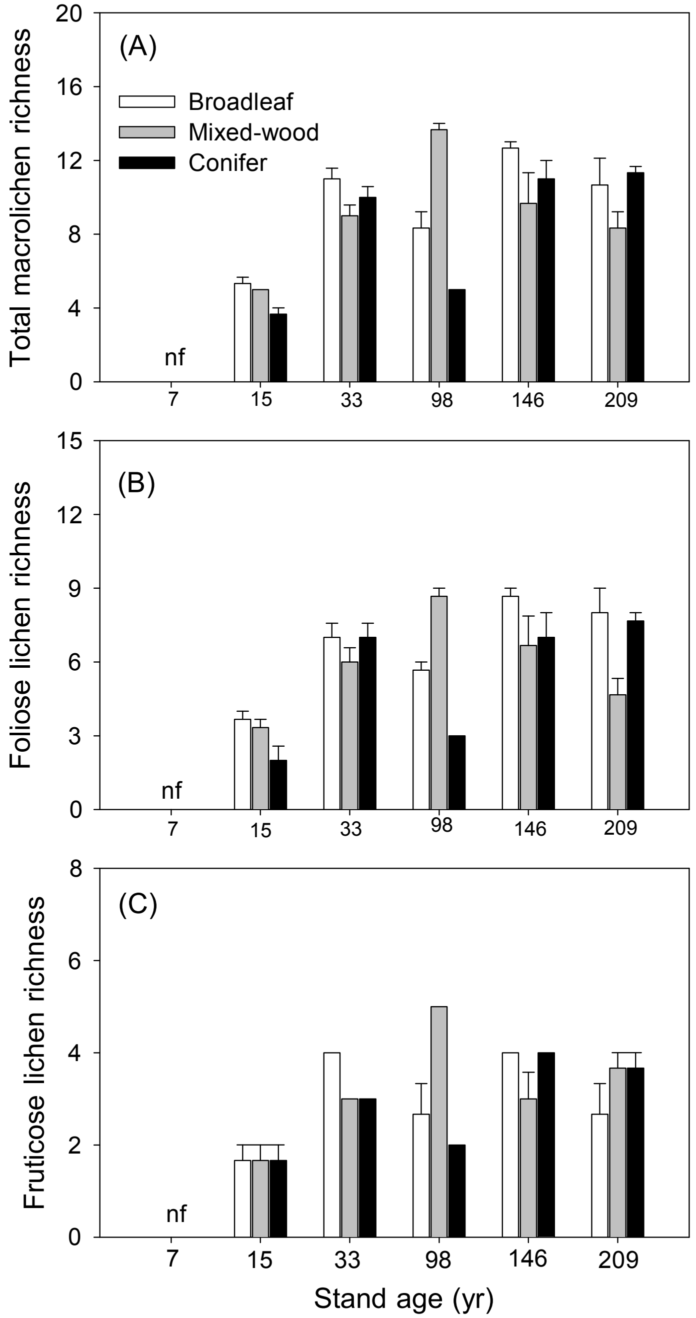


FIGURE 3-2. Epiphytic macrolichen species richness (mean + SE) in relation to stand age (7-, 15-, 33-, 98-, 146-, and 209-years) and overstory type (B = broadleaf, M = mixedwood, C = conifer). (A) total macrolichen species richness, (B) foliose lichen richness, and (C) fruticose lichen richness in stands of fire origin. The "nf" indicates that no epiphytic macrolichen species found in the 7-year-old stands. Note: no error bars indicates that all replicate stands had the same number (count) of species.

Epiphytic macrolichen species composition differed significantly between stand ages ($P < 0.001$, $R^2 = 0.44$) and overstory types ($P < 0.001$, $R^2 = 0.14$) and their interaction ($P < 0.001$, $R^2 = 0.24$, Table 3-2). When the trend in macrolichen species composition was visualized using nonmetric multidimensional scaling ordination, the two major axes captured 83.4% of the variance in the composition data; axis 1 (corresponding to stand age, $r^2 = 0.64$) explained 66.8%, whereas axis 2 (corresponding to overstory type, $r^2 = 0.10$) explained 16.6% of the variation. The young stands were grouped further apart from older stands in ordination space while macrolichen species composition was more similar between old age stands (i.e., 98-, 146- and 209-year-old stands, Fig. 3-3). Macrolichen species composition differed significantly between broadleaf and conifer stands, but there was an overlap between conifer and mixed-wood stands (Fig. 3-3).

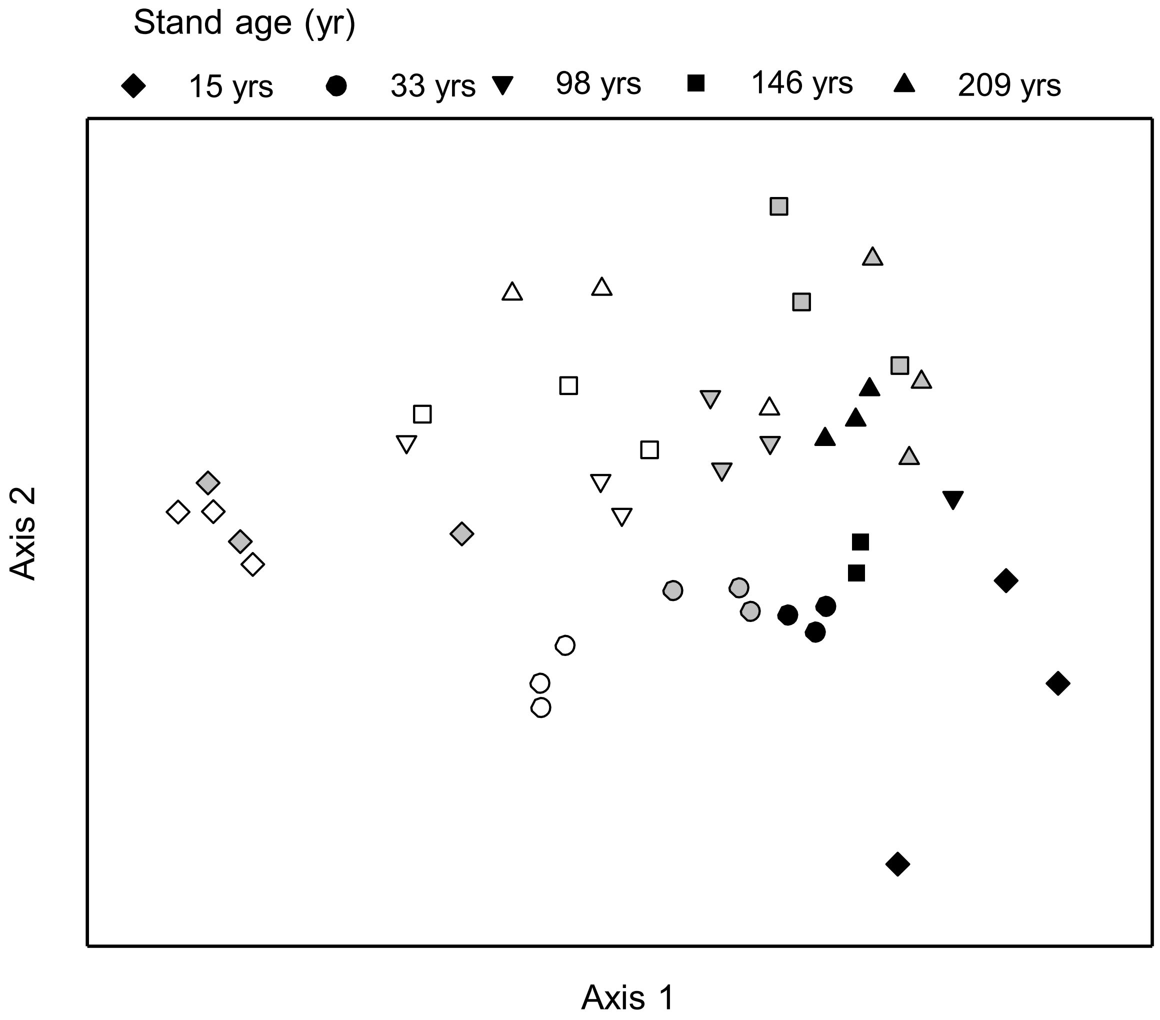


FIGURE 3-3. Nonmetric multidimensional scaling (NMDS) ordination of epiphytic macrolichen species composition. Stand types are broadleaf (white), conifer (black), and mixed-wood (gray). Best NMDS solution was reached at a stress of 0.162. Stands nearest each other in ordination space have similar floristic assemblages, whereas those located farther apart are dissimilar.

Indicator species analysis showed macrolichen species' affiliation to the different stand ages and overstory types. Each stand age and overstory type, except for the intermediate stand age, was associated with at least one indicator species (Table 3-3). The foliose lichens *Xanthoria ulophyllodes* and *Xanthoria fallax*, which occurred exclusively on aspen trees, were identified as indicator species in the 15-year-old and 33-year-old broadleaf stands, respectively. Similarly, the foliose lichen *Tuckermannopsis americana*, which was the most dominant species on pine and spruce trees in young stands, was an indicator species for 33-year-old conifer stands. Furthermore, *Lobaria pulmonaria*, a nitrogen-fixing lichen common in old-growth stands, was identified as an indicator species in 209-year-old conifer stands (Table 3-3).

TABLE 3-3. Indicator values and randomized indicator values for epiphytic macrolichen species that are indicators of the various stand ages and overstory types. Only indicator species with $P < 0.10$ are reported.

Stand age (years)	Overstory*	Species	Indicator values	Indicator values from randomization		
				Mean	SD	*P*
15	B	*Xanthoria ulophyllodes*	33.9	19.9	8.1	0.078
33	B	*Xanthoria fallax*	23.4	17.5	4.1	0.086
33	B	*Physcia stellaris*	96.2	27.3	13.4	0.001
33	C	*Tuckermannopsis americana*	60.1	28.4	7.8	0.001
33	C	*Evernia mesomorpha*	20.4	16	2.8	0.084
146	B	*Phaeophyscia pusilloides*	73	31.5	14.1	0.025
146	B	*Physcia aipola*	49.9	24.6	8	0.010
146	C	*Bryoria capillaris*	97.8	32.4	13.2	0.001
209	C	*Lobaria pulmonaria*	65.2	35.7	15.63	0.074
209	C	*Hypogymnia physodes*	31.5	19.2	5.5	0.027
209	C	*Parmelia sulcata*	23.9	18.5	3.7	0.090
209	M	*Usnea subfloridana*	20.4	15.6	2.5	0.037
209	M	*Ramalina dilacerata*	45.9	27.5	8.3	0.016

Notes: *Overstory types: B – broadleaf, C – conifer, and M – mixed-wood.

DISCUSSION

As we predicted, epiphytic lichen abundance increased continuously with stand development, reaching highest cover in 209-year-old stands. Absence or low abundance of epiphytic lichens in young stands (7-, and 15-year-old) is likely attributable to unfavourable local conditions including microclimate and unsuitable substrate conditions such as small diameter stems and branches with smooth barks (Dettki, Klintberg & Esseen 2000; Sillett *et al.* 2000; Ódor *et al.* 2013; Ruete, Fritz & Snäll 2014). Younger stands in the early stand initiation stage (i.e., 7-year-old) had no detectable macrolichens, but rather contained traces of undifferentiated lichen thalli, which suggests that macrolichen colonization begins directly after disturbance. High macrolichen abundance in older stands is attributable to long colonization time and more suitable substrates such as large diameter stems and branches with rough barks for macrolichen establishment and growth (Esseen, Renhorn & Petersson 1996; Lie *et al.* 2009). Areas made heterogeneous by the presence of canopy gaps, trees with large-diameter lower branches, as is the case in our 209-year-old stands, are considered lichen biodiversity hotspots (Neitlich & McCune 1997).

Epiphytic macrolichen species richness also increased with time since disturbance with highest richness in the canopy transition (i.e., 98- and 146-year-old). The increase of macrolichen species richness from young to intermediate stand ages reflects continuous colonization of different species with stand age (Snäll, Ribeiro Jr & Rydin 2003; Ódor *et al.* 2013; Ruete, Fritz & Snäll 2014). The decline of macrolichen species richness from intermediate to old stand ages is attributable to macrolichen mortality (Snäll, Ribeiro Jr & Rydin 2003) associated with age-related tree mortality of pioneer tree species (Luo &

Chen 2011) and canopy succession (Taylor & Chen 2011; Chen & Taylor 2012). The high macrolichen species richness coincides with high tree species richness at intermediate stages (Brassard *et al.* 2008), supporting the observations that epiphytic macrolichen diversity positively correlates with tree species diversity (Kiraly & Odor 2010; Kiraly *et al.* 2013). The peaks of epiphytic macrolichen diversity at intermediate stand ages suggest that the prediction of intermediate disturbance hypothesis (Connell 1978) is applicable to epiphytic macrolichen diversity.

While the increase in epiphytic macrolichen abundance and diversity with time since fire is consistent with studies that emphasize the influence of stand age on lichen communities (Hyvärinen, Halonen & Kauppi 1992; Price & Hochachka 2001; Nascimbene *et al.* 2009), so far, stand-age related patterns have been examined without considering the influence of overstory composition, whose variation can be attributed to forest age-related succession (Taylor & Chen 2011) and to propogule availability after stand-replacing disturbance (Ilisson & Chen 2009). By examining the independent effect of overstory composition type, we found that epiphytic macrolichen abundance was generally higher in conifer than broadleaf overstory types while it was comparable between conifer and mixed-wood stands. Epiphytic macrolichen diversity on the other hand was not different between broadleaf and conifer overstory types, but was higher in mixed-wood than broadleaf and conifer overstory types in the intermediate stages (i.e., 98-year-old). High macrolichen abundance and diversity in mixed-wood overstory types is consistent with the positive correlation between mixed composition of tree species and higher epiphyte diversity compared with broadleaf- or conifer-dominated old-growth stands (Cleavitt, Dibble & Werier 2009). We reasoned that mixed-wood types would support high lichen abundance and diversity as epiphytic species specific to broadleaf or conifer tree species can co-occur.

We found more foliose than fruticose lichens at the late stand initiation stage (i.e., 15-year-old), providing evidence for previous suggestions that colonization of foliose lichens due to the production of numerous propagules is more rapid than fruticose lichens due to the production of large propagules (Sillett & Goslin 1999; Dettki, Klintberg & Esseen 2000; Sillett *et al.* 2000). However, their responses to stand development and overstory composition were similar. These results indicate that, despite their morphological differences and colonization process, ecological drivers such as stand development and overstory composition have similar impacts on the both functional groups.

Macrolichen species composition changed with time since fire. Since our sampling design considered canopy succession based on thorough understanding of boreal forest dynamics (Chen & Popadiouk 2002; Taylor & Chen 2011; Chen & Taylor 2012), epiphytic macrolichens appear to undergo succession in conjunction with overstory species dynamics. Differences in macrolichen species composition were distinct between early and late successional stages. For instance, many of the lichen species found in old-growth stands such as *Usnea longissima* and *Lobaria pulmonaria* were absent in the younger stands. Even among the young stands, several lichen species such as *Evernia mesomorpha* and *Tuckermannopsis americana* that were common in 33-year-old stands were rarely found in 15-year-old stands. Lichen species composition was more similar in old age classes (98-, 146- and 209-year-old stands). Lichen species compositional overlaps between mature and old-growth stands have also been noted in other studies (Nascimbene, Marini & Nimis 2010).

Furthermore, broadleaf and conifer overstory types supported different macrolichen species composition while macrolichen species composition in mixed-wood stands was intermediate to broadleaf and conifer stands. The differences in lichen species composition between broadleaf and conifer overstory types was further highlighted by the results of indicator species analysis which revealed no common indicator species between broadleaf and conifer overstory types at any stage. The differences in lichen composition between broadleaf and conifer overstory types as well as occurrences on individual host tree species likely reflect host specificity (Laube & Zotz 2006; Cleavitt, Dibble & Werier 2009).

Epiphytic macrolichen abundance, diversity, and composition are strongly influenced by forest age and overstory composition, indicating that shifts in forest age structure and composition can have strong impacts on the successional dynamics of epiphytic macrolichens. For instance, high fire frequency and/or short rotation harvesting regimes that convert large portions of the landscape into young forest stands could result in the loss of macrolichen species with affinity for habitat conditions in older stands. Conversely, epiphytic lichens that are associated with pioneer tree species would go extinct with prolonged absence of stand-replacing disturbance. Furthermore, because broadleaf and conifer stands support different macrolichen abundance and composition, management intervention should aim at maintaining a diverse overstory type, especially mixed-wood stands in order to maintain distinct macrolichen communities in the landscape.

CONCLUSIONS

Epiphytic macrolichen abundance increased with time since fire, reaching highest cover in 209-year-old stands, indicating that epiphytic macrolichens require a long time to recover following stand-replacing disturbance. Epiphytic macrolichen diversity peaks at intermediate stand ages, with highest diversity in mixed-wood stands in the canopy transition stages. Epiphytic macrolichen species composition differed between young and old stands and among overstory types, indicating that different aged stands and overstory types are associated with distinct macrolichen communities. These results suggest that restoration and conservation of epiphytic macrolichen diversity and their ecological functions would require forest managers to maintain a diverse age structure and overstory composition in boreal forest landscapes. The results further highlight that all successional stages merit protection and that mature mixed stands especially should be prioritized in forest conservation planning.

CHAPTER FOUR: EPIPHYTIC MACROLICHEN COVER, RICHNESS AND COMPOSITION IN YOUNG SUCCESSIONAL BOREAL FOREST: A COMPARISON OF FIRE AND LOGGING DISTURBANCE

INTRODUCTION

Epiphytic macrolichens are an ecologically significant component of forest ecosystems (Bergamini and others 2005). They account for the majority of epiphytic floristic diversity and play crucial roles in nutrient and mineral cycling (Knops and others 1996; Matzek and Vitousek 2003). As structurally dependent flora, epiphytic lichens are sensitive to changes in forest structure and composition that are caused by natural disturbances and forestry practices (Hyvärinen and others 1992; Bartels and Chen 2012).

Epiphytic macrolichens are slow colonizers; therefore, time since disturbance, i.e., stand age, constitutes a determining factor of epiphytic lichen development (Hyvärinen and others 1992; Hedenas and Ericson 2000; Price and Hochachka 2001; Bartels and Chen 2012). In addition, canopy tree species composition has strong influence on epiphytic lichen communities (Price and Hochachka 2001; Cleavitt and others 2009; Kiraly and others 2013). In the boreal forests of North America, stand-replacing disturbances such as fire initiate stand development in multiple successional pathways, such that stands at any given stage of stand development can be dominated by either broadleaf or conifers or mixed species dominance (Chen and Popadiouk 2002; Taylor and Chen 2011). Yet, the independent effect of stand composition on the temporal development of epiphytic lichens in fire *vs.* logged stands has not been previously examined.

Wildfire is the most prevalent natural disturbance factor that shapes the structure and function of North American forests (Johnson 1996, Weber and Flannigan 1997). However, in recent years, harvesting, mostly in the form mechanical clearcut harvesting (hereafter logging), has emerged as an important stand-replacing disturbance in boreal forests as a result of increased demand for forest resources in the 21st century. In managed landscapes, logging is designed to emulate the natural wildfire disturbance (Canadian Council of Forest Ministers 2005), but few have examined its conservation potential for macrolichens relative to wildfire (Johansson 2008). Many previous studies have examined the consequences of disturbance on epiphytic lichens (Rolstad and others 2001; Hilmo and others 2005; Storaunet and others 2008). However, the effect of disturbance origin is too often confounded with stand age, as most studies compare young managed stands with old fire-origin stands (Hyvärinen and others 1992; Esseen and others 1996; Dettki and Esseen 1998; Kuusinen and Siitonen 1998; Ódor and others 2013).

In this paper, our objective was to evaluate the independent and interactive influences of disturbance type, stand age, and composition on epiphytic lichens during early forest development in post-fire and post-logged stands in the boreal forest of central Canada. Specifically, we determined whether the temporal dynamics of epiphytic lichen abundance, diversity, and composition differ between stands originating from wildfire and logging. We focused on epiphytic macrolichens because of their indicator statuses and conservation value (McCune 2000; Will-Wolf 2002; Bergamini and others 2005), but because the macrolichen functional groups (foliose and fruticose) may differ in their colonization of young forests (Dettki and others 2000), we also examined whether their responses to disturbance origin, stand development and overstory composition differed.

MATERIALS AND METHODS

Study Area and Sites

The study was conducted in the boreal forests north of Lake Superior and west of Lake Nipigon in the Black Spruce Forest, located approximately 100 km north of Thunder Bay, Ontario, Canada (49°23'N to 49°36'N, 89°31'W to 89°44'W). This study area falls within the Moist Mid-Boral (MBX) ecoclimatic region (Ecoregions Working Group 1989) and is characterized by warm summers and cold, snowy winters. The mean annual temperature is 2.5°C and precipitation is 712 mm (Environment Canada 2014). The soils on our sample sites are composed of deep glacial tills of the Brunisolic and Podzolic orders (Soil Classification Working Group 1998). Stand-replacing fire is the most dominant natural disturbance in the study area, with an average fire return interval of approximately 100 years for the past century (Senici et al. 2010).

The dominant overstory tree species in the area include jack pine, trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* [Mill] B.S.P.), balsam fir (*Abies balsamea* L. Mill), and white spruce (*Picea glauca* [Moench] Voss). Common understory shrub and herbaceous species in the area as studied by Hart and Chen (2008) include mountain maple (*Acer spicatum* Lam.), dwarf raspberry (*Rubus pubescens* Raf.), alder (*Alnus* spp.), beaked hazel (*Corylus cornuta* Marsh.), bluejoint reedgrass (*Calamagrostis canadensis* Michx.), Canadian mayflower (*Maianthemum canadense* Desf.), violet (*Viola* spp.) and large-leaved aster (*Aster macrophyllus* L.).

Commercial harvesting, mainly clearcut harvesting, began in the area in the 1970s. Dependent on management objectives for tree species composition, burned and logged sites are left to naturally regenerate for broadleaf forest type, whereas jack pine (*Pinus banksiana* Lamb.) is usually planted or aerial seeded for conifer and mixedwood forest types, with no intensive management such as thinning and pruning.

Sampling Design

To determine the effect of disturbance type and time since fire, we selected two 7 – 33-year chronosequences of fire and logging origin that shared similar developmental histories. Although some have expressed reservations on the use of the chronosequence method (Johnson and Miyanishi 2008), others have clarified that given careful site selection, replication, and demonstration of developmental links, the chronosequence method is well suited for studying successional processes over decadal to centennial time scales (Walker and others 2010). Because commercial harvesting only began in the 1970s, the temporal scale of our sampling for both post-fire and post-logged stands was limited to available harvested stands from the past 35 years. Our comparison was further constrained by the availability of independent, large, stand-replacing fires that occurred during the same time period as harvesting; however, we were able to sample three age classes (7-, 15-, and 33-years since fire or logging) that represented the stand initiation, early stem exclusion, and late stem exclusion stages of boreal stand development, respectively (Chen and Popadiouk 2002). Time since last stand-replacing fire (TSF) was determined from detailed fire records (Senici and others 2010) and time since harvesting was obtained from silviculture and forest management records.

Since stands of both fire and logging origin on mesic sites in the region can be dominated by conifer, broadleaf or mixed-wood in the overstory at any given stage of stand development (Frelich and Reich 1995; Chen and Popadiouk 2002; Ilisson and Chen 2009; Taylor and Chen 2011), we made every effort to sample all three overstory stand types for each age class. We sampled three replicates for each combination of stand age and overstory type for each stand origin, resulting in a total of 27 post-fire and 27 post-logged stands (Table 4-1). We avoided sampling stands of the same age in close proximity to one another to minimize the impact of spatial structure (Legendre and Legendre 1998). This was achieved by selecting stands of the same age class from different road accesses, resulting in distances between stands in the range of 0.5 to 10 km. In order to minimize site variability, we selected only stands located on mesic sites on flat-mid-slope positions, with no slope exceeding 5%. The stands were located on well-drained (sandy or silty loams) glacial moraines, >50 cm in thickness, which is the prevailing soil type in our study area. To ensure that each sample stand met these criteria, soil pits were dug in each candidate stand to verify whether the site was mesic, following the procedures described in Taylor and others (2000). The selected stands were > 1 ha in area, visually homogeneous in stem density and composition.

TABLE 4-1. Characteristics of 54 stands sampled in the boreal forest of Ontario, Canada.

Origin	Stand age (yrs)	Over-story*	*n*	Stand density (stems/ha) or basal area (m^2/ha)*, †	Tree species richness	Stand composition (%)†					
						Trembling aspen	White birch	Jack pine	Black spruce	Balsam fir	Others ‡
Fire	7	B	3	5783 (808)	3.0 (0.0)	58 (19)	28 (19)	15 (2)			
	7	C	3	5608 (2249)	2.3 (0.3)		2 (2)	97 (2)	<1.0		
	7	M	3	3275 (290)	3.7 (0.3)	38 (10)	15 (7)	43 (15)	4 (3)		
	15	B	3	10242 (60)	3.0 (0.0)	80 (5)	7 (1)	13 (5)			
	15	C	3	4433 (405)	3.0 (0.0)	29 (18)	2 (2)	69 (17)			
	15	M	3	6383 (736)	3.0 (0.0)	57 (8)	<1.0	34 (2)	9 (8)		
	33	B	3	33.4 (3.9)	3.0 (0.6)	89 (4)	4 (3)	4 (1)	1(1)		< 1.0
	33	C	3	32.2 (2.4)	3.3 (0.3)	4 (2)	1 (1)	94 (3)	< 1.0		
	33	M	3	25.6 (0.5)	2.7 (0.3)	36 (7)	< 1.0	55 (12)	8 (8)		
Logging	7	B	3	7717 (1910)	3.7 (0.7)	83 (12)	11 (9)		4 (2)		2 (1)
	7	C	3	1725 (189)	2.3 (0.9)	5 (5)		65 (32	23 (20)	7 (7)	
	7	M	3	2242 (639)	4.7 (0.3)	37 (19)	17 (4)	33 (17)	6 (3)	5 (5)	2 (1)
	15	B	3	10233 (755)	4.7 (0.3)	70 (9)	17 (7)	3 (3)	6 (1)		3 (1)
	15	C	3	3967 (820)	3.7 (0.3)	2 (1)	2 (2)	70 (14)	23 (11)	3 (2)	
	15	M	3	5833 (2285)	5.0 (0.0)	10 (6)	28 (13)	43 (10)	7 (5)	10 (5)	2 (2)
	33	B	3	24.1 (1.2)	3.7 (0.3)	79 (9)	16 (9)	1 (1)	2 (1)		2 (1)
	33	C	3	30.1 (1.1)	2.7 (0.3)	1 (1)		97 (1)	1(1)		<1.0

33	M	3	32.6 (2.3)	3.7 (0.9)	42 (8)	1 (1)	51 (5)	5(4)		1 (1)

Notes: *Overstory types: B – broadleaf, C – conifer, and M – mixed-wood.

†Values are means with 1 SE in parentheses. Stand density (stems/ha) was determined for the younger (7- and 15-year-old) stands and basal area (m^2/ha) for older stands.

‡The "Others" category includes white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera* L.), and mountain maple (*Acer spicatum*) with DBH > 5 cm.

Data Collection

In each selected stand, we established a 400-m^2 circular plot within which all data was collected. Plots were randomly located, but were at least 50 m from the forest edge in order to avoid edge effects. We identified all tree species and measured the diameter at breast height (DBH; 1.3 m above the root collar) of all trees of each sample plot for the 33-year old stands. For the younger (7- and 15-year old) stands, tree stems were counted by species. Stand density and basal area by species were summed to plot level and scaled up to level per hectare. Overstory types were assigned based on the relative density or basal area of broadleaf and conifer tree species in a plot. Broadleaf and conifer stands were defined as stands that composed of > 65% broadleaf or conifer tree species by stand basal area or stem density. Mixed-wood stands were defined as neither broadleaf nor conifer tree species > 65% by stand basal area or stem density (Table 4-1).

In each plot, we conducted a thorough reconnaissance of the entire plot area and sampled epiphytic lichens using the whole-plot ocular method (McCune and Lesica 1992). On each tree of the sample plot, we visually estimated the percent cover of all epiphytic macrolichen species present on the trunks and branches, similar to the visual estimation method used for ground vegetation (Mueller-Dombois and Ellenberg 1974). Individual trees were viewed as habitat units or quadrats (Burns 2007). Sampling included only macrolichen species occurring > 0.5 m above root collar to avoid inclusion of terricolous or saxicolous lichen species. The nomenclature of lichens follows that of Brodo et al. (2001).

Data Analyses

Epiphytic macrolichen abundance was calculated as the mean percent cover of all macrolichen species on all trees within each plot. Macrolichen diversity assessed as species richness was the total number of epiphytic lichen species recorded in the plot. In addition to total macrolichen cover and richness, we separately analyzed cover and richness of the two epiphytic macrolichen functional groups distinguished by their morphology, i.e., the shrubby or pendulous foliose lichens and the flattened or leafy fruticose lichens (Brodo and others 2001). Similarly, epiphytic macrolichen composition was at the plot level and was derived as the mean percent cover of each macrolichen species on all trees within each plot.

We tested whether epiphytic lichen cover and richness differ between stands of fire and logging origin using the following model:

$$Y_{ijkl} = \mu + A_i + T_j + O_k + A \times T_{ij} + A \times O_{ik} + T \times O_{jk} + A \times T \times O_{ijk} + e_{l(ijk)} \quad (1)$$

where Y_{ijkl} is cover or species richness (separately analyzed by total macrolichen, foliose, and fruticose lichen), μ is the overall mean, A is stand age class (i = 1, 2, 3), T is overstory type (j = 1, 2, 3), O is stand origin (k = 1, 2), and e is random sampling error from replications (l =1, 2, 3) within stand age, type, and origin.

Because macrolichen cover was estimated as percentage, we applied arcsine-square-root transformation, as recommended by Crawley (2007). Since both cover and richness did not confirm the assumptions of normality and homogenous variances for general linear models, we used a generalized linear model (GLM) with the Gaussian family error distribution and an identity link function for cover data, and a GLM with a Poisson error distribution and a logarithmic link function for species richness (count data) in R (R Development Core Team 2013). The initial models showed evidence of overdispersion; hence, we corrected the standard errors using a quasi-GLM model with the variance given by $ø \times \mu$, where ø is the dispersion parameter (Zuur and others 2009). The significance of the predictors was tested using F tests by means of analysis of deviance, and the deviance explained by each variable in the model was calculated as a percentage of residual deviance explained from the null model. The significance of differences among *A*, *T*, and *O* levels was tested using Tukey's multiple comparison in the *glht* function in the multcomp package (Hothorn and others 2008). Statistical significance was set at $\alpha = 0.05$.

We used permutational multivariate analysis of variance (PERMANOVA) to test the effects stand age, overstory compositional type, and stand origin on lichen species composition. PERMANOVA, which is a nonparametric, multivariate analysis that uses permutation techniques to test for compositional differences between more than one factor (Anderson 2001), was run using the Bray-Curtis dissimilarity and 1000 permutations of the compositional data. We then examined the trends in the compositional data using nonmetric multidimensional scaling (Kruskal 1964), which is an ordination method suitable for data that are non-normal or on discontinuous scales (McCune and Grace 2002) by specifying the Bray-Curtis dissimilarity index. All statistical analyses were performed using R (R Development Core Team 2013).

RESULTS

We recorded a total of 16 epiphytic macrolichen species, of which 12 were foliose lichens and 4 were fruticose lichens (Table 4-2). The 7-year-old stands in both post-fire and post-logged stands lacked epiphytic macrolichen species or only contained traces of undifferentiated lichen thalli (lichen body) mainly on beaked hazel (*Corylus cornuta*). Total macrolichen cover estimated per plot ranged from 1% to 53% (mean ± 1 SE: 9.2 ± 2.1) and the number of species per plot varied between 2 and 13 (7.4 ± 0.6).

Total macrolichen cover was significantly affected by stand age, overstory type, and stand origin with stand age accounting for the largest share of deviances (Table 4-3). Total macrolichen cover increased with stand age for all overstory types (Fig. 4-1A). While it did not differ between logging and fire origin stands for any overstory type in the 15-year-old stands, total macrolichen cover in the 33-year-old stands was significantly higher in conifer stands and marginally higher in mixed-wood stands of fire origin than logging origin, but did not differ between in broadleaf stands (Fig. 4-1A). When analysed by functional groups, both foliose lichen cover and fruticose lichen cover were influenced similarly as total macrolichen cover (Table 4-3 and Figs. 4-1B and 4-1C).

TABLE 4-2. Frequency (%) of epiphytic macrolichens species encountered, grouped by stand origin, age, and forest type.

Species/ Stand age		Fire			Logging		
	Growth form	Broadleaf	Mixedwood	Conifer	Broadleaf	Mixedwood	Conifer
Stand age (15 years)							
Evernia mesomorpha	fruticose	0.5	0.8	4.3	-	2.0	8.4
Parmelia sulcata	foliose	8.8	0.8	1.1	0.5	7.3	20.4
Physcia aipolia	foliose	0.5	0.8	-	-	-	-
Ramalina dilacerata	fruticose	0.2	-	-	-	-	-
Tuckermannopsis americana	foliose	-	-	5.6	-	1.9	8.2
Usnea subfloridana	fruticose	1.1	1.2	2.4	-	5.1	10.3
Vulpicida pinastri	foliose	-	-	0.6	-	-	1.3
Xanthoria fallax	foliose	20.4	19.9	-	8.8	1.9	0.6
Xanthoria ulophyllodes	foliose	11.6	7.2	-	11.6	-	-
Stand age (33 years)							
Bryoria capillaris	fruticose	7.1	-	-	3.2	4.4	9.9
Evernia mesomorpha	fruticose	20.3	62.2	93.4	41.6	64.0	99.2
Flavopunctelia flaventior	foliose	-	-	-	0.3	-	-
Hypogymnia physodes	foliose	12.9	38.3	93.6	5.0	51.9	98.7
Melanelia septentrionalis	foliose	1.9	-	-	11.2	4.1	-
Parmelia sulcata	foliose	19.6	27.2	3.3	46.6	59.1	35.4
Phaeophyscia pusilloides	foliose	-	-	-	0.3	-	-
Physcia aipolia	foliose	-	8.0	26.3	0.6	-	-
Physcia stellaris	foliose	58.9	1.7	1.5	44.5	29.6	0.4
Platismatia tuckermanii	foliose	-	-	-	2.9	-	-
Ramalina dilacerata	fruticose	15.1	16.3	2.7	14.5	19.3	0.4
Tuckermannopsis americana	foliose	11.3	62.3	93.9	10.9	60.7	98.7
Usnea subfloridana	fruticose	15.8	68.9	94.5	40.1	65.3	99.4
Vulpicida pinastri	foliose	6.8	8.5	14.6	4.1	11.1	10.8
Xanthoria fallax	foliose	79.7	21.3	5.5	62.2	37.8	0.4
Xanthoria ulophyllodes	foliose	0.5	-	0.5	0.6	0.5	-

TABLE 4-3. Analysis of deviance of the effects of stand age (A_i $i = 1, 2, 3$), overstory type (T_j $j = 1, 2, 3$), and stand origin (O_k $k = 1, 2$) on epiphytic lichen cover and richness in post-fire *vs.* post-logged stands. Bold fonts indicate statistical significance ($\alpha = 0.05$).

Source	df	Total lichen cover	Foliose lichen cover	Fruticose lichen cover	Total lichen richness	Foliose lichen richness	Fruticose lichen richness
		P-value (deviance explained %)	*P*-value (deviance explained %)	*P*-value (deviance explained %)	*P*-value (deviance explained %)	*P*-value (deviance explained %)	*P*-value (deviance explained %)
A_i	2	**<0.001** (68.02)	**<0.001** (71.15)	<**0.001** (62.50)	<**0.001** (96.41)	<**0.001** (93.93)	<**0.001** (87.63)
T_j	2	**<0.001** (5.58)	**0.022** (1.93)	<**0.001** (13.29)	<**0.001** (0.46)	<**0.001** (1.46)	0.171 (0.19)
O_k	1	0.064 (1.02)	**0.015** (1.92)	0.470 (0.12)	0.638 (0.01)	**0.034** (0.27)	0.999 (0.0)
$A \times T_{ij}$	4	<**0.001** (10.15)	<**0.001** (7.69)	<**0.001** (11.14)	**0.015** (0.35)	0.995 (0.01)	<**0.001** (2.57)
$A \times O_{ik}$	2	**0.026** (2.02)	**0.017** (2.89)	0.167 (0.90)	<**0.001** (0.49)	**0.008** (0.62)	**0.001** (0.85)
$T \times O_{jk}$	2	0.120 (1.03)	0.098 (0.96)	0.247 (0.80)	0.075 (0.13)	0.069 (0.32)	<**0.001** (2.36)
$A \times T \times O_{ijk}$	4	**0.036** (3.04)	**0.012** (3.84)	0.065 (2.39)	<**0.001** (1.27)	<**0.001** (1.33)	<**0.001** (4.33)

Notes: The columns give degrees of freedom (df), deviance explained (%), and the p-value when F-test is used to test for significance.

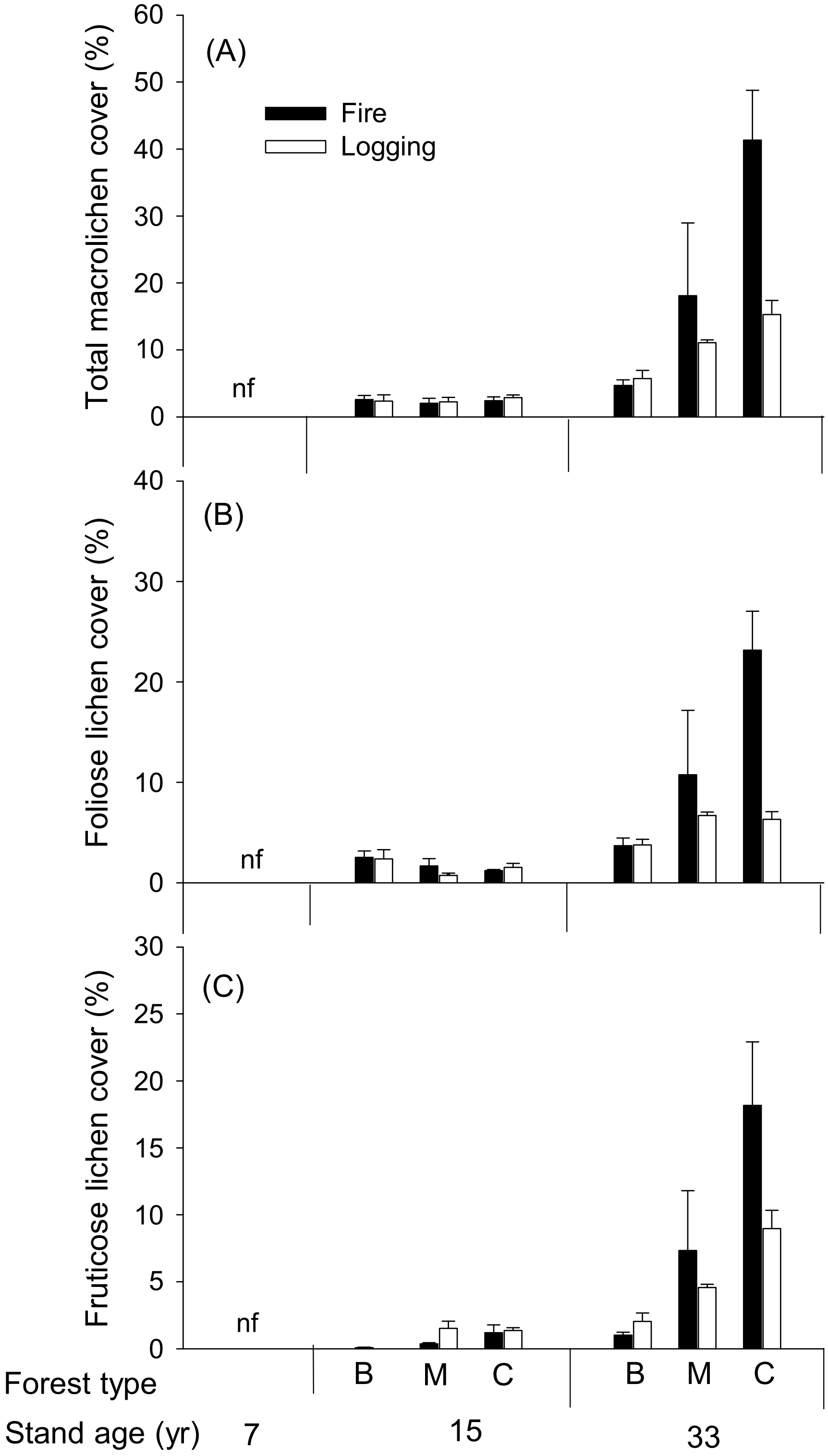


FIGURE 4-1. Effects of disturbance type (fire *vs.* logging), stand age (7-, 15-, and 33-years), and overstory type (B = broadleaf, M = mixedwood, C = conifer) on (A) total

epiphytic macrolichen cover, (B) foliose lichen cover, and (C) fruticose lichen cover (mean + 1SE). The “nf” indicates that no macrolichen species found in the 7-year-old stands.

Total macrolichen richness was significantly affected by stand age, overstory type, and stand origin (Table 4-3). It increased with stand age, which accounted for 96.4% of total deviance in species richness, for all overstory types (Fig. 4-2A). Total macrolichen richness in broadleaf overstory type in 15-year-old stands was higher in fire origin than logging origin stands, but it did not differ between conifer nor mixed-wood stand of fire *vs.* logging origin. In the 33-year-old stands, total macrolichen richness was higher in mixed-wood overstory types of logging-origin than fire origin stands, but did not differ between broadleaf and conifer overstory types of fire *vs.* logging origin (Fig. 4-2A). Like macrolichen cover, the trends of foliose lichen richness and fruticose lichen richness were similar to that of total macrolichen richness (Table 4-3, Figs. 4-2B and 4-2C).

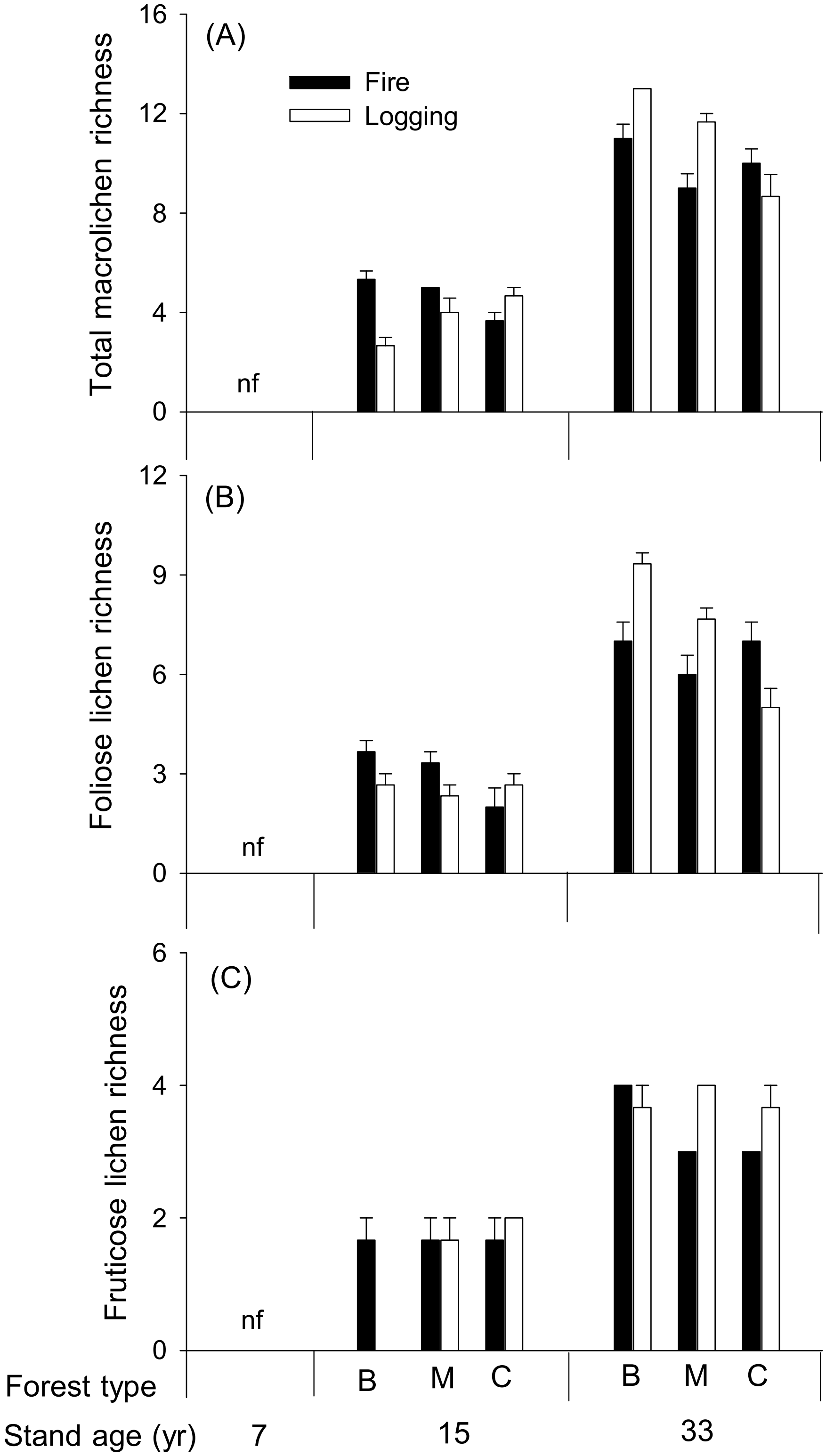


FIGURE 4-2. Effects of disturbance type (fire *vs.* logging), stand age (7-, 15-, 33-years), and overstory type (B = broadleaf, M = mixedwood, C = conifer) on (A) total epiphytic

macrolichen richness, (B) foliose lichen richness, and (C) fruticose lichen richness (mean + 1SE). The “nf” indicates that no macrolichen species found in the 7-year-old stands. Note: no error bars indicates that all three replicate stands had the same number (count) of species.

Permutational multivariate analysis of variance indicated significant differences in epiphytic macrolichen species composition between post-fire vs post-logged stands ($P = 0.003$, $R^2 = 0.043$), stand ages ($P \leq 0.001$, $R^2 = 0.209$), and overstory types ($P \leq 0.001$, $R^2 = 0.249$) and their interactions (Table 4-4). In nonmetric multi-dimensional scaling, stands of different ages and overstory types of fire and logging origin showed a strong separation along the NMDS2 axis in ordination space (Fig. 4-3). For both stand origins, lichen species composition varied between broadleaf and conifer stands with mixed-wood stands being intermediate (Fig. 4-3).

TABLE 4-4. Results of permutational multivariate analysis of variance (PERMANOVA) testing the effects of stand age (A_i $i = 1, 2, 3$), overstory type (T_j $j = 1, 2, 3$), and stand origin (O_k $k = 1, 2$) on lichen species composition. R^2 is proportional variance accounted for by each model term.

Source	df	SS	*F*	*P*	R^2
A_i	1	1.75	19.34	<0.001	0.181
T_j	2	2.40	13.31	<0.001	0.249
O_k	1	0.41	4.56	<0.001	0.043
$A \times T_{ij}$	2	1.68	9.31	<0.001	0.174
$A \times O_{ik}$	1	0.28	3.06	0.018	0.029
$T \times O_{jk}$	2	0.42	2.31	0.017	0.043
$A \times T \times O_{ijk}$	2	0.56	3.10	0.004	0.058
Error	24	2.17			

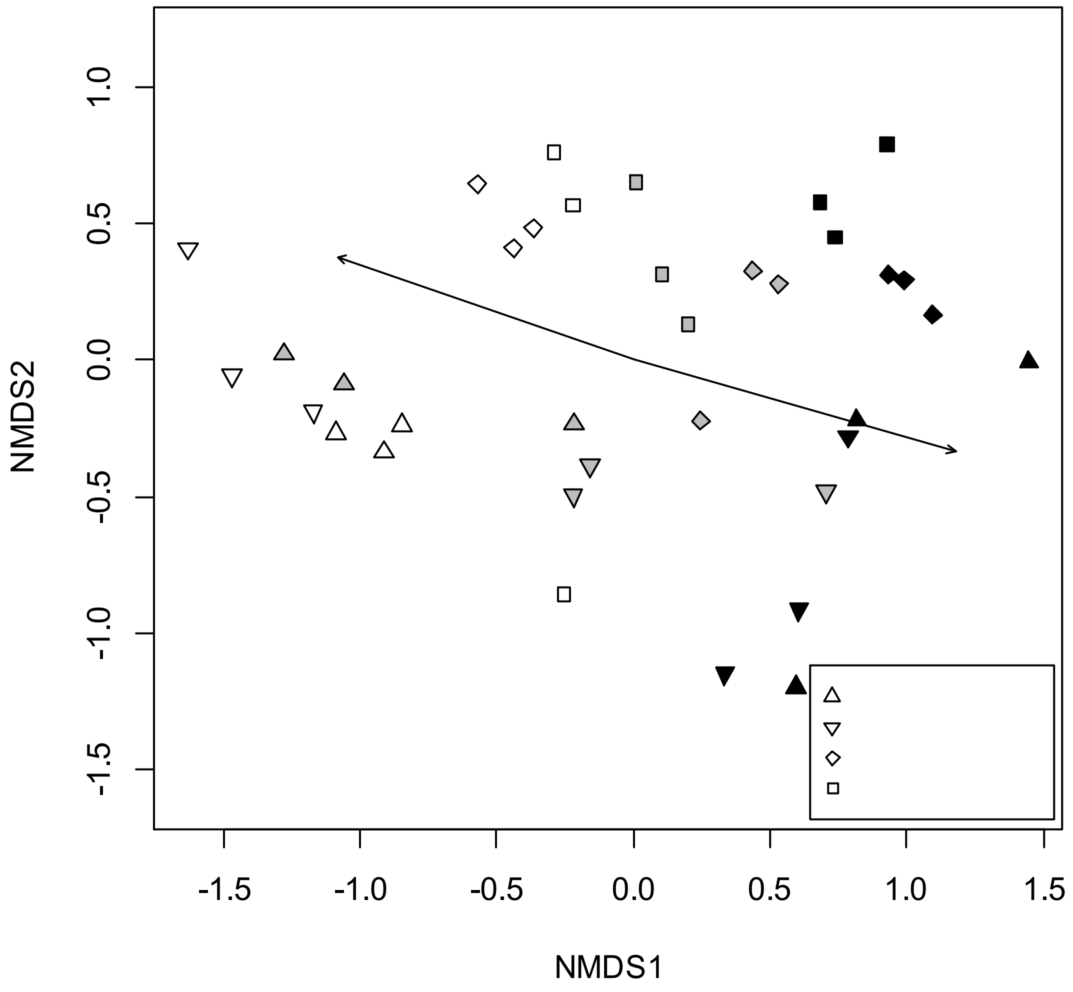


FIGURE 4-3. Nonmetric multidimensional scaling (NMDS) ordination of epiphytic macrolichen species composition for broadleaf (white symbol), conifer (black symbol), and mixed-wood (gray symbol) stands of age 15 and 33 years. Best NMDS solution was reached at a stress of 0.165. Axis 1 shows a good separation between overstory types while axis 2 shows a fair separation between stand origins. Stands nearest each other in ordination space have similar macrolichen composition whereas those located farther apart are less similar.

DISCUSSION

Unlike most previous studies that compare old post-fire stands with young managed stands (Hyvärinen and others 1992; Esseen and others 1996; Dettki and Esseen 1998; Kuusinen and Siitonen 1998; Ódor and others 2013), our study evaluates the independent and interactive effects of stand age, overstory composition, and stand origin on epiphytic macrolichen abundance, diversity, and composition. We found that epiphytic macrolichen cover and richness in both post-fire and post-logged stands consistently increased with time since disturbance for all overstory types, a phenomenon which is consistent with previous studies (Hyvärinen and others 1992; Price and Hochachka 2001; Boudreault and others 2009). We found, however, that epiphytic macrolichens had not recovered seven years after fire or logging, indicating that epiphytic macrolichens require sufficient time to re-establish after fire or logging. The absence or low cover and richness of epiphytic macrolichens in the young (7- and 15-year-old) stands may be due to establishment limitation such as lack of lichen propagules or unfavourable local conditions such as small diameter stems and branches with smooth barks (Dettki and others 2000; Sillett and others 2000; Boudreault and others 2009; Ódor and others 2013; Ruete and others 2014). Higher epiphytic lichen cover and richness in the 33-year-old stands reflect increased time available for colonization. The rapid increases of lichen cover and richness from 7- to 33-year-old stands indicate continuous species addition, i.e., the community remains unsaturated with the persistence of pioneers as well as later colonists (Ellis 2012).

In 15-year-old stands, we found higher epiphytic lichen species richness in fire- than logging-origin broadleaf stands, but no differences in conifer or mixed-wood stands. Evidently, *Physcia aipolia* and *Ramalina dilacerata* appeared in 15-year-old post-fire, but not in post-logged broadleaf stands (Table 2), contributing to the difference in species richness. In 33-year-old stands, macrolichen cover in conifer and mixedwood stands was higher in post-fire than in post-logged stands, whereas lichen richness in mixed-wood stands was higher in post-logged than in post-fire stands. More prominently, we found strong compositional differences between post-fire and post-logged stands as well as the influences of stand age and overstory type. Stand age effect reflects the difference of colonization processes among epiphytic lichen species since some are early colonizers and others are intermediate or late colonizers (Hedenas and Ericson 2000). The effect of overstory composition is attributable to host-specific associations between tree species and epiphytic lichen species (Price and Hochachka 2001; Cleavitt and others 2009; Kiraly and others 2013).

The underlying mechanisms for the observed differences between post-fire and post-logged stands of the same age and overstory composition are, however, unclear. We speculate that regeneration density and genetic makeup of trees may be contributing factors. First, post-fire conifer stands regenerated naturally by jack pine typically start with higher stem density than post-logged stands established by planting (*see* Table 4-1) and likely increase the probability of post-disturbance lichen colonization. Second, planted trees that could have narrower genetic diversity may have also affected the post-disturbance colonization process. Also, the higher lichen richness in the post-logged mixed-wood stands may be attributable to higher tree species richness in these stands (Taylor and others 2013), as high tree species richness promotes epiphytic lichen diversity (Kiraly and Odor 2010; Kiraly and others 2013). Furthermore, the differences in epiphytic macrolichen abundance, diversity, and composition between the stands of the two disturbance origins could be a result of their different effects on soil nutrient availability and stoichiometry (Shrestha and Chen 2010; Chen and Shrestha 2012), as evidenced by strong fertilization effects on the composition and productivity of epiphyte communities (Benner and Vitousek 2007).

In the first study to simultaneously examine independent and interactive effects of stand age, overstory composition, and stand origin on epiphytic lichen abundance, diversity, and composition in forest ecosystems, we show that logging does not influence epiphytic lichens similarly as fire, extending three decades after disturbance. We show that epiphytic lichens require substantial time for colonization in both post-fire and post-logged stands, but post-fire stands have higher than or similar cover and richness than post-logged stands except 33-year-old mixed-wood stands. More pronounced is the compositional difference of epiphytic lichens between post-fire and post-logged stands. The differences could be a result of multiple mechanisms varying from difference in regeneration density, genetic diversity of trees, and soil nutrient availability and stoichiometry. Furthermore, it is unclear whether the effect of fire and logging may eventually converge over time as stands continue to grow older. Long-term assessment of the effects of logging and wildfire on epiphytic lichen development would be useful in determining the conservation value of logging relative to the natural wildfire disturbance.

CHAPTER FIVE: SPECIES DYNAMICS OF EPIPHYTIC MACROLICHENS IN RELATION TO FOREST AGE AND HOST TREE SPECIES IN BOREAL FOREST

INTRODUCTION

Epiphytic macrolichens are a prominent feature of the boreal forest (Esseen et al. 1996, Campbell et al. 2010), and useful indicators forest health and successional sequence (Hedenas and Ericson 2000, McCune 2000). Many specialized macrolichens including cyanolichens are recognised for their contribution to nutrient and mineral cycling (Knops et al. 1996, Campbell et al. 2010). The lack of suitable habitat is a primary cause for population decline of many forest specialists over the last decades. Understanding the link between the dynamics of macrolichens and their hosting habitat is urgent to the conservation of epiphytic macrolichens.

Wildfire is the most prevalent natural, stand-replacing disturbance that shapes the structure and function of northern forests (Johnson 1996, Weber and Flannigan 1997). Most epiphytic lichen species are observed more frequently on old than on young trees (Fritz et al. 2009, Lie et al. 2009, Nascimbene et al. 2009) with some occurring almost exclusively in old-growth stands (Boudreault et al. 2000). Epiphytic lichens may differ in colonising ability; some can colonise substrates quickly, others colonise very slowly and can take hundreds of years to become fully established (Hedenas and Ericson 2000, Gjerde et al. 2012). Frequent occurrence of some epiphytic lichens on large trees and in older stands is attributable to time available for colonization (Snall et al. 2003, Snall et al. 2005). Time available for colonization, which reflects stand age in boreal forest, thus constitutes an important determinant of epiphytic lichen diversity (Hyvärinen et al. 1992, Price and Hochachka 2001, Nascimbene et al. 2010). Epiphytic lichen biomass also changes from young to old forests (Esseen et al. 1996, Boudreault et al. 2009), suggesting that epiphytic lichens may undergo succession in conjunction with the canopy succession of tree species. But the recolonization of epiphytic lichens following fire in the boreal forests is far from being fully understood (Johansson 2008). It is not clear as to which species are added or lost with stand development following stand replacing fire.

Individual host trees are habitat units that support epiphyte species by providing favorable conditions suitable for the species' survival and reproduction. It is generally viewed that each host tree species houses a specific subset of the local epiphytic species pool (Callaway et al. 2002, Laube and Zotz 2006). Some epiphytic species appear to be confined to specific hosts such as deciduous or coniferous tree species (Cleavitt et al. 2009, Kiraly and Odor 2010). However, the vast majority of studies in northern forests have examined epiphytic lichen occurrences on one or a few tree species (Esseen et al. 1996, Boudreault et al. 2000, Johansson and Ehrlén 2003, Hedenås and Hedström 2007, Nascimbene et al. 2010, Fedrowitz et al. 2012). It remains unknown for a wide range of host tree species considered in boreal forests, to what extent epiphytic lichens show preferences for tree species. Moreover, it is not known how epiphytic lichen species composition on the host tree is influenced by time since colonization and host tree identity.

The aim of this study is to examine the independent and interactive effects of time since disturbance and tree species on the dynamics of epiphytic macrolichen species in the central boreal forest of Canada. Specifically, we examine: (1) how the occurrence of epiphytic macrolichen species is influenced by time since wildfire, (2) how epiphytic macrolichen species are associated with host tree species, and (3) whether the occurrence and composition of epiphytic macrolichen species on individual tree species change through stand development.

MATERIALS AND METHODS

Study Area and Sites

We used data collected in the mixed-wood boreal forests of central Canada in an area located north of Lake Superior and west of Lake Nipigon in northwestern Ontario (49°23'N to 49°36'N, 89°31'W to 89°44'W). The closest meteorological station is located in Thunder Bay, Ontario, Canada. The study area falls within the Moist Mid-Boral (MBX) ecoclimatic region (Ecoregions Working Group 1989) and is characterized by warm summers and cold, snowy winters, with a mean annual temperature of 2.5°C and mean annual rainfall of 712 mm (Environment Canada 2014). The soils on the upland sites compose of deep glacial tills of the Brunisolic and Podzolic orders (Soil Classification Working Group 1998). The study area has an extensive history of stand-replacing fire, with an average fire return interval of approximately 100 years for the past century (Senici and others 2010). Within those areas managed for production, silvicultural intervention, particularly clear-cut harvesting has been in practice since the 1970s.

The vegetation of the area is dominated in the overstory by jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* [Mill] B.S.P.), balsam fir (*Abies balsamea* L. Mill), and white spruce (*Picea glauca* [Moench] Voss). Dominant understory shrub and herbaceous species in the area as studied by Hart and Chen (2008) include mountain maple (*Acer spicatum* Lam.), dwarf raspberry (*Rubus pubescens* Raf.), alder (*Alnus* spp.), beaked hazel (*Corylus cornuta* Marsh.), bluejoint reedgrass (*Calamagrostis canadensis* Michx.), Canadian mayflower (*Maianthemum canadense* Desf.), violet (*Viola* spp.) and large-leaved aster (*Aster macrophyllus* L.).

Sampling Design

We selected a wide range of stands of fire origin that shared similar developmental histories. Using information from detailed fire records (Senici et al. 2010), we selected chronosequences of stands at different stages of development; from 7 to 209 years old since last fire. Based on available fires in the area, we sampled six age classes: 7-, 15-, 33-, 98-, 146-, and 209-years since fire, each representing stand initiation, early stem exclusion, late stem exclusion, early canopy transition, late canopy transition, and gap dynamic stages of stand development, respectively, modified from Chen and Popadiouk (2002). Because at any given stand development stage on mesic sites in the region, stands originating from fire can be dominated by conifer, broadleaf, or the mixture of both group of species in the overstory (Frelich and Reich 1995, Ilisson and Chen 2009, Taylor and Chen 2011), we made every effort to sample fire-origin stands of varying overstory composition from dominance of conifer to broadleaf and various levels of their mixture for each age class. A total of 51 stands were sampled.

We avoided sampling stands of the same age in close proximity to one another in order to minimize the impact of spatial structure (Legendre and Legendre 1998). This was achieved by selecting stands of the same age class from different road accesses, resulting in distances between stands in the range of 0.5 to 10 km. In order to minimize site variability, we selected only stands that were located on mesic sites on flat-mid-slope positions, with no slope exceeding 5%. All stands were located on well-drained (sandy or silty loams) glacial moraines >50 cm in depth. To ensure that each sample stand met these criteria, soil pits were dug in each candidate stand to verify that the site was mesic, following the procedures described in Taylor et al. (2000). The selected stands were > 1 ha in area and visually homogeneous in stem density and composition.

Data Collection

In each selected stand, we established a 400-m^2 circular plot within which all data were taken. The plot locations were random, but were at least 50 m from the forest edge in order to avoid edge effects on epiphytic lichens (Esseen and Renhorn 1998; Hilmo and Holien 2002). We identified all trees by species and measured the diameter at breast height (DBH; 1.3 m above the root collar) of all trees present in stands ≥ 33 years. For the younger (7- and 15-year-old) stands, tree stems were counted by species. Stand density and individual tree basal area were summed and scaled up to level per hectare (Table 5-1).

In each plot, we conducted a thorough reconnaissance of the entire plot area and sampled epiphytic lichens using the whole-plot ocular method (McCune and Lesica 1992). Each tree of the sample plot was visually inspected and scored for presence of all epiphytic macrolichen species present on the trunks and branches. Individual tree species were viewed as habitat units or quadrats (Burns 2007). Sampling included only macrolichen species occurring > 0.5 m above root collar to avoid inclusion of terricolous or saxicolous lichen species. Epiphytic lichen species' names follow the nomenclature of Brodo and others (2001).

TABLE 5-1. Characteristics of 54 stands sampled in the boreal forest of Ontario, Canada

Time since fire (yrs)	Over-story*	*n*	Stand density (stems/ha) or basal area (m^2/ha)*, †	Stand composition (%)†					
				Trembling aspen	White birch	Jack pine	Black spruce	Balsam fir	Others‡
7	B	3	5783 (808)	58 (19)	28 (19)	15 (2)			
7	C	3	5608 (2249)		2 (2)	97 (2)	<1.0		
7	M	3	3275 (290)	38 (10)	15 (7)	43 (15)	4 (3)		
15	B	3	10242 (60)	80 (5)	7 (1)	13 (5)			
15	C	3	4433 (405)	29 (18)	2 (2)	69 (17)			
15	M	3	6383 (736)	57 (8)	<1.0	34 (2)	9 (8)		
33	B	3	33.4 (3.9)	89 (4)	4 (3)	4 (1)	1 (1)		<1.0
33	C	3	32.2 (2.4)	4 (2)	1 (1)	94 (3)	1 (1)		
33	M	3	25.6 (0.5)	36 (7)	<1.0	55 (12)	8 (8)		
98	B	3	56.2 (7.2)	95 (2)	2 (1)		1 (1)	1 (1)	1 (1)
98	C	1	49.1 (5.6)		4	60	29	7	
98	M	3	53.4 (3.5)	44 (12)	16 (12)	11 (7)	13 (7)	16 (3)	
146	B	3	65.2 (8.9)	85 (3)	8 (4)		3 (2)	1 (1)	3 (1)
146	C	2	63.0 (6.4)	<1.0	3 (2)	80 (2)	12 (4)	4 (2)	
146	M	3	45.8 (5.3)	44 (14)	18 (9)		11 (3)	25 (1)	2 (2)
209	B	3	49.0 (4.3)	57 (24)	25 (17)		11 (7)	8 (3)	
209	C	3	46.3 (9.0)	5 (4)	8 (4)		32 (7)	54 (16)	<1.0
209	M	3	48.2 (2.4)	14 (2)	31 (8)	3 (3)	29 (12)	23 (16)	

Notes: *Overstory types: B – broadleaf, C – conifer, and M – mixed-wood.

†Values are means with 1 SE in parentheses. Stand density (stems/ha) was determined for the younger (7- and 15-year-old) stands and basal area (m^2/ha) for older stands.

‡The "Others" category includes white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera* L.), and mountain maple (*Acer spicatum*) with DBH > 5 cm.

Data Analyses

To examine species-specific association between each epiphytic macrolichen with time since fire and host tree species, we analysed the presence/absence of each epiphytic lichen species. Response variable was the presence ($y_i = 1$) or absence ($y_i = 0$) of the focal epiphytic macrolichen species. Explanatory variables were time since fire (TSF; 7-, 15-, 33-, 98-, 146-, and 209-yr old), host tree species (which included the major tree species of the overstory canopy; *Pinus banksiana*, *Populus* spp., *Betula papyrifera*, *Picea* spp., and *Abies balsamea*), and the interaction between time since fire and host tree species. We used the following generalized linear model (GLM) which was fit to data by specifying binomial error distribution with a logit link function:

$$Logit\left(p_{ij}\right) = B_0 + \beta_1 \cdot TSF_{ij} + \beta_2 \cdot Tree\,species_{ij} + \beta_3 \cdot TSF_{ij} \times Tree\ species_{ij} \qquad (1)$$

where *logit* (p_{ij}) is the probability of occurrence of an epiphytic macrolichen species, TSF is time since fire (years), Tree species is host tree species identity, β_0 is the intercept term, β_1, β_2 and β_3 are coefficients of the respective covariates.

We examined epiphytic macrolichen species composition on each tree species and how it may change with forest age and tree species identity using permutational multivariate analysis of variance (PERMANOVA). PERMANOVA is a nonparametric, multivariate analysis that uses permutation techniques to test for compositional differences between more than one factors (Anderson 2001). PERMANOVA was run based on the Bray-Curtis dissimilarity and 999 permutations of the compositional data. Further, we used nonmetric multidimensional scaling (NMDS; Kruskal 1964), which is a robust ordination technique for community data that are non-normal or on discontinuous scales (Minchin 1987), to express the variation in lichen species composition among forest age and host tree species and to visualize the association between lichen species and host tree species in ordination space. NMDS was run on the frequency of occurrence of lichen species across all time periods, based on Bray-Curtis dissimilarity index. All statistical analyses were conducted in R (R Development Core Team 2013).

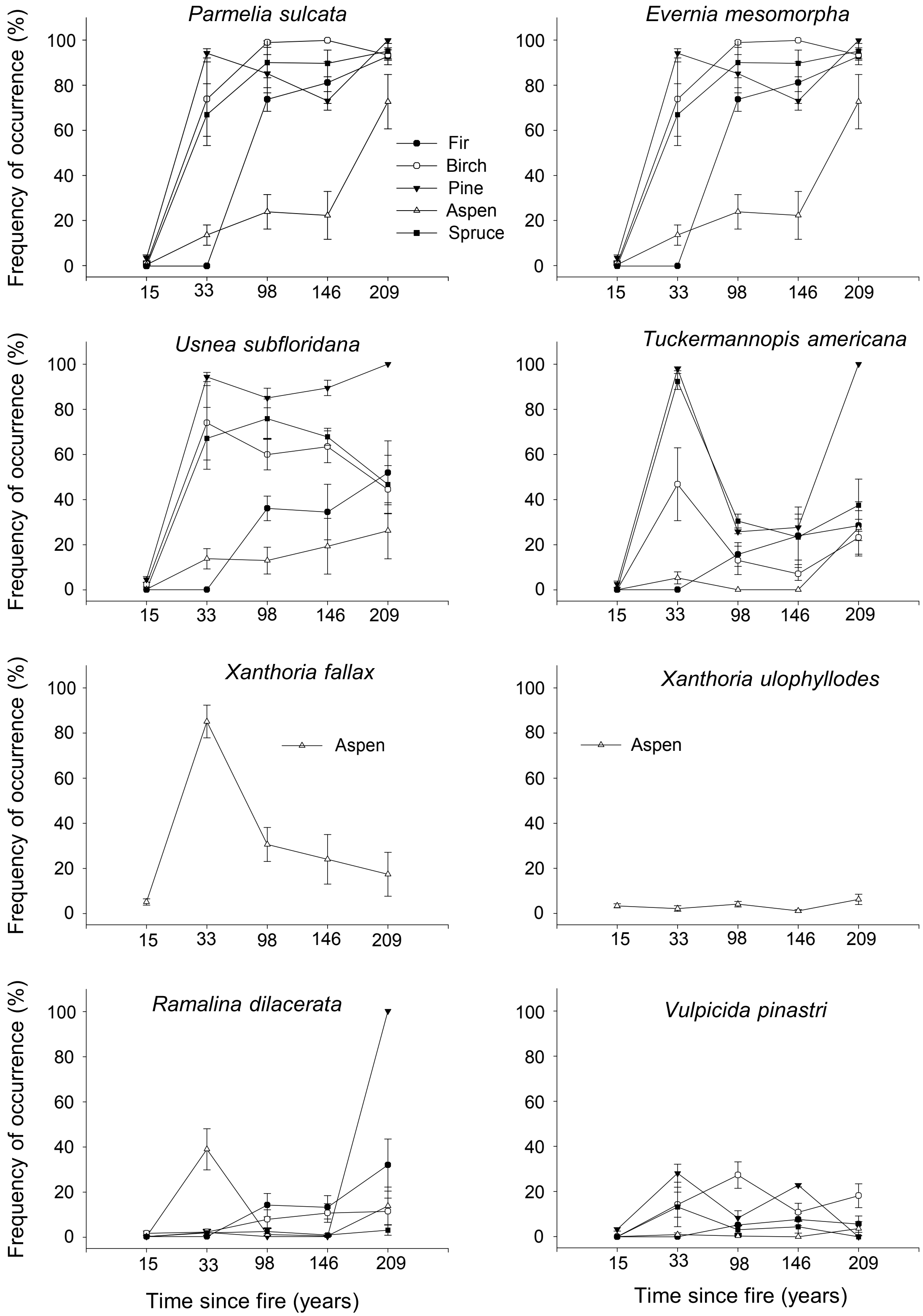
RESULTS

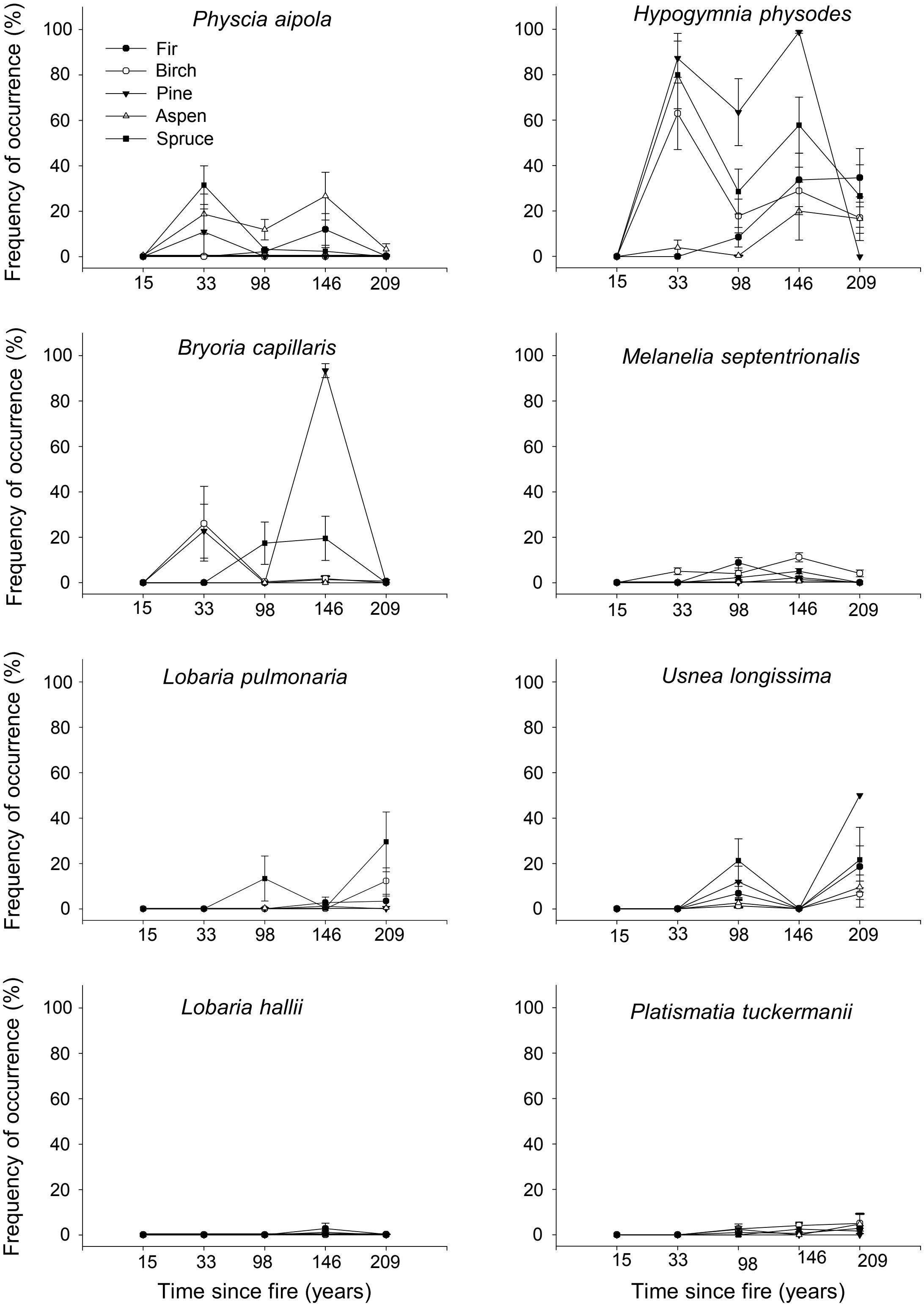
Individual epiphytic macrolichen species were influenced either by the independent or combined effects of time since fire and host tree species (Table 5-2). A significant interactive effect of time since fire and host tree species was observed for most epiphytic lichen species, except for the species that had limited occurrence in a particular stand age or host tree species (Table 5-2; Fig. 5-1). Time since fire in most instances explained much of the deviance in the logit models, whereas host tree species was an important predictor for the species that were restricted to particular tree species such as *Xanthoria fallax* and X. *ulophyllodes*. Frequency of occurrence of epiphytic macrolichen species on the host tree species changed with time since fire; it either increased consistently or declined at some point with stand age (Fig. 5-1). Frequency of occurrence for most species was low in the young (≤ 33 years old) stands compared with the older (≥ 98 years old) stands. However, some species occurred with particularly high frequencies in the young stands. Frequencies of species such as *Parmelia sulcata*, *Evernia mesomorpha*, and *Usnea subfloridana* on their host tree species increased consistently with time since fire, whereas frequency of occurrence of some other species such as *Tuckermannopsis americana*, *Physcia aipola*, *Ramalina dilacerata*, and *Vulpicida pinastri* on the host trees either peaked in the young 33-yr-old stands or gradually declined with increasing time since fire. For many other epiphytic lichen species, frequency of occurrence on the host tree species showed a unimodal or bimodal pattern with peaks at different time scales since fire.

TABLE 5-2. Analysis of deviance of the independent and interactive effects of time since fire (TSF; 7-, 15-, 33-, 98-, 146-, and 209-yrs) and host tree identity (fir, birch, pine, aspen, spruce) on the occurrence (presence/absence) of epiphytic macrolichen species modelled using multiple logistic regression. Degrees of freedom are 4, 4, and 14 for TSF, tree species identity, and their interaction, respectively. Bold fonts indicates statistical significance (α = 0.05).

	Time since fire (TSF)	Host tree species (Host)	TSF × Host
Species	*P*-value (deviance explained %)	*P*-value (deviance explained %)	*P*-value (deviance explained %)
Parmelia sulcata	**<0.001** (45.1)	**<0.001** (10.9)	**<0.001** (1.9)
Evernia mesomorpha	**<0.001** (32.3)	**<0.001** (24.8)	**<0.001** (2.1)
Tuckermannopsis americana	**<0.001** (34.2)	**<0.001** (30.7)	**<0.001** (2.4)
Ramalina dilacerata	**<0.001** (18.2)	**<0.001** (13.2)	**<0.001** (2.9)
Usnea subfloridana	**<0.001** (47.5)	**<0.001** (18.1)	**<0.001**(3.2)
Vulpicida pinastri	**<0.001** (14.2)	**<0.001** (10.9)	**<0.001** (1.8)
Physcia aipola	**<0.001** (15.6)	**<0.001** (5.1)	**<0.001** (4.7)
Xanthoria fallax	**<0.001** (15.6)	**<0.001** (43.8)	Insig.
Xanthoria ulophyllodes	**<0.001** (5.3)	**<0.001** (15.1)	Insig.
Melanelia septentrionalis	**<0.001** (17.3)	**<0.001** (11.6)	0.085 (4.3)
Lobaria pulmonaria	**<0.001** (31.1)	**<0.001** (4.8)	**0.005** (3.5)
Hypogymnia physodes	**<0.001** (32.4)	**<0.001** (31.1)	**<0.001** (2.7)
Bryoria capillaris	**<0.001** (34.3)	**<0.001** (22.9)	**<0.001** (7.1)
Usnea longissima	< **0.001** (27.5)	**<0.001** (4.3)	**<0.001** (3.6)
Physcia stellaris	**<0.001** (33.9)	**<0.001** (27)	Insig.
Physcia adscendes	**0.008** (27.4)	0.200 (11.9)	Insig.
Flavopunctelia flaventior	**<0.001** (23.9)	**0.042** (4.9)	0.998 (1.8)
Platismatia tuckermanii	**<0.001** (23.4)	**<0.001** (5.5)	0.733 (2.4)

Notes: Results are reported for the lichen species whose frequencies of occurrence were sufficient enough to allow for meaningful statistical analysis.
"Insig." denotes insignificant or insufficient data to test for interaction effect.
The columns give the p-value and deviance explained (%) for each predictor. Chi-square was used to test for significance.


Parmelia sulcata
Evernia mesomorpha
Usnea subfloridana
Tuckermannopis americana
Xanthoria fallax
Xanthoria ulophyllodes
Ramalina dilacerata
Vulpicida pinastri
Frequency of occurrence (%)
0
20
40
60
80
100
15
33
98
146
209
Fir
Birch
Pine
Aspen
Spruce
Aspen
Aspen
Time since fire (years)
Time since fire (years)


Physcia aipola
Hypogymnia physodes
Bryoria capillaris
Melanelia septentrionalis
Lobaria pulmonaria
Usnea longissima
Lobaria hallii
Platismatia tuckermanii
Fir
Birch
Pine
Aspen
Spruce
Frequency of occurrence (%)
0
20
40
60
80
100
15
33
98
146
209
Time since fire (years)

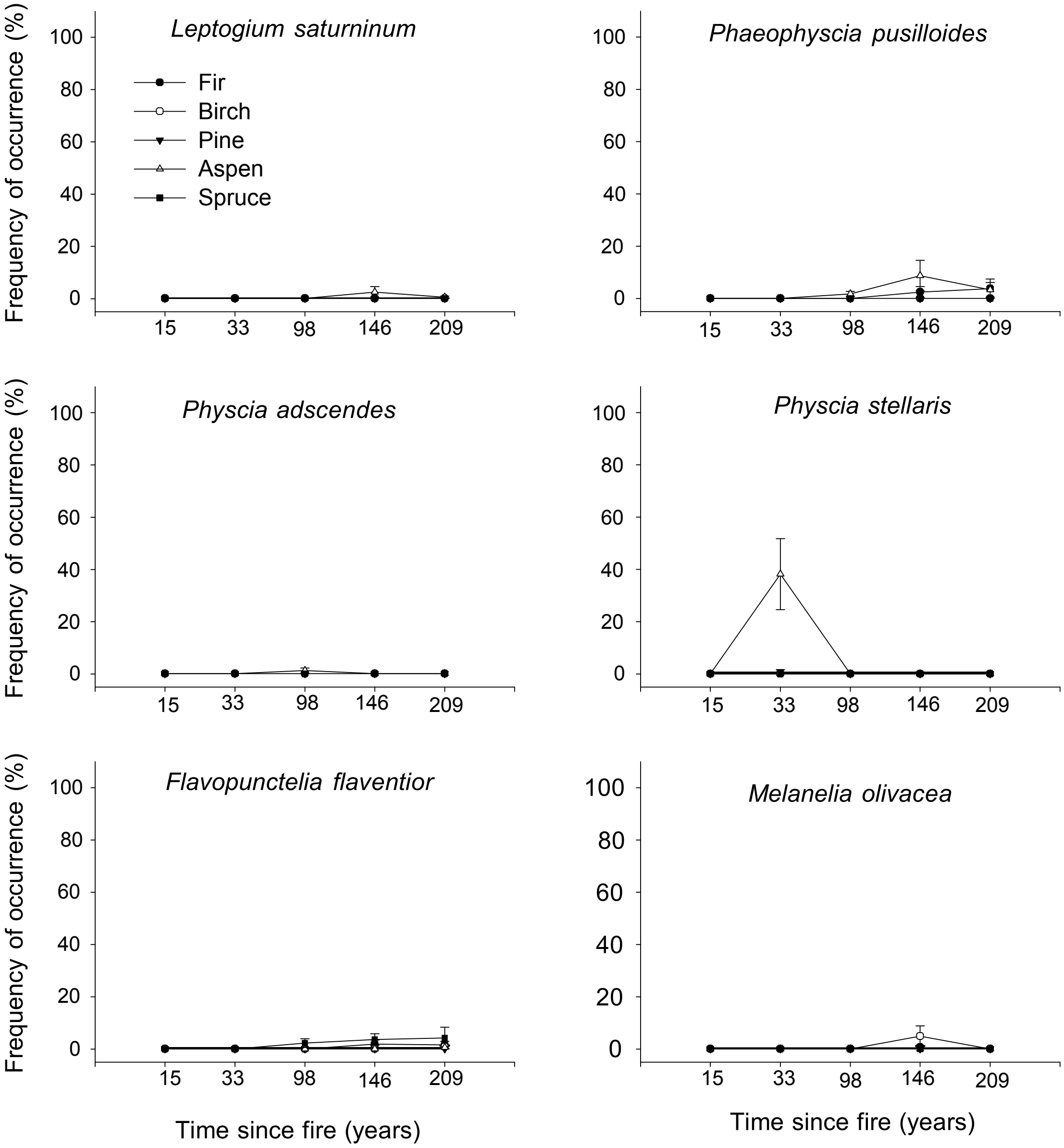


FIGURE 5-1. Influence of stand age and host tree species on frequency of occurrence (mean ± 1 SE) of epiphytic macrolichen species in the boreal forest.

Epiphytic macrolichen species composition differed significantly between stand age and host tree species (Table 5-3). Thus, epiphytic lichen species composition varied on the host tree species with time since fire. Differences in lichen species composition between the various stand ages and host tree species was also supported by non-metric multidimensional scaling ordination which showed a fair separation between stand ages and host tree species in ordination space (Fig. 5-2A)..

TABLE 5-3. Results of permutational multivariate analysis of variance (PERMANOVA) testing the effects of forest age (15-, 33-, 98-, 146-, and 209-year-old) and host tree species (*Populus* spp., *Pinus banksiana*, *Betula papyrifera*, *Picea* spp., and *Abies balsamea*) on epiphytic macrolichen species composition.

Source	df	SS	*F*	*P*	R^2
Age	4	8.685	22.965	<0.001	0.299
Tree species	4	4.869	12.875	<0.001	0.167
Age × Tree species	13	5.039	4.100	<0.001	0.173
Error	111	10.495			0.361

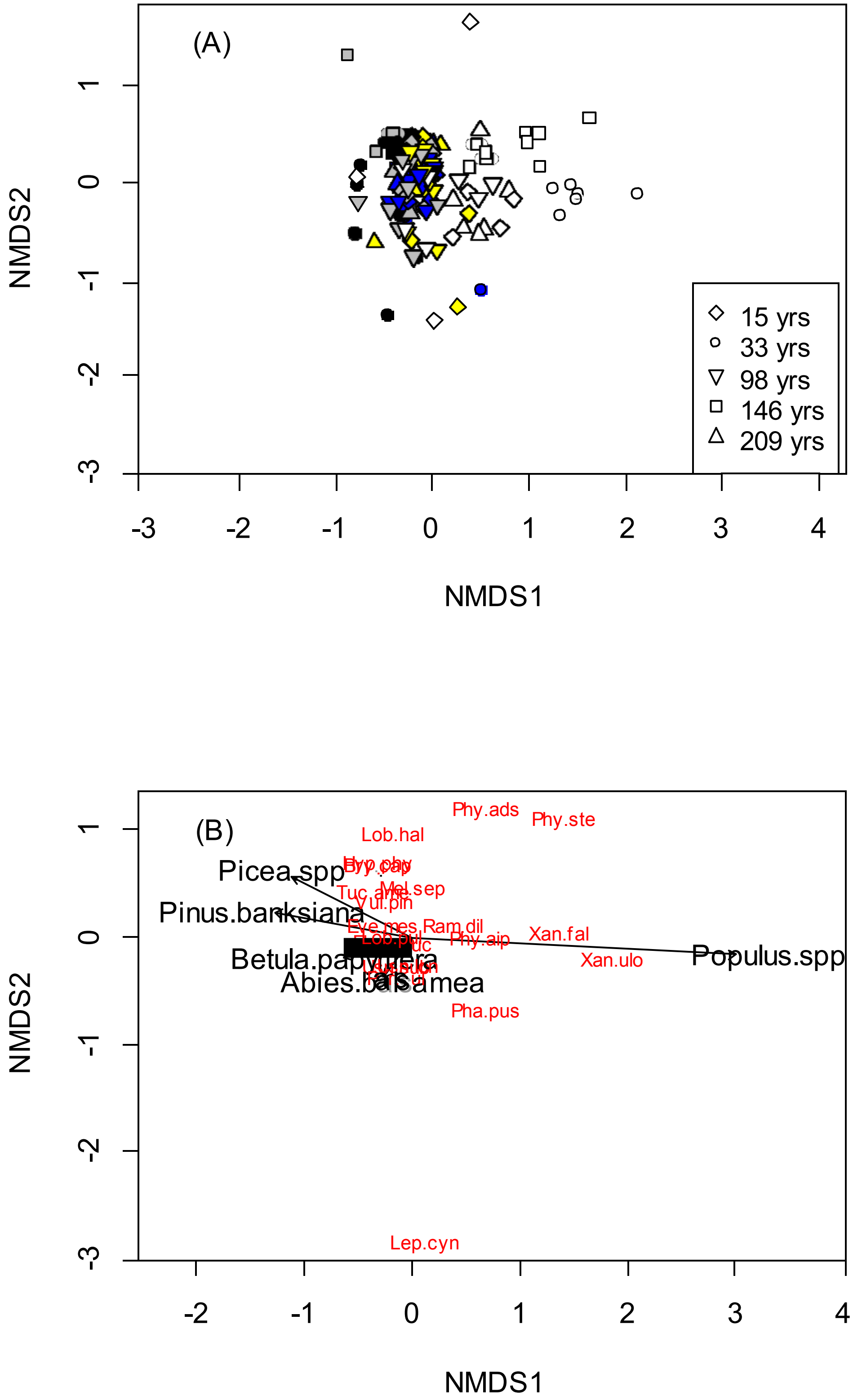

(A)
NMDS2
NMDS1
1
0
-1
-2
-3
-3
-2
-1
0
1
2
3
4
◇ 15 yrs
○ 33 yrs
▽ 98 yrs
□ 146 yrs
△ 209 yrs
(B)
NMDS2
NMDS1
Picea.spp
Pinus.banksiana
Betula.papyrifera
Abies.balsamea
Populus.spp
Phy.ads
Phy.ste
Lob.hal
Hyp.phy
Bry.cap
Tuc.ame
Mel.sep
Vul.pin
Eve.mes
Ram.dil
Lob.pul
Phy.aip
Xan.fal
Xan.ulo
Pha.pus
Lep.cyn
1
0
-1
-2
-3
-2
-1
0
1
2
3
4

FIGURE 5-2. Non-metric multidimensional scaling (NMDS) ordination showing a two-dimensional representation of epiphytic macrolichen species composition based on percent frequency of occurrence across 51 post-fire stands in the central boreal forest of Canada. Best NMDS solution was reached at a stress of 0.183. In (A): points represent mean lichen species occurrence in the different stand ages (15, 33, 98, 148, and 209 years since fire) and tree species (*Abies balsamea* (yellow), *Betula papyrifera* (blue), *Pinus banksiana* (black), *Populus tremuloides* (white) and *Picea mariana* (gray)). Axis 1 shows a separation between host tree species while axis 2 shows a separation between stand ages. Points nearest each other in ordination space have similar species composition whereas those located farther apart are less similar. In (B): individual epiphytic lichen species in ordination space. Species names are as follows: Bry.cap, *Bryoria capillaris*; Eve.mes, *Evernia mesomorpha*; Fla.pun, *Flavopunctelia flaventior*; Hyp. Phy, *Hypogymnia physodes*; Lep.sat, *Leptogium saturninum*; Lob.hal, *Lobaria hallii*; Lob.pul, *Lobaria pulmonaria*; Mel.oliv, *Melanelia olivacea*; Mel.sep, *Melanelia septentrionalis*; Par.sul, *Parmelia sulcata*; Pha.pus, *Phaeophyscia pusilloides*; Phy.ads, *Physcia adscendes*; Phy.aip, *Physcia aipola*; Phy.ste, *Physcia stellaris*; Pla.tuc, *Platismatia tuckermanii*; Ram.dil, *Ramalina dilacerta*; Tuc.ame, *Tuckermannopisis americana*; Usn.lon, *Usnea longissima*, Usn.sub, *Usnea subfloridana*; Vul.pin, *Vulpicida pinastri*; Xan.fal, *Xanthoria fallax*, Xan.ul, *Xanthoria ulophyllodes*. Vectors (arrows) indicate the correlation between epiphytic macrolichen species composition and host tree species (*Abies balsamea, Betula papyrifera, Pinus banksiana, Populus* spp., and *Picea* spp). Length of the vector represents the strength of the correlation.

Epiphytic macrolichens were absent in the 7-yr-old stands which only contained traces of undifferentiated lichen thalli (lichen reproductive body) mainly on the shrub, beaked hazel (*Corylus cornuta*). But, the number of epiphytic macrolichen species increased consistently with time since fire, with new species recruitment at each stand age (Table 5-4). A few epiphytic macrolichen species such as *Xanthoria fallax*, *X. ulophyllodes*, and *Leptogium saturninum* appeared to be specialist species with exclusive occurrence on *Populus tremuloides* (Table 5-5). Meanwhile, *Populus* spp. appeared to be a common substrate as they hosted the greatest number of epiphytic macrolichen species at all stand ages. About half of the epiphytic macrolichen species encountered appeared to be generalist species and occurred at least once on each particular host tree species. However, epiphytic lichen species composition was different on each tree species (Fig. 5-2B).

TABLE 5-4. Frequency (%) of epiphytic macrolichen species found at different time scales since fire.

		Time since disturbance (stand age)				
Macrolichen species	Form	15-yr	33-yr	98-yr	146-yr	209-yr
Xanthoria ulophyllodes	Foliose	2.5	0.3	1.6	0.4	2.4
Xanthoria fallax	Foliose	4.0	32.1	9.4	9.7	3.7
Vulpicida pinastri	Foliose	0.1	10.2	7.6	10.5	4.3
Usnea subfloridana	Fruticose	1.2	62.8	61.7	87.5	87.4
Tuckermannopsis americana	Foliose	1.0	59.4	10.8	17.8	28.6
Ramalina dilacerata	Fruticose	0.1	10.8	4.6	5.2	22.3
Physcia aipola	Foliose	0.3	12.7	5.2	9.8	1.5
Parmelia sulcata	Foliose	1.4	15.5	58.9	73.4	86.8
Evernia mesomorpha	Fruticose	1.5	61.8	40.1	50.6	51.7
Physcia stellaris	Foliose		18.5			
Melanelia septentrionalis	Foliose		0.4	4.2	2.7	0.6
Hypogymnia physodes	Foliose		51.9	18.0	44.4	33.9
Bryoria capillaris	Fruticose		2.0	1.4	25.7	0.6
Flavopunctelia flaventior	Foliose			0.2	0.6	2.4
Platismatia tuckermanii	Foliose			1.6	1.3	4.5
Usnea longissima	Fruticose			5.8	5.2	11.7
Physcia adscendes	Foliose			0.6		
Phaeophyscia pusilloides	Foliose			0.8	4.2	1.7
Lobaria pulmonaria	Foliose			0.6	6.7	10.8
Melanelia olivacea	Foliose				1.9	
Lobaria hallii	Foliose				1.1	0.2
Leptogium saturninum	Foliose				0.2	0.2

TABLE 5-5. Frequency (%) of epiphytic macrolichen species on *Populus* spp., *Pinus banksiana*, *Betula papyrifera*, *Picea* spp., and *Abies balsamea* tree species.

Lichen species	*Populus* spp.‡	*Pinus banksiana*	*Betula papyrifera*	*Picea* spp. ‡	*Abies balsamea*
Bryoria capillaris	<0.1	7.5	2.0	11.8	1.2
Evernia mesomorpha	4.4	56.9	47.5	53.7	56.1
Flavopunctelia flaventior	<0.1		0.3	1.9	1.7
Hypogymnia physodes	0.6	52.3	20.2	36.3	38.9
Leptogium saturninum	0.1				
Lobaria hallii		<0.1		<0.1	<0.1
Lobaria pulmonaria	0.4	0.5	4.5	11.2	4.1
Melanelia olivacea			2.3		0.2
Melanelia septenrionalis	0.1	0.1	6.1	0.9	2.9
Parmelia sulcata	7.5	14.9	77.8	73.3	89.5
Phaeophyscia pusilloides	1.4				0.5
Physcia adscendes	0.1				
Physcia aipola	5.7	8.2		1.2	1.7
Physcia stellaris	11.6	0.2			
Platismatia tuckermanii	0.1	0.1	4.8	0.9	2.6
Ramalina dilacerata	6.6	0.6	10.1	2.8	24.6
Tuckermannopsis americana	0.9	51.9	13.6	36.9	26.9
Usnea longissima	0.4	0.4	4.8	12.1	9.1
Usnea subfloridana	13.9	58.2	68.2	71.1	80.4
Vulpicida pinastri	0.3	9.5	15.7	4.9	5.5
Xanthoria fallax	29.2				
Xanthoria ulophyllodes	3.5				
Number of species	20	15	14	15	17

Notes: ‡*Populus* spp. included *Populus tremuloides* and *Populus balsamifera*.
‡ *Picea* spp. included *Picea mariana* and *Picea glauca*.

DISCUSSION

The dynamics of epiphytic macrolichen species in our system were moderated by forest stand age and host tree species. Species recruitment and frequency patterns of epiphytic macrolichens along the post-fire chronosequence varied with time since fire, a phenomenon which is consistent with other studies in the boreal region (Boudreault et al. 2000, Boudreault et al. 2009). While previous studies seldom include observations in young stands < 40 years, we found that epiphytic macrolichens had not recovered seven years after fire, but lichen recolonization had likely began as the 7-yr-old stands contained traces of undifferentiated lichen thalli. Nine species, representing about 40% of the total epiphytic macrolichen species, appeared to be pioneer or early-successional species, as they were found to have colonized regenerating stands at the stand initiation stage, but with low frequencies. Most of these pioneer species, prominent among them *Evernia mesomorpha*, *Parmelia sulcata*, and *Usnea subfloridana,* were asexually reproducing lichens. Therefore, our observation corroborates the view that likelihood of successful establishment is greater for lichens with vegetative than generative propagation (Dietrich and Scheidegger 1997).

Individual epiphytic lichen species showed strong dependence on stand age, while epiphytic lichen communities were different at each stand age. Some species such as the old man's beard lichen *Usnea longissima* and the nitrogen-fixing lichen *Lobaria pulmonaria* appeared to be late-successional, as they occurred exclusively in the older stands (≥ 98 years old). About half of the species, however, appeared to be mid-successional with occurrence within the mid-stages (i.e., 33- to 98-yr-old stands). For most lichens, frequency of occurrence was higher in the old (i.e., 146- and 209-yr-old) stands than in other stand ages. Such is consistent with previously reported high epiphytic species abundance and diversity in older stands in other studies (Hyvärinen et al. 1992, Esseen et al. 1996, Price and Hochachka 2001, Nascimbene et al. 2010, Bartels and Chen 2012). On the contrary, frequencies of occurrence of some lichen species such as *E. mesomorpha*, *T. americana*, and *Xanthoria fallax* were comparably high in the young, 33-yr-old stands, which may be may be attributed to the high stem densities of tree species, especially shade-intolerant jack pine and trembling aspen in stands belonging to the stem exclusion stage (Chen and Popadiouk 2002). The high frequencies also suggest that epiphyte communities at this stage, i.e., 33 years after fire, remain unsaturated and non-competitive and can still accommodate new species (Flores-Palacios and Garcia-Franco 2006, Ellis 2012).

The different tree species in our study system were hosts to significantly different epiphytic macrolichen species composition, which emphasizes the importance of tree species diversity in the boreal forest. It is commonly suggested that each host tree species harbors a specific subset of the local epiphytic species pool according to its own set of physical and chemical characteristics of the bark (Callaway et al. 2002, Merwin et al. 2003, Laube and Zotz 2006). Until present, however, there is scarce evidence of host specificity in epiphytic lichens as the majority of studies have either focused on a few dominant taxa or been limited to one or a few dominant tree species (Esseen et al. 1996, Boudreault et al. 2000, Johansson and Ehrlén 2003, Hedenås and Hedström 2007, Nascimbene et al. 2010, Fedrowitz et al. 2012, Berg et al. 2013). Herein, we found specific instances of exclusive occurrence of some epiphytic lichen species on particular host tree species, which suggested habitat preferences.

Although most epiphytic macrolichen species in our study tended to be generalist species, i.e., they were sighted at least once on a different host tree species, a few species such as *Xanthoria fallax* and *X. ulophyllodes* appeared to be specialist species with exclusive occurrence on *Populus* spp. In our study, *Populus* spp. tended to be species-rich and appeared to be favorable substrate for many epiphytic lichen species, an observation which is consistent with the studies of others (Uliczka and Angelstam 1999, Rogers and Ryel 2008). It also supports the view that aspen (*Populus tremuloides*) has more host-specific species associated with it than many tree species in the boreal forest (Hedenås and Hedström 2007). Consistent with other studies, our results also support the positive correlation between tree species diversity and composition and epiphyte species diversity and composition (Cleavitt et al. 2009, Kiraly et al. 2013).

As expected of dynamic communities, frequency of occurrence of epiphytic macrolichen species on the host tree species changed with time since fire. However; the pattern of change was not uniform for all the species, which is consistent with similar observations in previous studies in the boreal forest (Uliczka and Angelstam 1999). Frequency of occurrence of epiphytic lichen species on their host tree species either increased consistently with stand age or declined at some point. For most species, frequency of occurrence for most species was low in the young (≤ 33 years old) stands compared with the older (≥ 98 years old) stands. However, some species occurred with particularly high frequencies in the young stands. For some common lichen species that occurred in all stand ages such as *Parmelia sulcata, Evernia mesomorpha*, and *Usnea subfloridana*, frequency of occurrence on the different tree species increased gradually with stand age. For these species, frequency change was less drastic on *Populus* spp.

Frequency change on *Populus* was, however, drastic for the specialist species *Xanthoria fallax* and *X. ulophyllodes*, Frequency change of some epiphytic lichen species such as *Tuckermannopsis americana*, *Physcia aipola*, and *Vulpicida pinastri* also showed a unimodal or bimodal pattern, with peaks in either young or older stands. It is not clear, however, from this study whether the patterns of change reflect a change in individual epiphytic species preferences for particular tree species with time. These results nonetheless suggest the epiphytic lichen species dynamics are linked with the dynamics of the host tree species.

CONCLUSIONS

Epiphytic macrolichen species occurrence and composition on host tree species is strongly influenced by the independent and combined effects of time since colonization and host tree species. After stand-replacing fire, the pioneer, early-successional species that likely initiate the colonization process at the stand initiation stages appear to be those that are able to reproduce asexually. For some lichen species, frequencies of occurrence on the host tree species consistently increased with stand age whereas others only peaked at certain stages of stand development. Some epiphytic lichen species showed strict preference for particular tree species, but each tree species hosted significantly different epiphytic lichen species communities. *Populus* spp in particular appeared to be a favorable substrate for most epiphytic lichen species. Our results have implications for practical forest management and urge forest managers to promote tree species diversity, especially by retaining aspen, which is often discriminated against in favor of conifer, in order to maintain epiphytic macrolichen diversity and their ecological functions.

CHAPTER SIX: GENERAL CONCLUSION

The mechanisms underlying epiphyte species diversity can be grouped into inherent, local, and stand- and landscape-level mechanisms. The individual mechanisms involved are likely interrelated and therefore efforts to disentangle the mechanisms of epiphyte diversity need to rely on multi-scale approaches. Although the mechanisms proposed here adequately explain epiphyte species diversity patterns, it is likely that the various life forms of epiphytes, i.e., vascular and nonvascular epiphytes, would respond differently. Therefore, future studies should consider examining the mechanisms separately for the various epiphytic life forms. Also, considering the present limitations in the scope of the published studies, sufficient experimental and observational studies over broad spatial and temporal scales may be necessary for future predictions of epiphyte diversity patterns.

The dynamics of epiphytic macrolichens are strongly influenced by forest age and overstory composition. As a result, shifts in forest age structure and composition can have strong impacts on the successional dynamics of epiphytic lichens. For instance, high fire frequency and/or short rotation harvesting regimes that convert large portions of the landscape into young forest stands would result in the loss of the lichen species with affinity for old stands. Epiphytic lichen abundance, diversity, and composition differ among overstory types. For example, broadleaf and conifer stands support significantly different lichen composition. Therefore, management intervention should aim at maintaining a diverse overstory types, especially mixed-wood stands in order to maintain distinct lichen communities in the boreal landscape.

Logging does not seem to have the same effect on epiphytic lichens as fire. Post-fire stands tend to have higher or similar lichen cover and richness than post-logged stands. Multiple mechanisms varying from difference in regeneration density, genetic diversity of trees, and soil nutrient availability and stoichiometry may be accountable for the difference between fire and logged stands. It is unclear, however, whether the trajectories of epiphytic lichen development after fire and logging may eventually converge over time as stands continue to grow older. An assessment of the long-term effects of logging and wildfire on epiphytic lichen development would be useful in determining the conservation value of logging relative to the natural wildfire disturbance.

Finally, epiphytic macrolichen species occurrence and composition in the boreal forest is strongly influenced by the independent and combined effects of time since disturbance and host tree species. For some lichen species, frequencies of occurrence on the host tree species consistently increase with time whereas others show peaks at certain stages of stand development. Each tree species supports significantly different epiphytic lichen species composition, while some epiphytic lichen species show preferences for particular tree species. Therefore, maintenance of tree species diversity in the boreal forest must be prioritized in order to maintain epiphytic macrolichen diversity and their ecological functions.

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