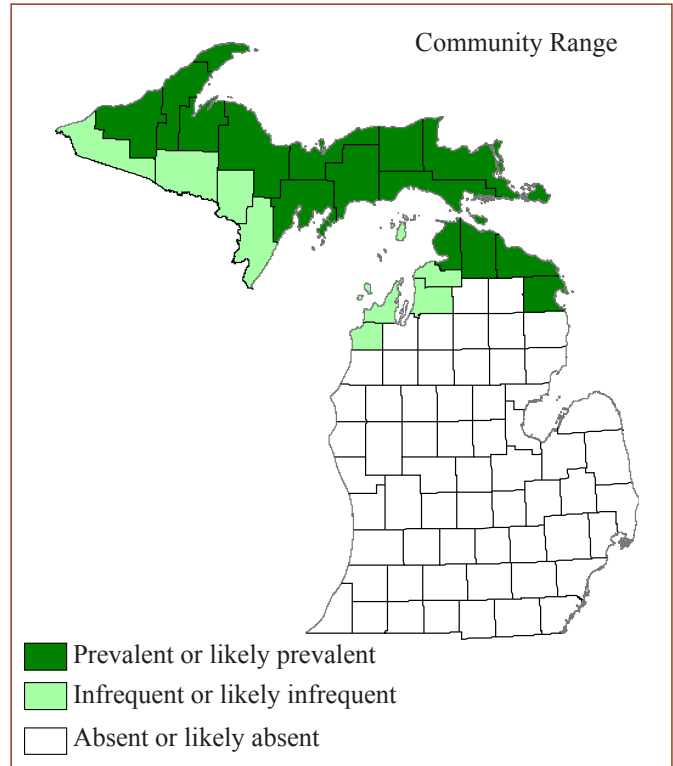




Photos by Joshua G. Cohen



Overview: Boreal forest is a conifer or conifer/hardwood forest type that is found on moist to dry sites characterized by species dominant in the Canadian boreal forest. Boreal forest occurs on upland sites along shores of the Great Lakes, on islands in the Great Lakes, and locally inland. This system is found primarily on sand dunes, in glacial lakeplains, and on thin soil over bedrock and cobble. Boreal forest is characterized by sand and sandy loam soils that are typically moderately acid to neutral, but heavier soils and more acid conditions are found. Proximity of boreal forest to the Great Lakes results in high levels of windthrow and climatic conditions characterized by high humidity, snowfall, summer fog and mist, and low summer temperatures. In addition to windthrow, fire and insect epidemics are important components of the natural disturbance regime.

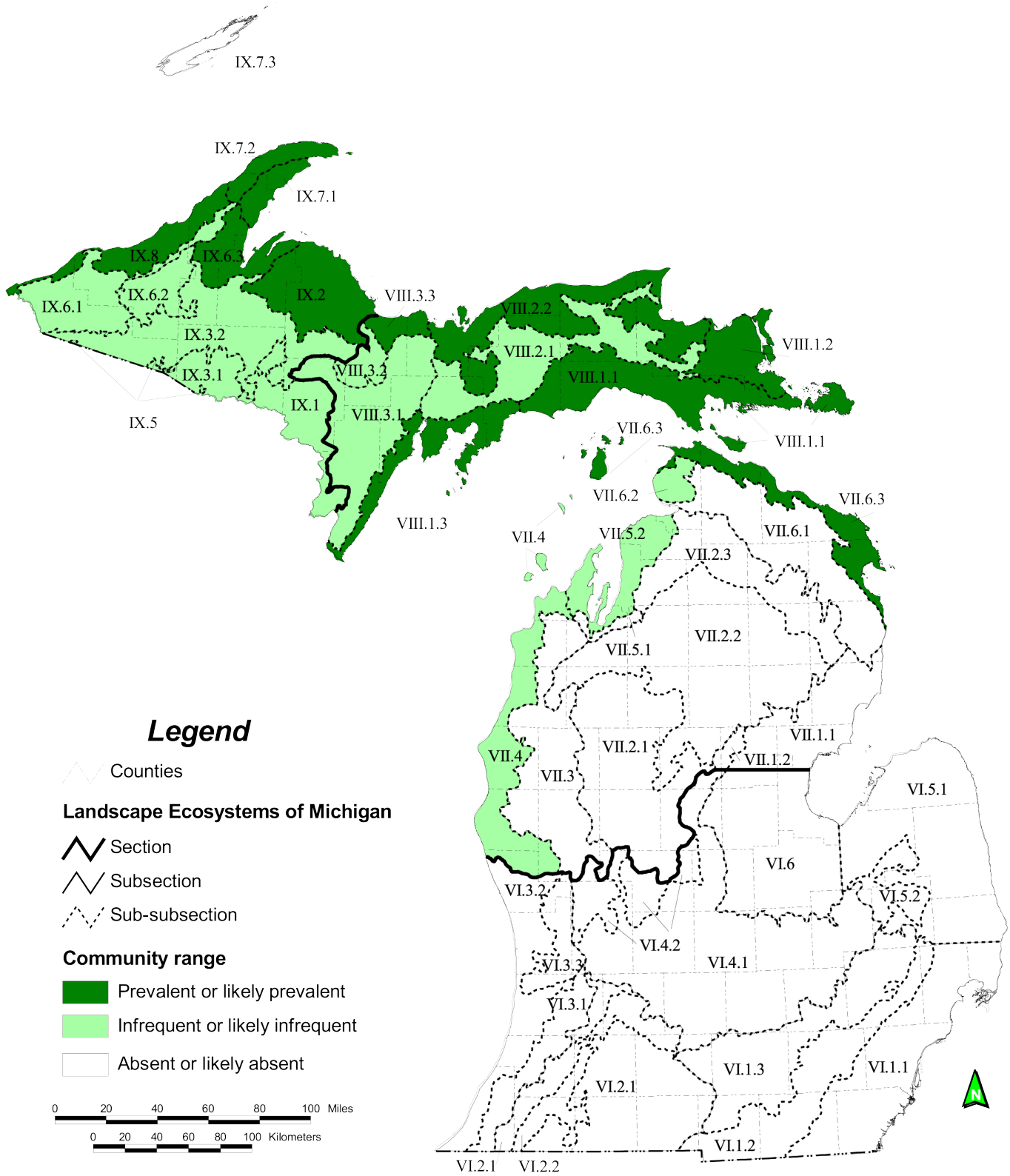
Global and State Rank: GU/S3

Range: Boreal forest is a circumboreal formation (Curtis 1959) that has existed as a dominant assemblage in the northern Great Lakes region of the United States and Canada for approximately 10,000 years, following the retreat of the Wisconsin or Pleistocene glaciers (Maycock and Curtis 1960, Holloway and Bryant 1985). In North America, boreal forest is primarily found throughout Canada, ranging into Alaska (Nichols 1935). In the Great Lakes region (the Lake states and Ontario province), boreal forest is found

in central Ontario, throughout northern Minnesota, along the tip of the Door Peninsula in Lake Michigan and along the Lake Superior shoreline in Wisconsin, and within northern Michigan (Grant 1934, Curtis 1959, Maycock and Curtis 1960, Stearns et al. 1982). Michigan boreal forests are predominantly found on Great Lakes islands and along coastal areas of the northernmost portion of the Lower Peninsula and throughout the Upper Peninsula; less frequently boreal forest occurs in localized inland areas of the Upper Peninsula. Interpretation of notes by General Land Office surveyors indicate that circa 1800, boreal forest primarily occurred in the northern Lower Peninsula in Alpena, Cheboygan, Charlevoix, and Emmet Counties and was concentrated in the Upper Peninsula in Keweenaw, Chippewa, Ontonagon, Delta, and Mackinac Counties (Comer et al. 1995).

Rank Justification: Boreal forests are uncommon features of the northern Great Lakes region, occurring sporadically in the northern Lower Peninsula and infrequently in the Upper Peninsula. Analysis of General Land Office survey notes in Michigan reveals that boreal forest once occupied approximately 385,000 hectares (just under 955,000 acres) (Comer et al. 1995). Recent estimates of boreal forest in Michigan reveal a significant decrease in extent with approximations for *Abies balsamea* (balsam fir) and *Picea glauca* (white





Ecoregional map of Michigan (Albert 1995) depicting distribution of boreal forest (Albert et al. 2008)



spruce) forests of around 88,000 ha (just over 215,000 ac) (MIRIS 1978) and more general estimations of mixed upland conifer and other upland conifer forest of approximately 230,000 ha (just under 575,000 ac) (Michigan DNR 2001a, 2001b). Twenty-five high-quality occurrences of boreal forest, which constitute 1,242 ha (just over 3,000 ac), have been documented by Michigan Natural Features Inventory. Turn-of-the-century logging of *Thuja occidentalis* (northern white-cedar) and other conifers from boreal forests and widespread fires following the harvests favored the conversion of mature and old-growth boreal forest to early-successional forest dominated by deciduous species [i.e., *Populus tremuloides* (trembling aspen) and *Betula papyrifera* (paper birch)] (Campbell and Campbell 2000, Reich et al. 2001, Frelich 2002). Where conifer seed trees were eliminated or drastically reduced, hardwoods have persisted (Bergeron et al. 2004b). Many inland sites formerly dominated by boreal forest and occurring on moist to wet lacustrine soils were drained and converted to agriculture, especially in Chippewa County.

The current anthropogenic disturbance factors impacting boreal forests are shoreline development and forest harvesting. While cedar has remained a valuable timber commodity, spruce and fir have become increasingly important sources for the burgeoning pulp industry (Curtis 1959, Reich et al. 2001). Forestry has replaced stochastic or random natural disturbances (i.e., fire, windthrow, and insect defoliation) as the primary and non-random disturbance factor influencing boreal forest structure and composition at the site and landscape scales (Niemela 1999, Ward et al. 2001, Bergeron et al. 2004a). Current silvicultural practices in boreal forests are typically even-aged management systems. Clear-cutting of boreal forests has resulted in the simplification of the age-class distribution, structural diversity, and landscape patterning of boreal forests (Thompson et al. 1998, Niemela 1999, Siitonen et al. 2000, Elkie and Rempel 2001, McCarthy 2001, Reich et al. 2001, Bergeron 2004, Didion et al. 2007). Late-seral and old-growth, uneven-aged boreal forests have been reduced from the increasingly homogenized landscapes where boreal forests are managed on short rotation periods (e.g., less than 100 years) (Thompson et al. 1998, Bergeron et al. 1999, Niemela 1999, Bergeron 2004, Bergeron et al. 2004a, Chapin et al. 2004, Didion et al. 2007).

In addition to the decline in older boreal forests, early-successional post-burn stands of boreal forest have also become increasingly scarce with the advent of fire suppression (Schmiegelow and Monkkonen 2002). Beginning in the 1920s, effective fire control by the U.S. Forest Service and state agencies reduced the acreage of fires ignited by humans or lightning (Swain 1973). Fire suppression in boreal forests is thought to have reduced the size of burns, the area burned, and fire frequency (Ward et al. 2001). Increasing forest fragmentation and road development have facilitated fire suppression efforts (Ward et al. 2001, Lesieur et al. 2002, Bergeron et al. 2004a). Fire suppression and forest harvesting have likely amplified the importance of balsam fir within these systems and thereby increased the potential impact for *Choristoneura fumiferana* (spruce budworm) infestations (Morin and Laprise 1997, Bergeron and Leduc 1998, Kneeshaw and Bergeron 1998, McCullough et al. 1998, Lesieur et al. 2002). In addition, herbivory by *Odocoileus virginianus* (white-tailed deer) is drastically altering the species composition and structure of these systems (Thompson et al. 1998). Most notably, high deer densities can result in the failure of cedar recruitment and benefit non-palatable species (i.e., balsam fir and white spruce) and browse-tolerant species [i.e., aspen and *Acer rubrum* (red maple)] (Waller and Alverson 1997, Van Deelen 1999).

Physiographic Context: Boreal forest typically occupies upland sites (often with local wet places) along shores of the Great Lakes, on islands in the Great Lakes (e.g., Isle Royale, Drummond Island, and Beaver Island), and locally inland [e.g., restricted areas in the Negaunee Michigan Highlands as described by Albert (1995)]. Coastal boreal forests occur primarily on sand dunes, in glacial lakeplains, and on thin soil over bedrock and cobble of both alkaline and acidic rock types (Cooper 1913, Darlington 1940, Stearns et al. 1982, Flakne 2003). Farther inland, moderately to poorly drained lakeplain and outwash deposits occasionally support these forests (Comer et al. 1995). Within lakeplain, boreal forest is often found in areas with poorly expressed dune and swale topography. Along shorelines, boreal forest often shares an abrupt boundary (Cooper 1913) with coastal communities such as cobble shore, sand and gravel beach, open dunes, limestone bedrock lakeshore, Great Lakes marsh, and Great Lakes barrens, and gradually grades to mesic northern forest or less frequently, rich conifer



swamp, limestone bedrock glade, or alvar inland from the lakeshore. Coastal boreal forests occurring along the mainland often form narrow, linear bands, while archipelagic boreal forests often occupy broader areas of variable shape along the island shoreline, especially along the southwestern portion of the island (Harman and Plough 1986). Near-shore boreal forests occupy peninsulas, former embayments, and coves. Topography of these systems ranges widely from gently sloping on lakeplain systems to steep topography (Potzger 1941) on high dune fields, especially where Aeolian features have developed upon moraines.



Photo by Ted Cline

Boreal forest in Delta County is concentrated in shoreline areas and occurs adjacent to coastal ecosystems such as limestone bedrock lakeshore and cobble shore. Juxtaposition near the Great Lakes results in modified climate with cool, even temperature, a short growing season, abundant available moisture during the growing season, and deep snows in the winter.



Photo by Joshua G. Cohen

Climate: Proximity of boreal forests to the Great Lakes results in modified climate with cool, relatively equable temperature, a short growing season, abundant available moisture during the growing season, often in the form of fog or mist, and deep snows in the winter (Cooper 1913, Darlington 1940, Potzger 1941, Curtis 1959, Maycock and Curtis 1960, Maycock 1961, Stearns et al. 1982, Harman and Plough 1986). The northern Lake States are characterized by a humid, continental climate with long cold winters, short summers that are moist and cool to warm, and a large number of cloudy days (Albert 1995). The Michigan range of boreal forest falls within the area classified by Braun (1950) as the Northern Hardwood-Conifer Region (Hemlock/White Pine/Northern Hardwoods Region) and within the following regions classified by Albert et al. (1986) and Albert (1995): Region II, Northern Lower Michigan; Region III, Eastern Upper Michigan; and Region IV, Western Upper Michigan. The mean number of freeze-free days is between 90 and 160, and the average number of days per year with snow cover of 2.5 cm or more is between 80 and 140. The normal annual total precipitation ranges from 740 to 900 mm with a mean of 823 mm. The daily maximum temperature in July ranges from 24 to 29 °C (75 to 85 °F), the daily minimum temperature in January ranges from -21 to -9 °C (-5 to 15 °F), and the mean annual temperature is 7 °C (45 °F) (Albert et al. 1986, Barnes 1991).

Soils: Sand, loamy sand, and sandy loam soils are typically moderately acid to neutral, but heavier soils (e.g., silty loam and clay loam) and more acid and alkaline conditions are found (Potzger 1941, Jones and Zicker 1955, Curtis 1959, Maycock and Curtis 1960, Stearns et al. 1982, Harman and Plough 1986). Boreal forests that occur over volcanic or limestone bedrock often are characterized by shallow organic soils or mor humus (Potzger 1941, Maycock 1961, Albert et al. 1995, Frelich and Reich 1995, Flakne 2003). Conifer dominance in the canopy results in a litter layer that is typically more acidic than the underlying organic and mineral soils. Water-retaining capacity of the soils is variable, with sandy soils typically being well-drained and soils with heavier texture, such as loams, ranging from moderately drained to poorly drained (Curtis 1959, Stearns et al. 1982). Drainage is impeded in locations where thin soils overlay bedrock. As noted above, inland boreal forest systems usually occur on moderately to poorly drained lakeplain or outwash (Comer et al. 1995).





Large stretches of boreal forest occur along the Lake Superior shoreline of the Keweenaw Peninsula.
Photos by Joshua G. Cohen.



Natural Processes: The species composition and structure, successional trajectory, and landscape patterning of boreal forests varies regionally and temporally depending on the complex interaction of microclimatic factors, abiotic site factors (i.e., soils, bedrock, and topography, see above), windthrow, insect defoliation, fire, and mammalian herbivory. Proximity to the Great Lakes results in the moderation of the microclimate of boreal forests with higher humidity, greater snowfall, lower summer temperatures, warmer winter temperatures, and greater summer fog and mist compared to the adjacent inland areas (Patzger 1941, Curtis 1959, Harman and Plough 1986). Fog genesis occurs as the result of the advection of warm moist air over a relatively cooler surface; fog forms as moist surface air passes over the cool waters of the Great Lakes. By increasing the relative humidity, fog and mist moderate extremes of temperature and evaporation by reducing solar radiation, evapotranspiration, and diurnal heating. Conifer dominants of boreal forests are adept at intercepting the moisture from fog because of the high surface area of their leaves and twigs (Harman and Plough 1986). Furthermore, proximity to the Great Lakes, by increasing moisture levels throughout the year, likely decreases the probability of fire disturbance and severe insect defoliation. In a study of maritime boreal forests in Newfoundland, McCarthy and Weetman (2006) speculated that wet cool climatic conditions may prevent the development of insect defoliator populations to the level that can cause severe tree and stand mortality. Finally, high levels of wind activity in near-shore areas increase the incidence of windthrow.

The natural disturbance regime of boreal forests in Michigan is characterized by frequent windthrow, less frequent insect epidemics, and infrequent catastrophic fire. Because many boreal forests lie next to the Great Lakes and trees are shallowly rooted, windthrow and snap-off rates are high. Balsam fir, which is prone to fungal attacks and diseases and subsequently root and butt rot, is especially susceptible to windthrow and breakage (Cooper 1913, Grant 1934, Buell and Niering 1957, Curtis 1959, Buell and Martin 1961, Comer et al. 1995, Peterson 2004, Senecal et al. 2004, McCarthy and Weetman 2006). In addition to blowdown, exposure to erosive winter winds can result in the exposure or re-exposure of mineral soil, which is favorable for conifer seedling establishment (Harman and Plough 1986). Mortality from windthrow likely decreases with distance from the lake edge (Senecal et al. 2004).



Photos by Joshua G. Cohen

In addition to creating canopy gaps that promote conifer regeneration, windthrow and spruce budworm mortality generate coarse woody debris that provides critical microsites for seedling establishment.

Mature to old-growth boreal forests are characterized by a mosaic of different-aged partial openings caused by windfall, senescence, and *Choristoneura fumiferana* (spruce budworm) defoliation (Cooper 1913, Kneeshaw and Bergeron 1998, Kneeshaw and Gauthier 2003, D'Aoust et al. 2004, Pham et al. 2004). Where fire disturbance is infrequent (> 200 years), uneven-aged conditions and the associated complex structural heterogeneity (i.e., canopy gaps, coarse woody debris and snags of all stages of decomposition and diameter classes) persist and gap phase dynamics control tree establishment, growth, and mortality (Bergeron 2000, De Grandpre et al. 2000, Greif and Archibold 2000, Bergeron et al. 2001, Elkie and Rempel 2001, McCarthy 2001, Clark et al. 2003, Kneeshaw and Gauthier 2003, Despons et al. 2004, Pham et al. 2004, McCarthy and Weetman 2006). Small-scale canopy openings (< 200 m²) created by individual or small-group tree mortality promote the regeneration of shade-tolerant conifers, such as balsam fir and cedar, and less frequently white spruce (Kneeshaw and Bergeron 1998, Greene et al. 1999, McCarthy 2001, Ruel and Pineau 2002, Pham et al. 2004). All of these species can reproduce sexually and vegetatively, but layering is most common for cedar (Greene et al. 1999). Advanced regeneration is typically correlated with the basal area density of parent trees (Greene et al. 1999). Small openings are often filled with dense thickets of balsam fir seedlings which establish on a variety of seedbeds and can remain suppressed for many decades (Cooper 1913, Buell and Niering 1957, Buell and Martin 1961, Morin and Laprise 1997, Kneeshaw and Bergeron 1998,



McCarthy 2001, D'Aoust et al. 2004). In addition to creating canopy gaps, windthrow generates uprooted tree pits and tip-up mounds with exposed mineral soil and fallen logs, which decompose and function as nurse logs. These microsites provide critical seedbeds for white spruce, cedar, *Tsuga canadensis* (hemlock), *Betula alleghaniensis* (yellow birch), and paper birch, small-seeded species that depend on these features for successful germination due to favorable moisture conditions and reduced competition (Maycock and Curtis 1960, Liefers et al. 1996, Kneeshaw and Bergeron 1998, Simard et al. 1998, Greene et al. 1999, Bergeron 2000, Ducey and Gove 2000, McCarthy 2001, Rooney et al. 2000, Charron and Greene 2002, Ruel and Pineau 2002, McCarthy and Weetman 2006). Larger gaps generated by blowdown and group mortality from spruce budworm infestation can foster the maintenance of shade-intolerant species such as trembling aspen and paper birch (birch seedling density has been found to be correlated to gap size) (Kneeshaw and Bergeron 1998, Greene et al. 1999, Bergeron 2000, McCarthy 2001, Lesieur et al. 2002, D'Aoust et al. 2004, Pham et al. 2004, McCarthy and Weetman 2006).

Gaps generated by windthrow and spruce budworm defoliation are intrinsically different. The particular process of tree mortality affects the spatial and temporal characteristics of gap formation, the microsites produced, the potential resources available to gap regenerators, and the rate of gap closure (McCarthy 2001, Pham et al. 2004). Trees succumbing to death from spruce budworm defoliation typically die standing, remain standing as snags for several years, and eventually snap when they fall to the ground (Kneeshaw and Bergeron 1998, McCarthy 2001, Pham et al. 2004). Compared to windthrown trees, standing trees create smaller gaps and they do not provide microsites associated with seedling establishment (pit and mound topography and nurse logs). In addition, the gap creation and gap filling processes in spruce budworm-generated gaps tend to be slower compared to windthrow dynamics since budworm-caused mortality occurs over a number of years (Blais 1981, Kneeshaw and Bergeron 1998, McCarthy 2001, Pham et al. 2004). Compared to temperate and tropical forests, gaps persist longer in boreal forest because of the prevalence of spruce budworm-induced gaps, the shorter growing season, and the restricted ability of conifers to grow lateral branches into openings (McCarthy 2001, Pham et al. 2004). As noted above, group mortality is often

associated with spruce budworm outbreaks (Kneeshaw and Bergeron 1998). The severity of spruce budworm defoliation events and size of subsequent canopy gaps are correlated with balsam fir basal area; mortality tends to be lower in mixed stands (Lynch and Witter 1985, Morin and Laprise 1997, Bergeron and Leduc 1998, Kneeshaw and Bergeron 1998, Greene et al. 1999, D'Aoust et al. 2004, Jasinski and Payette 2005). Timing of defoliation episodes also influences tree death with high mortality rates occurring if defoliation occurs before midsummer bud formation (Malmstrom and Raffa 2000). In addition, site factors influence impact from spruce budworm defoliation. Balsam fir occurring on very dry or very wet sites tends to suffer heavy damage from defoliation events (Lynch and Witter 1984, Hix et al. 1987). Although spruce budworm defoliates both white spruce and balsam fir, this biotic disturbance agent tends to be more detrimental to the latter (Curtis 1959, Blais 1981, Greene et al. 1999, Volney and Flemming 2000, Nealis and Regniere 2004). Spruce budworm epidemics often occur in 25- to 36-year intervals that are driven by weather conditions and correspond to synchronous budworm population cycles (Candau et al. 1998, Malmstrom and Raffa 2000, Volney and Flemming 2000, Despons et al. 2004). The outbreak potential of spruce budworm is thought to be tied to extended warm periods since drought can stress host trees and increase their susceptibility to attack and also decrease the population of pathogens and natural enemies that control spruce budworm (Malmstrom and Raffa 2000, Jasinski and Payette 2005). Spruce budworm-induced stand damage is a major facilitator of fire ignition and spread, and defoliation events can increase the extent and severity of fire in boreal forests (Rowe and Scotter 1973, Malmstrom and Raffa 2000, Volney and Flemming 2000, Jasinski and Payette 2005). Interactions of insect epidemics, climate (i.e., droughts), and blowdowns influence fire regimes of boreal forests (Heinselman 1973).

Infrequent catastrophic crown fire is an important disturbance factor of Great Lakes boreal forests, especially for inland occurrences (Cooper 1913, Buell and Gordon 1945, Buell and Niering 1957, Curtis 1959, Maycock and Curtis 1960, Buell and Martin 1961, Maycock 1961, Maycock 1965, Frelich and Reich 1995, Flakne 2003). Fire disturbance contributes to the landscape heterogeneity of boreal forests via variation in frequency and severity (Morissette et al. 2002, Purdon et al. 2004). The primary ignition source for





Photo by Joshua G. Cohen

Infrequent catastrophic crown fire in boreal forest is ignited by summer lightning strike.

fires within boreal forests is summer lightning strikes that occur during persistent high-pressure systems (Cooper 1913, Rowe and Scotter 1973, Bergeron 1991, Johnson 1992, Heinselman 1996, Johnson et al. 2001, Bergeron et al. 2004b); however, historically, fires were likely also started by Native Americans (Cooper 1913, Heinselman 1996, Loope and Anderton 1998). Probability of ignition from lightning strike is amplified by increasing conifer coverage in the canopy, stand age, and drought conditions (Cumming 2000, Krawchuck et al. 2006).

Estimations of fire return interval for Michigan boreal forests have yet to be determined. However, numerous studies across the vast expanse of Canadian boreal forest and in the boreal forest of Minnesota have examined fire disturbance regimes. Fire frequency, primarily influenced by climate, is highly and continuously variable in time and space and from one region to the next (Cumming 2000, Bergeron et al.

2001, Lesieur et al. 2002, Bergeron et al. 2004b, Pham et al. 2004). In the Canadian boreal forest, fire rotation gradually lengthens from west to east and decreases along with fire size and intensity with increasing landscape importance of fire breaks (i.e., lakes), topographic variability, and deciduous trees (Rowe and Scotter 1973, Bergeron et al. 2001, Hely et al. 2001, Lesieur et al. 2002, Bergeron et al. 2004b). Boreal forest in dry areas of flat topography exhibit short fire cycles (50 to 150 years), while systems occurring in maritime or humid regions exhibit fire cycles that can exceed 500 years (Kneeshaw and Bergeron 1998, Larsen and MacDonald 1998, Bergeron 2000, Gauthier et al. 2000, Arsenaault 2001, Asselin et al. 2001, Elkie and Rempel 2001, Henry 2002, Lesieur et al. 2002, Clark et al. 2003, de Groot et al. 2003, Bergeron et al. 2004b, Pham et al. 2004, Didion et al. 2007). Fire cycles of Minnesota boreal forests are short, ranging from 50 to 110 years (Heinselman 1973, Frelich and Reich 1995, Heinselman 1996, Frelich 2002). Given the prevailing



landscape position of most Michigan boreal forests (along the shoreline), the fire return interval for these systems is probably greater than 500 years with slightly shorter fire cycles for inland sites. Where fire cycles are shorter than the life-span of the dominant tree species, large even-aged stands dominate the landscape (Frelich and Reich 1995, Arsenault 2001, Johnson et al. 2001). Longer fire cycles generate landscapes characterized by a diverse mosaic of uneven-aged boreal forest (Johnson et al. 2001).

Fire behavior (i.e., intensity and burn size) in boreal forests is determined by the interaction of weather, vegetation (fuels), and landform (topography) (Johnson 1992, Hely et al. 2000b, Arsenault 2001, Cumming 2001, Hely et al. 2001, Johnson et al. 2001). Conifer density, drought conditions, and flat topography are all positively correlated with fire intensity and area burned (Rowe and Scotter 1973, Bergeron 2000, Hely et al. 2000b, Cumming 2001, Hely et al. 2001, Bergeron et al. 2004b, Krawchuk et al. 2006). Large fires tend to be more intense than small fires, killing a higher proportion of trees relative to area burned (Bergeron et al. 2004b). Boreal forests with a high proportion of deciduous trees tend to support less intense fires that burn smaller areas (Hely et al. 2000b, Hely et al. 2001). In addition, where deciduous species are part of the canopy, spring fires tend to be more intense than summer fires because of the capacity for deciduous leaves to intercept sunlight and generate a cooler and moister understory in the summer compared to the spring (Hely et al. 2000b). Characterized by horizontal and vertical continuity of fuels, boreal forests dominated by coniferous species are inherently prone to high-intensity crown fires (Rowe and Scotter 1973, Johnson 1992). The following traits of conifer-dominated boreal forests engender crowning: low crown heights; living and dead basal branches that function as fuel ladders; heavy loads of small diameter elements (small needles on small diameter branches); high resin and low moisture content of decay resistant needles and cones; and a well-developed and aerated needle mat (Johnson 1992, Hely et al. 2000b, Johnson et al. 2001, Krawchuk et al. 2006). Crown fires in boreal forests leave high densities of snags and scattered patches of living trees where partial burning occurs (Lee 1998, Greif and Archibild 2000, Hely et al. 2000a, Lesieur et al. 2002, Pedlar et al. 2002, Greene et al. 2004).

Post-fire regeneration dynamics are controlled by fire intensity, extent, shape, and interval, and also by

pre-fire canopy density and age and landscape seed source availability (Rowe and Scotter 1973, Johnson 1992, Greene and Johnson 1999, Greene et al. 1999, Bergeron 2000, Arsenault 2001, Lesieur et al. 2002, Bergeron et al. 2004b, Greene et al. 2004, Rydgren et al. 2004, Johnstone and Chapin 2006). Large, intense crown fires often foster the immediate replacement of conifer-dominated boreal forest by early-successional deciduous forest dominated by trembling aspen and paper birch [*Pinus banksiana* (jack pine) and *Picea mariana* (black spruce) are also prevalent in post-fire Canadian and Minnesotan boreal forests] (Curtis 1959, Heinselman 1973, Rowe and Scotter 1973, Frelich and Reich 1995, Greene et al. 1999, Bergeron 2000, Frelich 2002, Bergeron et al. 2004). These shade-intolerant species are capable of massive asexual reproduction through basal sprouting; birch sprouts from the stem or root collar while aspen regenerates vegetatively primarily through root suckers but also from root collar sprouts (Cooper 1913, Heinselman 1996, Greene et al. 1999, Bergeron 2000, Harper 2002, Bergeron et al. 2004b). The density of suckers and sprouts is positively correlated with pre-fire basal area, the amount of basal area killed by the fire, and stand age (sprouting capacity declines with tree age) (Greene and Johnson 1999, Greene et al. 1999, Greene et al. 2004). Following hot fires, aspen is often more abundant than birch because of aspen's capacity to sprout from deeply buried roots as opposed to solely from the root collar (de Groot et al. 2003).

Immediate sprouting by aspen and birch is followed by a pulse of conifer recruitment in the first decade following fire (Galipeau et al. 1997, Greene and Johnson 1999, Greene et al. 1999, Charron and Greene 2002, Greene et al. 2004). This initial conifer regeneration episode is transient as suitable seedbeds are quickly covered, aerial seedbanks of killed species (i.e., black spruce and jack pine) are soon depleted, and populations of granivores rebound (Johnson 1992, Greene et al. 2004). Conifers that do not have serotinous cones rely on seed from survivors to reinvade burnt areas (Johnson 1992, Bergeron 2000, Asselin et al. 2001, Charron and Greene 2002, Bergeron et al. 2004b). Post-fire conifer tree density is a function of burn severity and extent (Johnson 1992, Greene et al. 2004). Intense crown fires covering large areas are disadvantageous to balsam fir, cedar, and white spruce (Larsen and MacDonald 1998, Gauthier et al. 2000, Asselin et al. 2001). For these species, distance to seed



source is the primary factor influencing the spatial distribution of post-fire recruitment as regeneration density decreases abruptly with distance from remnant stands or trees (Johnson 1992, Galipeau et al. 1997, Cumming 2000, Asselin et al. 2001, Johnstone et al. 2004). In addition to seed availability, conifer establishment is sensitive to substrate conditions with exposed mineral soil and burnt humus being the primary establishment sites immediately following fire (Johnson 1992, Greene and Johnson 1999, Arsenault 2001, Charron and Greene 2002, Greene et al. 2004, Johnstone et al. 2004, Jayen et al. 2006, Johnstone and Chapin 2006). Severe fires typically result in a higher proportion of suitable seedbeds with seedbed frequency varying along a gradient of soil burn severity and conifer seedling germination and seedling survival increasing with degree of soil combustion (Johnson 1992, Arsenault 2001, Greene et al. 2004, Jayen et al. 2006, Johnstone and Chapin 2006). In addition, depth of burn can influence the ratio of deciduous to conifer recruits since deciduous sprouters decrease in importance with increasing depth of burn (Schimmel and Granstrom 1996).

The initial recruitment pulse of conifers and sprouting deciduous species is followed by several decades of low levels of conifer establishment in the understory of the initial cohort. Conifer recruitment increases as more suitable microsites for establishment develop with the break-up of the early-successional canopy and the accumulation of decomposing coarse woody debris (Cooper 1913, Liefers et al. 1996, Simard et al. 1998, Greene et al. 1999, Bergeron 2000, de Groot et al. 2003, Johnstone et al. 2004). Shade-tolerant conifer regeneration is often dominated by balsam fir, which has a competitive advantage over cedar and white spruce in that fir has the capacity to establish on thick leaf litter due to its larger seeds and does not rely as heavily on exposed mineral soil, burnt humus, and nurse logs (Simard et al. 1998, Bergeron 2000, Asselin et al. 2001, Lesieur et al. 2002). When the post-fire canopy cohort senesces and dies (usually starting 40 to 60 years after fire), the advanced regeneration of shade-tolerant conifers is released (Bergeron 2000, Cumming et al. 2000, De Grandpre et al. 2000, Senecal et al. 2004). As more time elapses, forest composition and structure change with even-aged, deciduous-dominated boreal forests succeeding to uneven-aged, conifer-dominated systems (Frelich and Reich 1995, Bergeron 2000, Greif

and Archibold 2000, Hely et al. 2000a, Arsenault 2001, Bergeron et al. 2001, Lesieur et al. 2002).

Through the course of boreal forest succession, mammalian herbivory influences boreal forest vegetative composition and structure (Dlott and Turkington 2000). Voracious and selective foraging by *Alces alces* (moose) in the Upper Peninsula of Michigan can result in the alteration of species composition, community structure, litterfall dynamics, nutrient cycling, and ultimately forest successional patterns of boreal forests (Snyder and Janke 1976, Risenhoover and Maass 1987, Pastor et al. 1988, McInnes et al. 1992, Pastor et al. 1993). Like boreal forests, moose have a circumpolar distribution. A single moose can consume 15 kg of dry food per day or five to six metric tons per year (Pastor et al. 1988). On sites with white spruce and balsam fir, moose preferentially browse on balsam fir, retarding fir vertical growth, limiting fir abundance, and imparting a competitive imbalance to unpalatable white spruce, which contains high concentrations of lignins and resins (Risenhoover and Maass 1987, Pastor et al. 1988, McInnes et al. 1992). Where deciduous species are prevalent, moose browsing can hinder the growth and recruitment of paper birch, *Sorbus americana* (mountain ash), *Acer spicatum* (mountain maple), and aspen, shift dominance to evergreens (especially spruce), and thereby modify litterfall quantity and quality and reduce soil microbial activity and nutrient availability (Snyder and Janke 1976, Pastor et al. 1988, McInnes et al. 1992, Pastor et al. 1993, Pastor et al. 1999, Connor et al. 2000). Periods of low moose density and large-scale disturbance events (i.e., fire, blowdowns, and severe spruce budworm events) are likely important for the recruitment of species preferentially browsed by moose (McInnes et al. 1992). White-tailed deer can also impact the species composition and structure of boreal forests by limiting the recruitment of cedar and reducing populations of *Taxus canadensis* (Canadian yew), a species also intensively browsed by moose (Snyder and Janke 1976, Janke et al. 1978, Alverson et al. 1989, Allison 1990, Van Deelen et al. 1996, Van Deelen 1999, Connor et al. 2000, Rooney et al. 2002).

Large-scale fires affect populations of small rodents such as mice, voles, shrews, and squirrels that are important conifer seed and seedling predators (Malmstrom and Raffa 2000, Charron and Greene 2002, Peters et al. 2003, Greene et al. 2004). Post-fire



rodent densities and granivory rates are likely inversely proportional to fire severity with rodent populations plummeting following intense fires (Charron and Greene 2002, Greene et al. 2004). As noted above, initial pulses of conifer recruitment are likely influenced by rodent population crashes following wildfires (Greene et al. 2004).



Photo by Joshua G. Cohen

The dense canopy of boreal forest is dominated by spire-shaped conifers (i.e., cedar, white spruce, and balsam fir).

Vegetation: The boreal forest flora is circumboreal in distribution and as a result, boreal forests display a high degree of floristic homogeneity with many ubiquitous species (Curtis 1959, Stearns et al. 1982). Floristic similarity between sites tends to diminish with increasing distance (Curtis 1959), and floristic diversity tends to decrease with increasing latitude (Kenoyer 1940). The canopy of boreal forests is characterized by a prevalence of conical-shaped evergreens, which often form a closed canopy (Cooper 1913, Potzger 1941). The spire shape of the canopy conifers functions as an adaptation to shed heavy snow loads (Thompson and Sorenson 2000) and facilitates the interception of low-angle solar radiation (McCarthy 2001, Henry 2002, Pham et al. 2004). The dense tree coverage often results in a scattered understory and a sparse groundcover due to the low levels of light transmitted through the canopy (Potzger 1941, Buell and Gordon 1945, Buell 1956, Buell and Niering 1957, Greene et al. 1999) and dense sod formed by the extensive network of the shallowly rooted trees (Buell and Gordon 1945, McCarthy 2001). In addition to low light levels, boreal flora are also

adapted to low winter temperatures, brief cool growing seasons, and low soil fertility. Many boreal plants are long-lived perennials that exhibit stress-tolerant traits such as nitrogen fixing, low rates of flowering, and slow relative growth rates (Dlott and Turkington 2000). The stringent environment of boreal forests likely contributes to the paucity of non-native invasive plants (La Roi 1967). Floristic composition of boreal forests is driven by available pools of species, abiotic factors (i.e., surface deposits and local climate), and disturbance dynamics (Gauthier et al. 2000, Legare et al. 2001).

The canopy of boreal forests is dominated by *Abies balsamea* (balsam fir), *Picea glauca* (white spruce), and *Thuja occidentalis* (northern white-cedar) along with *Betula papyrifera* (paper birch) and *Populus tremuloides* (trembling aspen) (Cooper 1913, Darlington 1940, Potzger 1941, Jones and Zicker 1955, Curtis 1959, Maycock and Curtis 1960, Maycock 1961, La Roi 1967, Stearns et al. 1982, Harman and Plough 1986, Pastor et al. 1988, McInnes et al. 1992, Pastor et al. 1993, Rutowski and Stottlemeyer 1993, Albert et al. 1995, Comer et al. 1995, Flakne 2003). Dominance shifts towards early-successional, shade-intolerant aspen and birch following fire, large-scale blowdown, and/or spruce budworm events, and towards shade-tolerant conifers in the absence of such disturbance (Maycock and Curtis 1960, Maycock 1961, Comer et al. 1995). Cedar dominance is most pronounced in sand dunes and on thin soils over neutral to alkaline bedrock or glacial deposits, such as in the Straits of Mackinac (Comer et al. 1995). White spruce, which occurs typically at low densities, is more prevalent on drier sites, while balsam fir and cedar are more common on wetter sites (Cooper 1913, Curtis 1959, Maycock and Curtis 1960, Greene et al. 1999); all three of these species increase in importance with time since fire, especially cedar (Greene et al. 1999, Bergeron 2000, Gauthier et al. 2000, Lesieur et al. 2002). Additional canopy associates include *Pinus strobus* (white pine), *Populus balsamifera* (balsam poplar), and *Tsuga canadensis* (hemlock), and less frequently *Picea mariana* (black spruce), *Pinus resinosa* (red pine), *Pinus banksiana* (jack pine), *Acer rubrum* (red maple), *Betula alleghaniensis* (yellow birch), and *Quercus rubra* (red oak) (Cooper 1913, Darlington 1940, Potzger 1941, Jones and Zicker 1955, Curtis 1959, Maycock and Curtis 1960, Maycock 1961, La Roi 1967, Stearns et al. 1982, Harman and Plough 1986, Pastor et al. 1988, Penskar et al. 2001, Frelich 2002, Penskar et al. 2002, Flakne 2003).



Inland boreal forests are often characterized by an increased canopy component of white pine and hemlock and deciduous species (Curtis 1959, Comer et al. 1995). In general, evergreen species are more prominent in the canopy on infertile soils (Legare et al. 2001). *Acer spicatum* (mountain maple), *A. pensylvanicum* (striped maple), *Sorbus americana* (American mountain ash), and *S. decorus* (mountain ash) are characteristic of the subcanopy and understory (Cooper 1913, Grant 1934, Curtis 1959, Maycock and Curtis 1960, Maycock 1961, La Roi 1967, Stearns et al. 1982, McInnes et al. 1992, Despons et al. 2004).

Where aspen and/or paper birch dominate the canopy, conifers (i.e., balsam fir, white spruce, and/or cedar) are prevalent in the subcanopy and understory (Curtis 1959, Frelich and Reich 1995). Conifer regeneration is also prevalent in small windthrow gaps, while birch seedlings are abundant in larger areas of blowdown (Cooper 1913). Balsam fir is typically the most abundant conifer represented in the seedling bank, while white spruce occurs sporadically (Cooper 1913, Buell and Niering 1957, Maycock 1961, Greene et al. 1999, McCarthy and Weetman 2006) and cedar is concentrated in localized areas. Additional understory or tall shrub species include *Cornus rugosa* (round-leaved dogwood), *Shepherdia canadensis* (soapberry), *Alnus rugosa* (tag alder), and less frequently *A. crispa* (mountain alder) and *Taxus canadensis* (Canadian yew) (Cooper 1913, McInnes et al. 1992, Rutowski and Stottlemeyer 1993). Characteristic low shrubs include *Lonicera canadensis* (American fly honeysuckle), *Arctostaphylos uva-ursi* (bearberry), Canadian yew, *Ribes cynosbati* (prickly gooseberry), *Vaccinium myrtilloides* (Canada blueberry), *V. membranaceum* (bilberry), *Diervilla lonicera* (bush honeysuckle), *Juniperus communis* (ground juniper), *Rubus parviflorus* (thimbleberry), and *R. pubescens* (dwarf raspberry) (Cooper 1913, Grant 1934, Darlington 1940, Potzger 1941, Buell and Niering 1957, Maycock 1961, Maycock 1965, La Roi 1967, Grigal and Ohmann 1975, Stearns et al. 1982, McInnes et al. 1992, Rutowski and Stottlemeyer 1993, Heinselman 1996). Where they are abundant, shrub species, such as Canadian yew, mountain maple, and *Rubus* spp. can compete with overstory species (Cooper 1913, Kneeshaw and Bergeron 1998).

Ground layer plants are a mix of species found in mesic northern forest and northern swamp types, and most bloom in early spring or summer (Stearns et al. 1982). Prominent among the boreal ground flora are *Actaea rubra* (red baneberry), *Aralia nudicaulis* (wild sarsaparilla), *Aster macrophyllus* (big-leaved aster), *Carex eburnea* (bristleleaf sedge), *C. deweyana* (Dewey sedge), *Clintonia borealis* (bluebead lily), *Coptis trifolia* (goldthread), *Cornus canadensis* (bunchberry), *Dryopteris* spp. (woodfern species), *Galium triflorum* (fragrant bedstraw), *Gaultheria procumbens* (wintergreen), *Goodyera oblongifolia* (Menzie's rattlesnake plantain), *G. repens* (creeping rattlesnake plantain), *Linnaea borealis* (twinflower), *Maianthemum canadense* (Canada mayflower), *Mitella nuda* (naked miterwort), *Mitchella repens* (partridge berry), *Oxalis acetosella* (northern wood sorrel), *Pteridium aquilinum* (bracken fern), *Polygala paucifolia* (gay wings), *Pyrola elliptica* (large-leaved shinleaf), *Smilacina stellata* (starry false Solomon seal), *Streptopus roseus* (rose twisted stalk), *Trientalis borealis* (starflower), and *Viola* spp. (violet species) (Cooper 1913, Grant 1934, Darlington 1940, Kenoyer 1940, Potzger 1941, Jones and Zicker 1955, Buell and Niering 1957, Curtis 1959, Maycock and Curtis 1960, Buell and Martin 1961, Maycock 1961, Maycock 1965, La Roi 1967, Grigal and Ohmann 1975, Stearns et al. 1982, De Grandpre et al. 1993, Rutowski and Stottlemeyer 1993, Heinselman 1996, Penskar et al. 2001, NatureServe 2006, Michigan Natural Features Inventory Database). *Cypripedium arietinum* (ram's head orchid, state special concern) and *Iris lacustris* (dwarf lake iris, state and federally threatened) are uncommon, but characteristic (Kost et al. 2007).



Photos by Joshua G. Cohen

Dense tree coverage results in low levels of light transmission to the sparsely vegetated understory and ground cover of boreal forests.



Clubmosses, such as *Lycopodium annotinum* (stiff clubmoss), *L. clavatum* (running ground pine), and *L. obscurum* (ground pine), are often locally abundant (Cooper 1913, Grant 1934, Buell and Niering 1957, Maycock 1961, Maycock 1965, La Roi 1967, Grigal and Ohmann 1975, Ruttowski and Stottlemeyer 1993), with ground pine more common following fire (Reich et al. 2001). Mosses, liverworts, Usnea lichens, and saprophytic fungi often are common due to favorable, moisture conditions (Cooper 1913, Curtis 1959, Stearns et al. 1982, Heinselman 1996, Despons et al. 2004).



Photo by Joshua G. Cohen

Proximity to the Great Lakes and coniferous canopy coverage generate moisture conditions suitable for a diverse array of non-vascular flora such as Usnea lichens.

Other Noteworthy Species: Boreal forests are utilized by a wide variety of species including numerous rare plants and animals. Rare plants associated with boreal forests include *Calypso bulbosa* (calypso orchid, state threatened), *Cypripedium arietinum* (ram's head orchid, state special concern), *Disporum trachycarpum* (northern fairy bells, state threatened), *Iris lacustris* (dwarf lake iris, state and federally threatened), *Luzula parviflora* (small-flowered woodrush, state threatened), *Oplopanax horridus* (Devil's-club, state threatened) (Cooper 1913), *Phacelia franklinii* (Franklin's phacelia, state threatened), *Piperia unalascensis* (Alaska orchid, state special concern), *Pterospora andromedea* (pinedrops, state threatened), *Viburnum edule* (squashberry or mooseberry, state threatened), and *Viola epipsila* (northern palustrine violet or marsh violet, state endangered).

Rare herptiles that utilize boreal forests include *Emydoidea blandingii* (Blanding's turtle, state special concern), *Pseudacris maculata* (boreal chorus frog,

state special concern), and *Sistrurus catenatus catenatus* (eastern massasauga, state special concern). Rare insects associated with boreal forest include *Polygonia gracilis* (hoary comma, state special concern butterfly) and *Proserpinus flavofasciata* (yellow-banded day-sphinx, state special concern moth). If suitable nesting trees or snags are available, *Haliaeetus leucocephalus* (bald eagle, state special concern), *Falco columbarius* (merlin, state threatened), and *Pandion haliaetus* (osprey, state special concern) can be found nesting in these systems. Other rare birds that could occur in boreal forest are *Accipiter gentilis* (northern goshawk, state special concern), *Falcapennis canadensis* (spruce grouse, state special concern), and *Picoides arcticus* (black-backed woodpecker, state special concern). Black-back woodpecker and *Picoides dorsalis* (three-toed woodpecker) are associated with post-wildfire boreal forests that have numerous snags for foraging wood-boring insects (Hobson and Schieck 1999, Morissette et al. 2002, Nappi et al. 2003, Nappi et al. 2004). Many additional animals depend on or are periodically concentrated in recently burned areas (Morissette et al. 2002, Bergeron et al. 2004a). *Alces americanus* (moose, state special concern), *Canis lupus* (gray wolf, state threatened), *Felis concolor* (cougar, state endangered), and *Lynx canadensis* (lynx, state endangered) utilize boreal forest habitat (Curtis 1959, Heinselman 1996, Henry 2002, Fisher and Wilkinson 2005). Wolf use of an area shifts seasonally in conjunction with fluctuation of their prey base. Lynx are closely tied to *Lepus americanus* (snowshoe hare), which are typically concentrated in mid-successional systems that have dense understories (Fisher and Wilkinson 2005). As noted above, selective browsing by moose and deer can result in changes to boreal forest floristic composition and structure. *Sorex fumeus* (smoky shrew, state threatened) and *Vallonia gracilicosta albula* (land snail, state special concern) can also be found within boreal forests. Paleontologists believe that *Mammot americanum* (mastodon, extinct) were associated with spruce-dominated forests and that spruce was a staple in their diet (Halsey and Vitt 2000).

As a predominantly coastal system, Michigan boreal forest and associated communities provide critical feeding, roosting, and perching habitat for migrating shorebirds, waterfowl, and songbirds in the spring. The majority of shrubs found within boreal forest have fleshy fruit, an important food source for birds such as grosbeaks, crossbills, warblers, and sparrows (Curtis



1959). Boreal forests are utilized by numerous bat species (Kalcounis et al. 1999, Hogberg et al. 2002). Mature boreal forests are particularly important for bat foraging and roosting (Kalcounis et al. 1999, Fisher and Wilkinson 2005). Bats depend on large live or dead trees, prevalent in mature and old-growth boreal forest, since they roost in crevices beneath loose bark and in abandoned cavities (Kalcounis et al. 1999, Fisher and Wilkinson 2005). As noted above, small rodents (i.e., mice, voles, shrews, and squirrels) are significant granivores within boreal forests. The primary vertebrate seed predator of white spruce is *Sciurus vulgaris* (red squirrel) (Peters et al. 2003). The small mammal guild in boreal forest serves additional functions including disseminating seeds, spores, and propagules of vascular plants, bryophytes, fungi, and lichens; mixing soils; facilitating decomposition of organic matter and litter; regulating invertebrate populations; and providing prey for terrestrial and avian predators (Pearce and Venier 2005). Composition of mammalian assemblages and species shifts with successional stages. For example, red-backed voles (*Myodes* spp.), arboreal sciurids (e.g., red and flying squirrels), mustelids [e.g., *Martes pennanti* (fisher) and *M. americana* (marten)] are prevalent in mature forests, while *Peromyscus* spp. (deer mice) and white-tailed deer are most abundant following disturbance (Fisher and Wilkinson 2005, Pearce and Venier 2005). Where boreal forests occur near wetland systems, *Castor canadensis* (beaver) can have profound impacts through flooding, and felling and browsing of aspen (Jones and Zicker 1955, Naiman et al. 1986, Pastor et al. 1988, Naiman et al. 1994).

Conservation and Biodiversity Management: Boreal forest is an uncommon type in the Great Lakes region that contributes significantly to the overall biodiversity of northern Michigan by providing habitat for a unique suite of plants and a wide variety of animal species, including numerous rare flora and fauna. When the primary conservation objective is to maintain native biodiversity in boreal forests, the best management is to leave large tracts unharvested and allow natural processes (i.e., windthrow, insect defoliation, and fire) to operate unhindered and stochastically generate a range of successional stages (Kneeshaw and Gauthier 2003). It is crucial to allow dead and dying wood to remain within these systems to become snags, stumps, and fallen logs (Morissette et al. 2002, Harper et al. 2005). Within areas managed solely for biodiversity, resource practitioners should refrain from salvage

harvesting following fire, wind, and insect disturbance. Salvage logging, especially after wildfire, can severely diminish nutrient pools and site productivity in addition to reducing structural heterogeneity (Brais et al. 2000, Morissette et al. 2002, Nappi et al. 2004). As noted above, recently burned areas, which provide critical habitat for a host of species, are rare within fire-suppressed and managed landscapes (Schmiegelow and Monkkonen 2002, Bergeron et al. 2004a).



Photo by Joshua G. Cohen

Recently burned expanses of boreal forest provide critical but rare and ephemeral habitat for unique species such as the black-backed woodpecker.

Where boreal forests are being actively managed, maintaining boreal forests in different age-classes within the historic range of variability and retaining stand-level structural attributes associated with natural disturbance will contribute to the preservation of regional biodiversity and ecological integrity (Bergeron et al. 1999, Niemela 1999, Peltzer et al. 2000, Bergeron et al. 2001, Legare et al. 2001, Lesieur et al. 2002, Morissette et al. 2002, Kneeshaw and Bergeron 2003, Bergeron 2004, Didion et al. 2007). Numerous researchers believe that management of boreal forests should emulate the scale, intensity, and frequency of natural disturbances since native organisms are adapted to the environmental forces with which they have evolved over the millennia (Hobson and Schieck 1999, Niemela 1999, Bergeron et al. 2001, McCarthy 2001, Bergeron et al. 2004a, D'Aoust et al. 2004, Fisher and Wilkinson 2005). Examination of regional natural disturbance regimes and the associated range of variability of cover types, age-classes, scale of perturbation, and structural attributes can help managers determine which silvicultural techniques to employ. Determining whether to manage using even-aged or



uneven-aged silvicultural systems should depend on the natural disturbance context of the system. For example, within landscapes with short fire cycles (< 100 years), managers should consider using short rotation even-aged management, while in regions with long fire cycles, uneven-aged silviculture and extended rotations are more appropriate (Lesieur et al. 2002, Bergeron et al. 2004a).

Although boreal forests are typically managed with even-aged silviculture, uneven-aged management is both technically and biologically feasible, especially in fire-resistant landscapes. Partial and selective cutting within boreal forests can be used to simulate gap-generating disturbance such as small-scale windthrow and spruce budworm defoliation events (Bergeron et al. 2001, McCarthy 2001, Harper et al. 2003, Kneeshaw and Gauthier 2003). Gap-based silvicultural systems mimic natural gap size and frequency through carefully planned patch or selective cutting (McCarthy 2001). Recruitment following uneven-aged management can be from both advanced regeneration (i.e., layers and seedlings) and seeding with primary reliance on advanced regeneration. Protection of advanced regeneration through careful logging is paramount to effective uneven-aged management (Morin and Laprise 1997, Greene et al. 1999, McCarthy 2001). Harvesters can avoid damage to advanced regeneration and residual trees by planning ahead of time where to travel, where to drop felled trees (directional felling), and where to process and pile the bucked logs (Pothier et al. 1995, MacDonnell and Groot 1997). Also critical is the maintenance of old-growth attributes and structural diversity, which can be realized by retaining large living trees, snags, and logs (Siitonen et al. 2000, Kneeshaw and Gauthier 2003). In addition, extended rotations and explicit management constraints (e.g., no harvesting of forests over a given age) can be employed to increase old-growth and overmature boreal forest and old-growth characteristics that have decreased in managed landscapes (Bergeron et al. 1999, Siitonen et al. 2000, Harper et al. 2003, Didion et al. 2007). Long rotation periods (over 100 years) are favorable for numerous species, such as epiphytic lichen, saprophytic fungi, trunk foraging birds, and bats that depend on old, large trees and/or coarse woody debris (Brais et al. 2000, Siitonen et al. 2000, Harper et al. 2003).

Even-aged management of boreal forests should be focused in landscapes with short fire cycles, and timber rotations should reflect site-specific fire return intervals. A common misconception about even-aged management of boreal forests is that clear-cuts or final harvests are surrogates for crown fires (Niemela 1999, McCarthy 2001, Harper et al. 2003). Even-aged management typically generates a more uniform landscape than fire disturbance with many structural attributes missing or depleted (Niemela 1999, Despons et al. 2004). Stand-replacing crown fires kill the majority of canopy trees, generate patches of residual live trees, create numerous snags, and produce suitable seedbeds for post-fire conifer recruitment. Even-aged management of boreal forests should strive to maintain patches of residual trees and numerous snags, and provide suitable seedbeds, such as exposed mineral soil, through scarification while minimizing soil compaction. Coarse woody debris in recently burned boreal forests is dominated by standing deadwood, while clear-cuts typically generate small pieces of recently downed material (Niemala 1999, Pedlar et al. 2002). Active management for the long-term supply of snags can be realized by retaining numerous standing dead trees as well as live trees to provide future snags (Lee 1998, Hobson and Schieck 1999, Greif and Archibold 2000, Fisher and Wilkinson 2005). As noted earlier, salvage logging is a common practice following wildfires. Adequate retention of standing dead trees is particularly important during salvage logging because recently burnt areas function as critical but ephemeral and rare habitat for numerous species (e.g., black-backed woodpecker) that depend on dead-burnt snags for foraging and perching (Hobson and Schieck 1999, Morissette et al. 2002, Nappi et al. 2003). Following wildfire and even-aged management, residual patches of live trees provide important habitat for wildlife (e.g., remnant patches in logged boreal forest are utilized by bats and squirrels for foraging and roosting/nesting, and by ungulates and carnivores for cover) (Hogberg et al. 2002, Fisher and Wilkinson 2005). Scattered or clumped seed trees are an important source for natural regeneration (Greene et al. 1999, Peters et al. 2003). Dominant trees with large live crown ratios and strong tapering boles should be selected as seed trees (Asselin et al. 2001).

In addition to providing ample seed trees as a source for recruitment, managers must strive to protect existing advanced regeneration through careful logging (as



noted above) and reduction of deer-browse pressure. Chronically high deer densities over the last half-century have limited tree recruitment of Great Lakes forests and drastically altered their floral composition and structure (Rooney and Dress 1997, Waller and Alverson 1997, Woods 2000, Zhang et al. 2000, Abrams 2001). Woody plant species unpalatable to deer or tolerant of browsing (i.e., aspens, balsam fir, spruce, and red maple) have increased, while species intolerant of deer browsing have decreased (i.e., cedar, hemlock, white pine, Canadian yew, and yellow birch) (Van Deelen et al. 1996). Reducing deer-browse pressure on cedar recruitment is a particular concern in the Straits of Mackinac, where cedar is a prevalent canopy dominant.

Research Needs: Boreal forest has a broad distribution and exhibits subtle regional, physiographic, and edaphic variants. The lack of a universally accepted classification system of boreal forest and the diversity of variations throughout its range demands the continual refinement of regional classifications that focus on the inter-relationships between vegetation, physiography, microclimate, and disturbance (Barnes et al. 1982). Systematic surveys for boreal forests are needed to help prioritize conservation and management efforts. Classification and survey efforts should incorporate nonvascular species, an often understudied group in boreal systems (Desponts et al. 2004).



Photo by Joshua G. Cohen

Systematic surveys of both coastal and inland boreal forest are needed to improve the classification of these systems and to allow for the prioritization of conservation and management efforts.

As noted above, the current paradigm for ecosystem management in boreal forests is the emulation of natural disturbance factors. Achieving this goal requires a regional understanding of the scale, intensity, and

frequency of natural disturbance and the range of variability of landscape patterning (i.e., size and distribution of successional stages and forest types) and stand-level attributes (i.e., snag density and gap size and distribution) generated by complex interactions of fire, windthrow, and insect epidemics (Johnson et al. 1998, Pastor et al. 1999, Cumming et al. 2000, Elkie and Rempel 2001, McCarthy 2001, Schmiegelow and Monkkonen 2002, Kneeshaw and Gauthier 2003). Scientists should continue investigating what primary factors drive the severity, frequency, and longevity of spruce budworm defoliation episodes (Malmstrom and Raffa 2000). Research is lacking on the fire regimes of Michigan boreal forests. Of particular importance is the study of how fire periodicity and intensity change depending on landscape context. Understanding the complex interaction of fire, insect defoliation, and wind disturbance and how these disturbance factors will be affected by climate change are critical research needs (Engelmark et al. 1993, Malmstrom and Raffa 2000, McCarthy 2001, Bergeron et al. 2004b, Jasinski and Payette 2005). The effects of climate change will likely be most pronounced in southern boreal ecosystems, such as those found in the Great Lakes region (Rutowski and Stottlemyer 1993, Chapin et al. 2004).

A better understanding is needed of the ecological consequences of anthropogenic disturbances on boreal forests and how they interact with natural disturbance processes over large spatial and temporal scales (Messier and Bergeron 1999, Niemela 1999, Bergeron et al. 2001, Didion et al. 2007). Little is known about how the replacement of fire by clear-cutting affects the resilience and biodiversity of these systems and the distribution of disturbed areas across the landscape (Bergeron et al. 1999, Hobson and Schieck 1999). Effects of management within boreal forests should be monitored to allow for assessment and refinement. Experimentation with uneven-aged management of boreal forests in fire-resistant landscapes is needed and will provide insights about alternatives to even-aged silviculture (Kneeshaw and Gauthier 2003). Guidance regarding retention of snags within managed systems can be developed by assessing snag density, longevity, and rate of accrual in unmanaged forests (Greif and Archibold 2000). Ecologically oriented management guidelines need to be developed for salvage logging operations (Morissette et al. 2002, Nappi et al. 2004). Sustainable management of boreal forests requires assessment of methods for establishing



conifer regeneration, especially where high deer densities limit recruitment. Seed tree selection and distribution are integral to successful regeneration and need to be further researched. In addition, a thorough understanding of the temporal variation of seed production will facilitate the optimal timing of management (Greene et al. 1999).

Similar Communities: alvar, dry-mesic northern forest, dry northern forest, Great Lakes barrens, hardwood-conifer swamp, limestone bedrock glade, mesic northern forest, poor conifer swamp, rich conifer swamp, wooded dune and swale complex

Other Classifications:

Michigan Natural Features Inventory Circa 1800 Vegetation (MNFI): Spruce-Fir-Cedar Forest (4223)

Michigan Department of Natural Resources (MDNR): F-spruce/fir (upland), C-northern white cedar, A-aspen, B-paper birch

Michigan Resource Information Systems (MIRIS): upland conifer (422), lowland conifer (423), aspen/birch (413), balsam fir upland conifer (42234), white spruce (42216), other upland conifer (4224), undifferentiated upland conifer (42202), balsam fir wetland conifer (42353), balsam fir/white spruce wetland conifer (42346), and undifferentiated lowland conifer (42306)

The Nature Conservancy National Classification:

CODE; ALLIANCE; ASSOCIATION; COMMON NAME

I.A.8.N.c; *Picea glauca* – *Abies balsamea* Forest Alliance; *Abies balsamea* – *Betula papyrifera* / *Diervilla lonicera* Forest; Balsam Fir – Paper Birch / Bush-Honeysuckle Forest; Balsam Fir – Paper Birch Forest

I.A.8.N.c; *Picea glauca* – *Abies balsamea* Forest Alliance; *Picea glauca* – *Abies balsamea* / *Acer spicatum* / *Rubus pubescens* Forest; White Spruce – Balsam Fir / Mountain Maple / Dewberry Forest; Spruce – Fir / Mountain Maple Forest

I.A.8.N.c; *Picea glauca* – *Abies balsamea* Forest Alliance; *Picea glauca* – *Abies balsamea* / *Pleurozium schreberi* Forest; White Spruce – Balsam Fir / Feathermoss Forest; Spruce – Fir / Feathermoss Forest

I.A.8.N.c; *Thuja occidentalis* Forest Alliance; *Thuja occidentalis* / *Abies balsamea* – *Acer spicatum* Forest; Northern White-Cedar / Balsam Fir – Mountain Maple Forest; White-Cedar – Boreal Conifer Mesic Forest

I.B.2.N.b; *Populus tremuloides* - *Betula papyrifera* Forest Alliance; *Populus tremuloides* - *Betula papyrifera* / (*Abies balsamea*, *Picea glauca*) Forest; Aspen - Birch / Boreal Conifer Forest

I.B.2.N.b; *Betula papyrifera* Forest Alliance; *Betula papyrifera* / *Diervilla lonicera* – (*Abies balsamea*) Forest; Paper Birch / Bush Honeysuckle – (Balsam Fir) Forest; Paper Birch / Fir Forest

I.C.3.N.c; *Picea glauca* – *Abies balsamea* – *Populus* spp. Forest Alliance; *Picea glauca* – *Abies balsamea* – *Populus tremuloides* / Mixed Herbs Forest; White Spruce – Balsam Fir – Quaking Aspen / Mixed Herb Forest; Spruce – Fir – Aspen Forest

NatureServe Ecological Systems Classification:

CES103.021: Boreal White Spruce-Fir-Hardwood Forest

Related Abstracts: alvar, black-backed woodpecker, Blanding's turtle, calypso orchid, dry-mesic northern forest, dry northern forest, dwarf lake iris, eastern massasauga, limestone bedrock glade, merlin, mesic northern forest, pine-drops, poor conifer swamp, ram's head orchid, rich conifer swamp, hardwood-conifer swamp, wooded dune and swale complex

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Photo by Joshua G. Cohen

Boreal forest with numerous windthrow gaps occurring on thin soils over limestone cobbles on Bois Blanc Island.

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