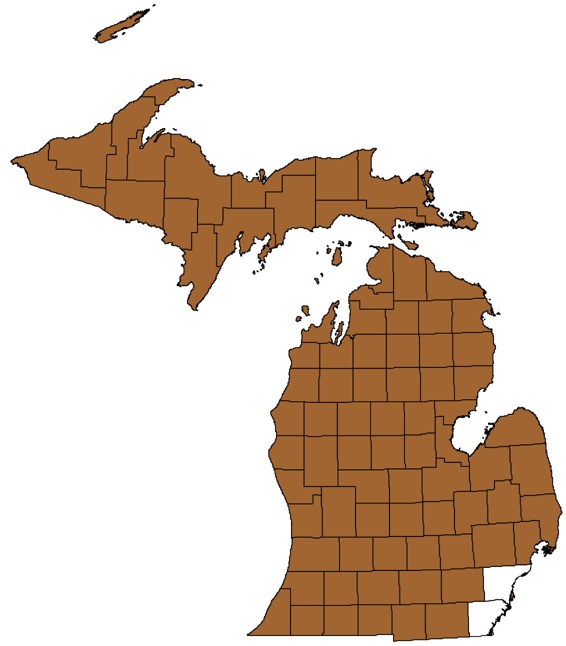
Hardwood-Conifer Swamp Community Abstract

Photo by Joshua G. Cohen

State Distribution



Overview: Hardwood-conifer swamp is a minerotrophic forested wetland dominated by a mixture of lowland hardwoods and conifers, occurring on organic soils and poorly drained mineral soils throughout Michigan. The community occurs on a variety of landforms, often associated with headwater streams and areas of groundwater discharge. Species composition and dominance patterns vary regionally. Windthrow and fluctuating water levels are the primary natural disturbances that structure hardwood-conifer swamp.

Global and State Rank: G4/S3

Range: Forested wetlands dominated by a mixture of hardwoods and conifers occur throughout the upper Great Lakes region, northeastern United States, and adjacent Canadian provinces (Faber-Langendoen 2001, NatureServe 2006). Species composition and dominance patterns vary across this range, which includes Minnesota, Wisconsin, Michigan, Ontario, Ohio, Pennsylvania, New Jersey, New York, Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, Maine, New Brunswick, and Nova Scotia. In Michigan, hardwood-conifer swamp is widespread north of the climatic tension zone, with occurrences in southern Lower Michigan limited to areas within the regionally local ranges of white pine, hemlock, and northern white-cedar (Voss 1972, MNFI Biotics Database 2007).

Rank Justification: The acreage of hardwood-conifer swamp present in Michigan at the time of European settlement is difficult to determine. Analysis of General Land Office (GLO) survey notes in Michigan reveals that lowland forest dominated by a mixture of conifers and hardwoods covered approximately 290,000 acres (115,000 ha) circa 1800. Because the dominant trees in these mixed stands varied, only a fraction of this acreage likely represented hardwood-conifer swamp as it is currently defined (Kost et al. 2007). Hemlock- and white pine-dominated lowland forests, which are considered variants of hardwood-conifer swamp, covered an additional 60,000 ac (24,000 ha) and 5,000 ac (2,200 ha), respectively. The total acreage covered by mixed conifers and hardwood-, hemlock-, and white pine-dominated lowland forests (350,000 ac, or 140,000 ha) is a small fraction of the 5,600,000 ac (2,300,000 ha) covered by the broad category of conifer-dominated lowland forest circa 1800. The majority of conifer-dominated lowland forest was comprised of mixed conifers (3,000,000 ac, or 1,200,000 ha) and northern white-cedar (1,300,000 ac, or 510,000 ha), rather than the white pine, hemlock, and mixed conifer and hardwood stands characteristic of hardwood-conifer swamp. A small portion of acreage comprised of mixed

Michigan Natural Features Inventory
P.O. Box 30444 - Lansing, MI 48909-7944
Phone: 517-373-1552

conifers and northern white-cedar may have represented hardwood-conifer swamp, but most of this acreage likely represented other natural community types (e.g., rich conifer swamp). Historically, hardwood-conifer swamp covered less acreage than rich conifer swamp and other forested peatlands because it is typically confined to ecotones bordering uplands and more extensive wetland systems, or areas around headwater streams where groundwater seepage, rather than over-the-bank flooding, controls vegetative composition and structure.

MIRIS data (MIRIS 1978) indicated approximately 1,800,000 ac (700,000 ha) of lowland coniferous forest and about 2,300,000 ac (900,000 ha) of lowland deciduous forest occurred in Michigan as of the 1970s. The percentage of this acreage representing hardwood-conifer swamp is unknown. The current status of hardwood-conifer swamp is poorly understood because this system has not been systematically surveyed in Michigan. Currently, 30 occurrences of hardwood-conifer swamp are tracked in the MNFI statewide database, totaling over 7,000 ac (2,800 ha) (MNFI, Biotics Database 2007). Only 11 of these occurrences are estimated to be of excellent (A-rank) or good (B-rank) viability.

Following European settlement, hardwood-conifer swamp was significantly impacted by logging activities, including removal of mature seed trees, increased exposure and drying of soil, and slash fires. These disturbances resulted in a significant decline in lowland conifers, including northern white-cedar, white pine, and hemlock, throughout the region (Whitney 1987, Zhang et al. 2000, Leahy and Pregitzer 2003). In one 300,000 ac (120,000 ha) section of the Huron National Forest in northeastern Lower Michigan, for example, lowland conifers have declined to 26% of their former extent (Leahy and Pregitzer 2003). In southern Lower Michigan, where conifers characteristic of hardwood-conifer swamp were local or absent in upland communities, logging and removal of mature seed-producing trees likely eliminated seed sources and contributed to the conversion of hardwood-conifer swamp to southern hardwood swamp (Comer et al. 1995). In addition, because seedlings of conifers and yellow birch regenerate primarily on large-diameter rotting wood, such as well-decomposed logs and stumps, the removal of mature trees resulted in a reduction in suitable niches for seedling establishment (St. Hilaire and Leopold 1995, McGee 2001, Forrester et al. 2005). Following removal of conifers, shading and litterfall by hardwood species may have reduced diversity of ground layer vegetation and the suitability of the seedbed for conifer seedlings (Laidig and Zampanella 1999, Kost 2001a, 2001b). Current logging practices continue to degrade hardwood-conifer swamp throughout its range (MNFI Biotics Database 2007).

In addition to historic and recent logging pressures, acreage of hardwood-conifer swamp has been reduced by conversion of wetlands for agriculture and other human uses. Wetland acreage in Michigan is estimated to have been reduced by greater than 50% since the beginning of European settlement (Dahl 1990). The shallow organic or poorly drained mineral soils supporting hardwood-conifer swamp were easier to convert for agricultural purposes than the deep peats characteristic of rich conifer swamp and other forested peatlands, resulting in a significant reduction of hardwood-conifer swamp acreage following European settlement. Several tracked occurrences of hardwood-conifer swamp show evidence of hydrologic disturbance, including ditching and the conversion of adjacent uplands for agricultural or residential uses (MNFI Biotics Database 2007).

At the present time, excessive deer herbivory threatens the viability of hardwood-conifer swamp throughout its range. High white-tailed deer (*Odocoileus virginianus*) density is leading to considerable browse pressure on conifer seedlings and saplings throughout Michigan and the Great Lakes region (Frelich and Lorimer 1985, Mladenoff and Stearns 1993, Alverson and Waller 1997, Long et al. 1998, Rooney and Waller 1998, Rooney et al. 2002, Krueger and Peterson 2006). Deer browse also reduces frequency and cover of understory shrubs and herbs (Balgooyen and Waller 1995, Augustine and Frelich 1998, Rooney and Waller 2003, Kraft et al. 2004). The result of heavy deer browse is significant alteration of community structure consisting of impacts to all vegetative strata.

Physiographic Context: The Michigan range of hardwood-conifer swamp is statewide, falling within the following regions classified by Albert et al. (1986) and Albert (1995): Region I, Southern Lower Michigan (concentrated in the interlobate regions and near Lake Michigan), Region II, Northern Lower Michigan, Region

III, Eastern Upper Michigan, and Region IV, Western Upper Michigan. This broad area is characterized by a cool snow-forest climate with warm summers. 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). 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 (Albert et al. 1986, Barnes 1991). The impacts of hardwood-conifer swamp on local climate are poorly known, but seasonal temperature fluctuations likely vary less in hardwood-conifer swamp relative to the surrounding landscape due to local moss cover and groundwater input (see Curtis 1959 for discussion). Moderation of climatic extremes is better understood for bog and fen peatlands with high moss cover (Heinselman 1963, McKenzie et al. 2007).

Hardwood-conifer swamp occurs on a variety of landforms, including poorly-drained outwash channels and outwash plains and depressions on medium- to coarse-textured end moraines, ground moraines, and glacial lakeplains (Kost et al. 2007). The community occupies sites influenced by groundwater seepage, usually where the water table is at or near the soil surface. Hardwood-conifer swamp occurs on gently sloping to flat topography along headwater streams or in association with relatively inactive portions of floodplains of low order streams, where it forms back swamps or occurs in meander scars (Tepley et al. 2004). Shallow kettle depressions and the margins of large forested and non-forested peatlands may also support hardwood-conifer swamp, but the community is absent from areas where significant peat accumulation isolates the rooting zone from contact with mineral-rich groundwater. Occurrences of hardwood-conifer swamp are typically narrow (<500 m, or 1,600 ft, wide), occupying outwash channels along streams and following slope contours. Large occurrences (to >250 ac, or 100 ha) are often associated with branched stream channels (MNFI Biotics Database 2007).

Hardwood-conifer swamp is bordered by a variety of natural community types. Adjacent uplands support either fire-prone systems, including oak barrens, oak openings (historically), dry-mesic southern forest, dry southern forest, dry-mesic northern forest, dry northern forest, and oak-pine barrens, or gap-phase systems, such as mesic southern forest and mesic northern forest. A variety of open to forested wetland communities may occur in adjacent lowlands, including southern wet meadow, northern wet meadow, prairie fen, northern fen, poor fen, bog, muskeg, interdunal wetland, southern shrub-carr, northern shrub thicket, southern hardwood swamp, northern hardwood swamp, rich tamarack swamp, and rich conifer swamp.


Photo by Bradford S. Slaughter

Hardwood-conifer swamp is often associated with headwater streams.

Substrate conditions are heterogeneous, and are often highly variable within a single stand. The most common condition is a thin layer of organic soil over a poorly drained mineral substrate. Organic soils are typically saturated, highly decomposed, sapric peat (i.e., muck) and frequently contain pieces of coarse wood throughout their profiles. Areas of deep (>1 m) organic deposits are common, especially in seeps. Substrate pH is also highly variable. Saturated mucks are typically of circumneutral pH, but may be acidic near the surface, especially where associated with sphagnum mosses or where coniferous needle mats accumulate. Mineral soils are often acidic. Vegetation (living and dead), depth to the water table, and groundwater movement all influence substrate alkalinity.

Natural Processes: The primary natural processes structuring hardwood-conifer swamp are small-scale windthrow and dynamics of surface water and groundwater. Patchy windthrow is the dominant natural disturbance, creating small-scale canopy gaps (Forrester et al. 2005). Hardwood-conifer swamp often occurs on structurally weak organic soils where trees root shallowly due to anaerobic conditions and are thus particularly susceptible to windthrow. Accumulation of ice and snow in tree crowns increases the likelihood of windthrow or trunk snap, particularly for trees weakened by pests or fungal pathogens (Christensen et al. 1959). In addition to toppling and snapping trees, wind may also tip trees rooted in unstable organic soils, which produces the pit-and-mound microtopography characteristic of many forested systems (Christensen et al. 1959). Tipping is responsible for the occurrence of northern white-cedars with upward-curving boles.

Photo by Bradford S. Slaughter

Tipping associated with windthrow produces the pit-and-mound topography characteristic of hardwood-conifer swamp.

Those boles in contact with the substrate can produce vertically-growing branches that eventually form a straight line of stems, a process characteristic of cedar-dominated swamps (i.e., rich conifer swamp) called layering (Christensen et al. 1959). Plot data collected by the Minnesota Department of Natural Resources (2003) indicate curved trees are less common on firmer substrates, including mucky mineral soil or shallow peat over mineral soil, substrates that often support hardwood-conifer swamp in Michigan. Nevertheless, small-scale windthrow shapes the structure of hardwood-conifer swamp through the combined effects of tipping and snapping of its canopy trees, and this impact varies based on substrate characteristics and tree species composition.

The creation of canopy gaps and associated microtopographic heterogeneity has important consequences for the establishment and recruitment of canopy trees. Seedlings of several characteristic hardwood-conifer swamp canopy species (e.g., yellow birch, white pine, northern white-cedar, and hemlock) preferentially germinate and establish on root hummocks and/or decaying logs versus muck or litter-covered depressions (i.e., hollows) (Holcombe 1976, St. Hilaire and Leopold 1995, Rooney and Waller 1998, Allison and Ehrenfeld 1999, McGee 2001, Rooney et al. 2002). In comparison to hollows, hummocks and decaying logs have high moss cover, high moisture content, coarse substrate texture, and stable hydrology, characteristics which may favor the germination and establishment of small seeds with low nutrient reserves (Coffman 1978, St. Hilaire and Leopold 1995, McGee 2001). The degree to which hummocks differ from hollows varies depending on moss cover. Ehrenfeld (1995) found that sphagnum-covered hummocks had similar moisture content to hollows, possibly due to strong hydraulic conductivity within surficial sphagnum peat and the living mat itself. Litter-covered hummocks, in contrast, were significantly drier than hollows, and were prone to seasonal drought, leading to dessication and mortality of conifer seedlings. Studies in the Great Lakes region have illustrated a strong association of northern white-cedar and hemlock seedlings with rotting wood versus raised mounds, which may be due to differences in moss cover and the ability of rotting wood to remain moist during periods of drought (Rooney and Waller 1998, Rooney et al. 2002). Hardwood-conifer swamp tends to occur on shallow peats and mucks or poorly drained mineral soils, where conditions are not conducive to the development of a continuous moss layer, unlike the deep peats that support moss cover characteristic of rich conifer swamp (Kost 2002). Relatively low moss cover may be one factor that favors greater representation of large-seeded hardwoods in hardwood-conifer swamp versus moss-covered forested peatlands of northern white-cedar, tamarack, balsam fir, and black spruce.

Although hummocks and decaying logs are important sites for the germination and establishment of tree seedlings, these sites do not necessarily increase long-term tree survival (St. Hilaire and Leopold 1995, Rooney and Waller 1998, Rooney et al. 2002). Recruitment to the subcanopy and canopy is related to stand-scale factors, including the distribution and size of canopy openings, and may require the establishment of mycorrhizal connections by seedlings (Rooney and Waller 1998, McGee 2001, Webster and Lorimer 2005). Canopy composition may exert a strong control on seedling recruitment. Shading and litterfall associated with hardwood-dominated canopies may reduce the suitability of the seedbed for conifer seedlings, and may reduce diversity of ground layer vegetation (Laidig and Zampanella 1999, Kost 2001a, 2001b, Simard et al. 2003). Accumulation of conifer needle litter also appears to negatively impact conifer regeneration (Simard et al. 2003). Ascertaining the relative impact of hardwood litter versus conifer litter on conifer regeneration requires additional study, but the greater surface area of hardwood leaves, in addition to complete annual turnover, suggests hardwood litter may have a more significant negative impact on conifer establishment. Despite the relatively narrow range of conditions suitable for conifer germination and establishment, replacement of wetland conifers by hardwoods may take centuries in the absence of large-scale disturbances (Zampanella et al. 1999).

The creation of canopy gaps and complex microtopography also has important impacts on ground layer diversity. Anderson and Leopold (2002) found that the degree of microtopographic variability and wetness beneath canopy gaps had more significant impacts than light variability on plant species richness. Wetland obligates (i.e., species that occur in wetlands with >99% probability) were concentrated in gaps (defined in their study as visible canopy openings), whereas hummock-dwelling species of broader ecological amplitude (i.e., species not restricted to wetlands) were concentrated in non-gaps. Paratley and Fahey (1986) noted a tendency for ground layer species to favor either mounds or depressions, and found that species richness was positively correlated with microtopographic variability, high base status (i.e., concentration of base cations, including calcium and magnesium), and magnitude of water table drawdown. The development of microsite preferences in ground layer herbs typical of hardwood-conifer swamp can be explained by the variation in substrate moisture and texture between mounds (including decaying wood) and depressions. In sum, the canopy gaps that result from windthrow promote high species diversity by increasing light availability, creating tip-up mounds, coarse woody debris, and hollows that increase microsite heterogeneity. Canopy gaps generate spatial variability in depth to the water table and seasonal periods of inundation, resulting in fine-scale spatial, seasonal, and temporal gradients in soil chemistry (Paratley and Fahey 1986, Anderson and Leopold 2002).

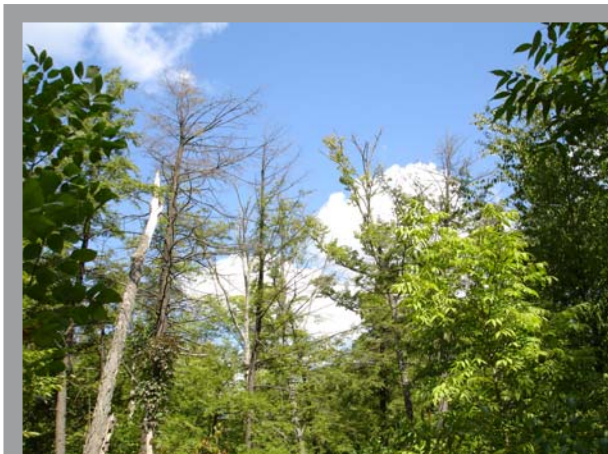


Photo by Bradford S. Slaughter

Windthrow is responsible for the patchy canopy characteristic of hardwood-conifer swamp. Increased light and soil moisture associated with gaps enhances plant species richness and diversity.

Although small-scale windthrow is the dominant natural process shaping hardwood-conifer swamp, stand-replacing windthrow is rare in conifer-dominated lowland forests. Estimates of return intervals range from 365 years in Minnesota to >1000 years in northern Lower Michigan (Whitney 1986, Minnesota Department of Natural Resources 2003).

Groundwater and surface water dynamics also shape hardwood-conifer swamp structure and impact succession. Significant hydrological processes impacting hardwood-conifer swamp include groundwater seepage, water table fluctuation, seasonal inundation, and flooding events. Groundwater seepage typically occurs at hydrologic breaks, such as where outwash channels bisect moraines (Amon et al. 2002). Seepages also occur away from slopes, where groundwater moves upward through breaches in otherwise impermeable deposits underlying the wetland (Amon et al. 2002). Groundwater seepages are often rich in calcium and magnesium carbonates and have high pH values, resulting from movement of groundwater through base-rich glacial deposits. In addition, water levels are more stable in groundwater seeps than in other wetland zones, in part due to the presence of most seeps at the bases of slopes that do not collect surface water (Amon et al. 2002, Bedford and Godwin 2003). Several vascular and non-vascular plant species are concentrated in groundwater seepage zones, including many calciphiles, and add to the diversity of wetland systems (Amon et al. 2002, Bedford and Godwin 2003, Bowles et al. 2005). However, groundwater seepages and associated concentrations of calciphilic species are less characteristic of hardwood-conifer swamp than rich conifer swamp and fen communities (Faber-Langendoen 2001, Kost 2001a, 2001b, 2002, NatureServe 2006, Kost et al. 2007).

Water table fluctuation, including seasonal inundation, is characteristic outside the immediate vicinity of groundwater seepages in hardwood-conifer swamp (Paratley and Fahey 1998, Anderson and Leopold 2002). As noted above, water table fluctuation interacts with canopy gap size, such that mid- and large-sized gaps may flood quickly during rain events, presumably due to the lack of canopy to intercept precipitation and lack of transpiration by large trees (Anderson and Leopold 2002). These wet gaps create microheterogeneity within hardwood-conifer swamp that results in increased diversity of vascular plant species, including many species otherwise characteristic of open wetland types (Anderson and Leopold 2002).

Beaver flooding can also shape hardwood-conifer swamp structure and direct successional pathways. Natural community surveys in Newaygo and Luce Counties found both inactive and active beaver dams and associated flooding in several forested wetlands, including hardwood-conifer swamp (MNFI Biotics Database 2007, Slaughter et al. 2007). The areas that were inundated were typically closest to the stream or lake and lowest in elevation. Stands of dead northern white-cedar and/or tamarack were characteristic of inundated zones. Wetland margins and elevated areas within the wetlands dominated by white pine, hemlock, and hardwoods were less significantly impacted. Following beaver flooding, graminoid-dominated communities develop and sometimes persist for several decades, resisting conifer invasion (Terwilliger and Pastor 1999). In addition, the graminoid-covered substrate favors establishment of red maple, black ash, and alder (Allison and Ehrenfeld 1999), which may drive succession towards hardwood dominance or towards conversion to northern shrub thicket. The impacts of beaver on hardwood-conifer swamp succession require further study, but the primary forested communities affected by beaver dam construction are likely low-lying peatlands immediately adjacent to streams and lakes (e.g., rich conifer swamp and poor conifer swamp).

Photo by Bradford S. Slaughter

Beaver disturb hardwood-conifer swamp through dam-building activities that can flood low-lying tracts and promote shrubs and graminoids.

Changes in drainage patterns due to peat accumulation, growth of vegetation, erosion, or other disturbances can also drive succession and result in site heterogeneity, rather than uniform climax forest, over time (Paratley and Fahey 1986, Futyma and Miller 2001). The effects of watershed-scale hydrologic disturbances on forested wetlands are less well understood, and may be outweighed, at least over short time periods, by finer-scale disturbances affecting local hydrology (Laidig and Zampanella 1999).

Fire is another natural disturbance that shapes hardwood-conifer swamp. In northern Lower Michigan, Cleland et al. (2004) found historic fire rotations of 120 years for wetlands adjacent to fire-prone uplands (generally, oak- and upland conifer-dominated systems), and 684 years for wetlands adjacent to northern hardwoods. Wetlands in both landscapes were dominated by tamarack, hemlock, spruce, and balsam fir, but wetlands occurring in fire-prone landscapes had an increased proportion of fire-dependent species (e.g., pine, white birch, aspen, and oak) and very low proportions of fire-intolerant hardwoods (e.g., sugar maple, beech, elm, and basswood) (Cleland et al. 2004). Acreage of lowland hardwood-conifer cover in northern Lower Michigan at the present time is roughly split between the two fire regimes described by Cleland et al. (2004). Despite the shorter fire return interval for forested wetlands adjacent to fire-prone uplands, broad-scale, stand-replacing fires appear to have been infrequent. For example, Whitney (1986) estimated a return interval of 3,000 years for destructive crown fires in conifer-dominated swamps in north-central Lower Michigan.

In the Great Lakes region, high densities of northern white-cedar and hemlock seedlings have been recorded on burned organic and mineral soils, often following slash fires (Curtis 1959, Rooney and Waller 1998, Rooney et al. 2002). In addition, the wind-borne samaras of red maple make it a successful invader of burned, open substrate (Allison and Ehrenfeld 1999). The relative contribution of fire to hardwood-conifer swamp structure and succession is unknown, but fire appears to provide suitable sites for the establishment of new cohorts of several canopy dominants, and may shape regional variation of structure and vegetative composition by selecting for fire-dependent canopy species and against fire-intolerant northern hardwoods and conifers (Cleland et al. 2004).

Vegetation Description: Hardwood-conifer swamp is a broadly defined natural community type, encompassing several regional, edaphic, and physiographic variants. Several vegetative associations are included within this type and are described below. In general, stands classified to this type contain at least 25% coniferous cover or basal area. Hardwoods range from dominant to uncommon or locally absent. Canopy, subcanopy, and ground layer density vary depending on species composition and local disturbance history. Throughout its range, hardwood-conifer swamp is characterized by high diversity, which can be attributed to its complex microtopography, spatially and temporally variable water table, and patchy canopy (Paratley and Fahey 1986, Vivian-Smith 1997, Anderson and Leopold 2002). The species listed below are derived from hardwood-conifer swamp occurrences tracked by MNFI (Biotics Database 2007), in addition to Curtis (1959), Brewer (1966), Voss (1972, 1985, 1996), Faber-Langendoen (2001), and NatureServe (2006). Although hardwood-conifer swamp occurs with greater frequency north of the climatic tension zone, the vegetation of occurrences south of the climatic tension zone is described first. Examples of hardwood-conifer swamp in southern Lower Michigan exhibit strong similarities in vegetative structure and composition due to the presence of only three characteristic conifers (white pine, northern white-cedar, and tamarack) in this region.

Southern Lower Michigan: In southern Lower Michigan, canopy dominance is often by red maple (*Acer rubrum*) and black ash (*Fraxinus nigra*), occasionally with high importance of yellow birch (*Betula alleghaniensis*) and white pine (*Pinus strobus*). Canopy associates include basswood (*Tilia americana*), northern white-cedar (*Thuja occidentalis*), tamarack (*Larix laricina*), and, locally, hemlock (*Tsuga canadensis*) and tulip-tree (*Liriodendron tulipifera*). Northern white-cedar often occurs in southern Lower Michigan as small patches within larger tamarack- or hardwood-dominated forested wetlands (Thompson 1953, Wenger 1975, Comer et al. 1995, Kost 2001a, Kost 2002, Slaughter and Skean 2003). Stands of significant size and of strong (>75%) northern white-cedar dominance are classified as a southern variant of rich conifer swamp (Kost 2002). Tree species typical of upland forests [e.g., red oak (*Quercus rubra*)] are sometimes present in the canopy, but are more commonly present as seedlings. American elm (*Ulmus americana*) was an important canopy tree prior to the introduction and spread of elm blight, but is now primarily an understory species, where it associates with saplings of the canopy species (Barnes 1976).

The tall shrub layer is characterized by blue-beech (*Carpinus caroliniana*), spicebush (*Lindera benzoin*), juneberries (*Amelanchier* spp.), red-osier dogwood (*Cornus stolonifera*), gray dogwood (*C. foemina*), silky dogwood (*C. amomum*), smooth highbush blueberry (*Vaccinium corymbosum*), poison sumac (*Toxicodendron vernix*), hazelnut (*Corylus americana*), Michigan holly (*Ilex verticillata*), red-berried elder (*Sambucus racemosa*), elderberry (*S. canadensis*), nannyberry (*Viburnum lentago*), wild-raisin (*V. cassinoides*), prickly-ash (*Zanthoxylum americanum*), witch-hazel (*Hamamelis virginiana*), Bebb's willow (*Salix bebbiana*), hoary willow (*S.

candida), pussy willow (*S. discolor*), slender willow (*S. petiolaris*), and autumn willow (*S. serissima*). Canada yew (*Taxus canadensis*) was once an important component of the hardwood-conifer swamp understory, but its populations have been significantly reduced and locally extirpated through deer browsing. Low shrubs include alder-leaved buckthorn (*Rhamnus alnifolia*), Canada fly honeysuckle (*Lonicera canadensis*), wild black currant (*Ribes americanum*), prickly gooseberry (*R. cynosbati*), and swamp gooseberry (*R. hirtellum*).

The ground layer, which is dense in light gaps and sparse under the shade of conifers, is characterized by the development of moss and litter-covered hummocks, interspersed with areas of level, saturated or inundated depressions. Characteristic species of hummocks and decomposing wood include wild sarsaparilla (*Aralia nudicaulis*), lady fern (*Athyrium filix-femina*), long-awned wood grass (*Brachyelytrum erectum*), goldthread (*Coptis trifolia*), crested woodfern (*Dryopteris cristata*), intermediate woodfern (*D. intermedia*), Canada mayflower (*Maianthemum canadense*), partridge berry (*Mitchella repens*), bishop's-cap (*Mitella diphylla*), naked miterwort (*Mitella nuda*), and starflower (*Trientalis borealis*). Typical species of depressions include jack-in-the-pulpit (*Arisaema triphyllum*), side-flowering aster (*Aster lateriflorus*), beggar-ticks (*Bidens* spp.), marsh marigold (*Caltha palustris*), wood reedgrass (*Cinna arundinacea*), small enchanter's-nightshade (*Circaea alpina*), honewort (*Cryptotaenia canadensis*), water horsetail (*Equisetum fluviatile*), common horsetail (*E. hyemale*), woodland horsetail (*E. sylvaticum*), purple avens (*Geum rivale*), fowl manna grass (*Glyceria striata*), spotted touch-me-not (*Impatiens capensis*), northern bugleweed (*Lycopus uniflorus*), sensitive fern (*Onoclea sensibilis*), cinnamon fern (*Osmunda cinnamomea*), royal fern (*O. regalis*), dwarf raspberry (*Rubus pubescens*), golden ragwort (*Senecio aureus*), rough goldenrod (*Solidago rugosa*), and skunk-cabbage (*Symplocarpus foetidus*), the last species a frequent ground layer dominant. Sedges are well-represented in hardwood-conifer swamp, including *Carex bromoides*, *C. crinita*, *C. disperma*, *C. gracillima*, *C. hystericina*, *C. intumescens*, *C. lacustris*, *C. lupulina*, and *C. stricta*. Species richness is generally higher in canopy gaps, where higher water tables support many wetland obligates that are absent or rare in non-gaps (Paratley and Fahey 1986, Anderson and Leopold 2002). Large canopy gaps support species typical of open wetlands and may be grass- or sedge-dominated. Species typical of large canopy gaps include swamp milkweed (*Asclepias incarnata*), bluejoint grass (*Calamagrostis canadensis*), sedges, turtlehead (*Chelone glabra*), swamp thistle (*Cirsium muticum*), joe-pye-weed (*Eupatorium maculatum*), boneset (*E. perfoliatum*), cut grass (*Leersia oryzoides*), white grass (*L. virginica*), arrow-leaved tear-thumb (*Polygonum sagittatum*), mad-dog skullcap (*Scutellaria lateriflora*), common skullcap (*S. galericulata*), common water horehound (*Lycopus americanus*), and broad-leaved cat-tail (*Typha latifolia*). Twining herbs and woody vines are also a common feature of canopy gaps, represented most commonly by hog peanut (*Amphicarpaea bracteata*), groundnut (*Apios americana*), poison-ivy (*Toxicodendron radicans*), Virginia creeper (*Parthenocissus quinquefolia*), and riverbank grape (*Vitis riparia*).

<u>Northern Lower Michigan and Upper Peninsula</u>: In and north of the climatic tension zone, conifers increase in importance relative to hardwoods. Hemlock, which occurs in monodominant stands or in association with yellow birch, red maple, and white pine, locally dominates shallow, poorly-drained depressions and peatland margins (Barrett et al. 1995, Comer et al. 1995, MNFI Biotics Database 2007). These sites are

Rotting, moss-covered wood provides a suitable substrate for conifer seedlings and a variety of ferns and forbs.

often referred to as hemlock or hemlock-hardwood swamps (NatureServe 2006), and are widespread in the northeastern United States and adjacent Canadian provinces. In Michigan, this type is most common in the western Upper Peninsula, where hemlock and yellow birch occur on moderately- to poorly-drained till plain, on outwash, and on lake margins in close association with upland sugar maple-hemlock forests (Frelich et al. 1993, Comer et al. 1995). In addition to hemlock, other common canopy constituents in northern Michigan hardwood-conifer swamps include balsam fir (*Abies balsamea*), black ash, northern white-cedar, tamarack, and black spruce (*Picea mariana*), with the latter two species occurring primarily on the wettest substrates. Paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*) can be common canopy and subcanopy species, especially in stands with recent disturbance history (Braun 1950). In addition, white spruce (*Picea glauca*) is occasionally present as scattered overstory individuals. In general, stands in northern Michigan have greater presence of boreal conifers and hardwoods than stands in southern Lower Michigan, but the majority of species are common to both regions. Continued inventory and research is necessary to identify additional variants.

Photo by Bradford S. Slaughter

Yellow birch (left) and hemlock (right) are characteristic trees, often found in close association.

Common small tree and shrub species in addition to those found in southern Lower Michigan include mountain maple (*Acer spicatum*), striped maple (*A. pensylvanicum*), blueberry (*Vaccinium angustifolium*), swamp red currant (*Ribes triste*), and Labrador-tea (*Ledum groenlandicum*). Smooth highbush blueberry and spicebush are generally absent, except in the tension zone. Tag alder (*Alnus rugosa*) often forms dense colonies at the lowland margin of hardwood-conifer swamps, as along streams, and also occupies canopy gaps within forested wetlands. Small individuals of canopy species are prevalent in the understory. Northern white-cedar and hemlock are characteristic in the understories of sites with low deer densities, including areas characterized by high snowfall, and where large-diameter coarse woody debris provides ample microsites for seedling establishment.

The ground layer includes many of the same species found in southern Lower Michigan. Species occurring with greater frequency in northern Michigan include bluebead lily (*Clintonia borealis*), bunchberry (*Cornus canadensis*), oak fern (*Gymnocarpium dryopteris*), Indian cucumber root (*Medeola virginiana*), gaywings (*Polygala paucifolia*), large-leaved shinleaf (*Pyrola elliptica*), interrupted fern (*Osmunda claytoniana*), creeping snowberry (*Gaultheria hispidula*), twinflower (*Linnaea borealis*), and northern wood-sorrel (*Oxalis acetosella*). Golden saxifrage (*Chrysosplenium americanum*) is locally common on exposed muck. Skunk-cabbage is sporadic north of the tension zone, whereas it frequently dominates the ground layer in southern Lower Michigan (Voss 1972, MNFI Biotics Database 2007).

The bryophyte community of hardwood-conifer swamps is poorly understood. Holcombe (1976) documented 72 species in a northern Michigan rich conifer swamp (cedar swamp), including 50 mosses and 22 liverworts. Mat-forming mosses, including *Heterophyllium haldanianum* and *Pleurozium schreberi*, dominated decomposing logs. Sphagnum mosses are also occasional dominants in rich conifer swamp (Kost 2002). The presence of pronounced hummock-hollow development, in which hollows are often inundated, concentrates moss development in hardwood-conifer swamp to the hummocks, and a continuous moss layer is generally not characteristic of these systems (NatureServe 2006).

Noteworthy Animal Species: Through flooding and herbivory, beaver can cause tree mortality and the conversion of hardwood-conifer swamp to open wetlands such as shallow ponds, emergent marsh, wet meadows, or fens. Insect outbreaks and plant parasites can set back or kill conifers, altering community composition and structure. Pests of potentially significant impact include the hemlock woolly adelgid (*Adelges tsugae*), which has the potential to cause hemlock mortality if it establishes in Michigan, and the emerald ash borer (*Agrilus planipennis*), which has already decimated the ash population in southeastern Michigan (Haack et al. 2002, McCullough and Roberts 2002, MacFarlane and Meyer 2005). Other insects affecting conifers include larch sawfly (*Pristophora erichsonii*) and larch casebearer (*Coleophora laricella*), which can repeatedly defoliate and kill tamarack, and spruce budworm (*Choristoneura fumiferana*), which defoliates black spruce and balsam fir. Because tamarack, black spruce, and balsam fir are rarely dominant trees in hardwood-conifer swamp, impacts of the latter three insects on this natural community type are generally modest.

Conservation and Biodiversity Management: Conservation and management of hardwood-conifer swamp should focus on the following key areas: preservation of the coarse woody debris resource, protection of mature seed-bearing trees, maintenance of canopy gap structure, protection of groundwater and surface water hydrology, reduction of deer browse pressure, and control and monitoring of invasive species, including plants, animals, and pathogens.

Regeneration of hardwood-conifer swamp canopy trees, particularly of conifers, relies on the presence of suitable sites for germination and establishment within the stand. Management should focus on protecting large-diameter decaying logs and hummocks that are favored germination sites for yellow birch, white pine, northern white-cedar, and hemlock (Holcombe 1976, St. Hiliare and Leopold 1995, Rooney and Waller 1998, Allison and Ehrenfeld 1999, McGee 2001, Rooney et al. 2002). Maintaining mature, senescent, and dead canopy trees within hardwood-conifer swamp stands ensures a continuing source of the large-diameter coarse woody debris important for seedling germination and survival. In addition to providing suitable germination sites for tree seedlings, coarse woody debris and snags create microtopographic variability on the forest floor that is associated with high species richness and diversity (Paratley and Fahey 1986, Anderson and Leopold 2002). Removal of coarse woody debris or senesced trees from hardwood-conifer swamps should be avoided to ensure the continued viability of the system.

Protection of mature, seed-bearing trees is necessary for the continued viability of hardwood-conifer swamp occurrences. Historic logging activities significantly reduced the acreage of lowland and upland conifers throughout Michigan, through direct mortality and reduction of regeneration capacity (Whitney 1987, Zhang et al. 2000, Leahy and Pregitzer 2003). Where conifers are absent in the uplands, removal of mature seed-bearing conifers occurring in the wetlands can convert the affected stands to hardwood-dominated systems (e.g., southern hardwood swamp). Mature, seed-bearing conifers in wetlands also serve as potential seed sources for the regeneration of conifers in adjacent upland forests, and wetland systems provide a refuge for hemlock during climatically dry periods (Mladenoff and Stearns 1993). Removal of mature conifers from hardwood-conifer swamps should be carefully managed to ensure the continued presence of seed sources within the wetland.

Expansion of red maple in some stands, often following logging or hydrologic disturbance, limits conifer seedling establishment and recruitment by reducing light availability at the ground level. An increase in deciduous canopy trees leads to an increase in deciduous leaf litter, which creates an unfavorable seed bed for conifers (Mladenoff and Stearns 1993). Harvest in closed-canopy, hardwood-dominated stands that formerly supported hardwood-conifer swamp should focus on creating canopy gaps suitable for colonization and establishment of species intolerant of dense shade, such as yellow birch (Webster and Lorimer 2005). Conifers, preferably from a native, local seed source, can be established in these stands by underplanting of appropriate species in light gaps and protecting them from deer browse.

Protection of groundwater and surface water hydrology is critical to maintaining the integrity of the hardwood-

Rare Plants Associated with Hardwood-Conifer Swamp (E, Endangered; T, Threatened; SC, species of special concern).

Scientific Name	Common Name	State Status
Berula erecta	Cut-leaved water-parsnip	T
Calypso bulbosa	Calypso or Fairy-slipper	T
Carex seorsa	Sedge	T
Cypripedium arietinum	Ram's head lady's-slipper	SC
Dentaria maxima	Large toothwort	T
Hydrastis canadensis	Goldenseal	T
Lonicera involucrata	Black twinberry	T
Mimulus glabratus var. *michiganensis*	Michigan monkey-flower	E
Poa paludigena	Bog bluegrass	T
Trillium undulatum	Painted trillium	E

Rare Animals Associated with Hardwood-Conifer Swamp

Scientific Name	Common Name	State Status
Accipiter cooperii	Cooper's hawk	SC
Accipiter gentilis	Northern goshawk	SC
Alces alces	Moose	SC
Appalachina sayanus	Spike-lip crater	SC
Ardea herodias	Great blue heron	*
Asio otus	Long-eared owl	T
Buteo lineatus	Red-shouldered hawk	T
Canis lupus	Gray wolf	T
Emys blandingii	Blanding's turtle	SC
Glyptemys insculpta	Wood turtle	SC
Gomphus quadricolor	Rapids clubtail	SC
Haliaeetus leucocephalus	Bald eagle	T
Incisalia henrici	Henry's elfin	SC
Pachypolia atricornis	Three-horned moth	SC
Pandion haliaetus	Osprey	T
Planogyra asteriscus	Eastern flat-whorl	SC
Sistrurus catenatus catenatus	Eastern massasauga	SC
Tachopteryx thoreyi	Grey petaltail	SC
Terrapene carolina carolina	Eastern box turtle	SC
Williamsonia fletcheri	Ebony boghaunter	SC

*Protected by the Migratory Bird Treaty Act of 1918 conifer swamp community. Hydrologic disturbances, including road construction and ditching, cause peat subsidence and decomposition and alter water tables by draining water or blocking its flow (Bradof 1992, Hillman 1997, Amon et al. 2002). Logging and hydrologic disturbances associated with logging roads and railroads in the late 19th and early 20th centuries converted many conifer-dominated stands to hardwood stands. Urban development also degrades water quality and disrupts hydrology, but the effects of urbanization may be unpredictable for any given site (Ehrenfeld and Schneider 1993). The degree to which forested wetland vegetation is impacted by hydrologic disturbance may be related to characteristics of the pit-and-mound microtopography (Ehrenfeld and Schneider 1993). Natural hydrologic disturbances, including flooding associated with beaver dams, also profoundly impact hardwood-conifer swamp structure (see Natural Processes). Bradof (1992) notes that drainage projects involving the creation of ditches facilitate beaver colonization of large areas of previously uncolonized wetlands, causing widespread flooding and tree-kill. Several measures can be taken to protect the integrity of hardwood-conifer swamp hydrology. A relatively wide upland buffer zone can be established to prevent surface water run-off and protect groundwater seepage zones. Construction of new ditches should be avoided, as should new road construction and stream maintenance projects (e.g., dredging, straightening, and removal of fallen wood). Tree harvest should take place in winter to avoid significant degradation of organic soils. Trapping and removal of beaver may be necessary in isolated nature preserves where the maintenance of hardwood-conifer swamp is a conservation priority, and where flooding is likely to eliminate species of conservation concern.

High white-tailed deer density has led to significant browse pressure on conifer seedlings and saplings throughout Michigan and the Great Lakes region (Frelich and Lorimer 1985, Mladenoff and Stearns 1993, Alverson and Waller 1997, Long et al. 1998, Rooney and Waller 1998, Rooney et al. 2002, Krueger and Peterson 2006). In addition, deer browse reduces frequency and cover of understory shrubs and herbs, altering structure of all strata and producing a cascade of effects extending to pollinators of affected plant species (Balgooyen and Waller 1995, Augustine and Frelich 1998, Rooney and Waller 2003, Kraft et al. 2004). In forests impacted by high deer densities, microsites, including treefall mounds, may serve as refugia for deer-favored species such as hemlock (Krueger and Peterson 2006). Protection of the coarse woody debris resource is an important component of any strategy to promote conifer regeneration, particularly in landscapes characterized by high deer density. Salvage logging of blowdowns should be avoided, as piles of toppled trees create physical barriers to deer and thus promote conifer recruitment.

Photo by Bradford S. Slaughter

Blowdowns serve as refugia for conifer seedlings and saplings in sites impacted by high deer density.

In addition, hemlock recruitment appears to be facilitated by balsam fir, a relatively unpalatable conifer that grows in dense patches and restricts access by deer (Borgmann et al. 1999). Therefore, maintaining high balsam fir cover in managed forest stands should be considered along with protecting the coarse woody debris resource to promote hemlock regeneration. At the landscape scale, reduction of deer densities will promote recovery of tree seedling, shrub, and herb populations. In areas where reducing the number of deer is not feasible, or in small, isolated stands of high-quality hardwood-conifer swamp, deer exclosures should be considered in order to promote conifer regeneration and recruitment.

Invasive plant species can establish within hardwood-conifer swamps in canopy gaps and in openings along streams. Species of particular concern include reed canary grass (*Phalaris arundinacea*), common reed (*Phragmites australis*), purple loosestrife (*Lythrum salicaria*), autumn-olive (*Elaeagnus umbellata*), and glossy buckthorn (*Rhamnus frangula*), although many other non-native plant species of lesser impact are of frequent occurrence (MNFI Biotics Database 2007). Fragmentation and isolation of hardwood-conifer swamp occurrences by residential, commercial, and industrial development, particularly in southern Lower Michigan, locally threatens this natural community type by restricting dispersal of native species and increasing the propagule pressure of commonly planted non-native trees, shrubs, and herbs. Hydrologic disturbances, including flooding and nutrient loading via surface water run-off, facilitate invasion of otherwise intact systems (Zedler and Kercher 2004). Monitoring and removal of invasive species should focus on those species which threaten to alter community composition and structure (e.g., glossy buckthorn and purple loosetrife). Management activities should avoid soil and hydrologic disturbances that favor spread of invasive plant species.

Other pests of potentially significant impact include the hemlock woolly adelgid (*Adelges tsugae*), which has the potential to cause significant hemlock mortality if it establishes in Michigan, and the emerald ash borer (*Agrilus planipennis*), which has already decimated the ash population in southeastern Michigan (Haack et al. 2002, McCullough and Roberts 2002, MacFarlane and Meyer 2005). Urgent measures must be taken to restrict the access of these species to unaffected swamps.

Research Needs: Hardwood-conifer swamp is a relatively poorly studied wetland type in Michigan and across its range, as the majority of research on lowland forests has been conducted in peatlands (e.g., rich conifer swamp, poor conifer swamp) and hardwood-dominated floodplain forests. A systematic survey for hardwood-conifer swamp in Michigan, including the collection of plot data, is necessary to assess the statewide and ecoregional conservation status of this natural community type, and to determine if any of the above described variants warrant splitting as separate natural community types. Additional inventory for hardwood-conifer swamp in northern Michigan is required, as few occurrences have been documented despite the community's widespread distribution in that region (MNFI Biotics Database 2007). Additional research is necessary to study the edaphic and climatic characteristics and successional pathways associated with hardwood-conifer swamp. The impacts of fire, windthrow, and beaver flooding on hardwood-conifer swamp in Michigan are poorly understood and should be investigated. Deer browse is a significant disturbance, but its impacts on hardwood species, shrubs, and ground layer species typical of hardwood-conifer swamp require further research. The most effective means of limiting the impacts of deer herbivory in this system must also be determined. The potential impacts of emerald ash borer and hemlock woolly adelgid on hardwood-conifer swamp should be studied and modeled. The interaction of natural and anthropogenic disturbances, and their impacts on hardwood-conifer swamp should also be elucidated. For example, the impacts of beaver in anthropogenically disturbed versus undisturbed forested wetlands should be studied to help improve land management and protection strategies. Additional research on conifer regeneration in hardwood-conifer swamp will improve management techniques and conservation strategies for this natural community type.

Similar Communities: *Rich tamarack swamp* is a tamarack-dominated peatland located primarily in the interlobate regions of southern Lower Michigan, where it was the most common forested wetland type circa 1800 (Kost 2001a). *Rich conifer swamp* is a northern white-cedar – dominated peatland, with tamarack, black spruce, and balsam fir as common associates. Lowland hardwoods are of low importance in rich conifer swamp. This system occurs primarily in cool regions of the state where climate limits peat decomposition, although isolated stands of rich conifer swamp, typically associated with tamarack and lowland hardwoods, are documented from southern Lower Michigan (Kost 2002). *Poor conifer swamp* is an oligotrophic forested wetland dominated by black spruce and tamarack on deep sphagnum peats (Cohen 2006). *Southern hardwood swamp* is dominated by hardwood species tolerant of seasonal hydrologic fluctuation (e.g., silver maple and green ash), and typically occurs on shallow muck or seasonally inundated mineral soils south of the climatic tension zone. Conifers are generally absent or of limited occurrence (Kost et al. 2007). *Northern hardwood swamp* is a black ash-dominated community on shallow muck or seasonally inundated mineral soils north of the tension zone (Weber et al. 2007). *Floodplain forest* is a broadly defined community occurring on third order or greater streams; hardwood-conifer swamps sometimes occur within floodplain forests in meander scars no longer subject to over-the-bank flooding (Tepley et al. 2004). Hardwood-conifer swamp can also occur as a zone in *wooded dune and swale complexes*.

Other Classifications:

Michigan Department of Natural Resources (MDNR): Q – Mixed Swamp Conifers; E – Swamp Hardwoods; C – Northern White Cedar; H – Hemlock

The Nature Conservancy U.S. National Vegetation Classification and International Classification of Ecological Communities (Faber-Langendoen 2001, NatureServe 2006):

CODE; ALLIANCE; ASSOCIATION; COMMON NAME

I.A.8.N.g; *Tsuga canadensis* Saturated Forest Alliance; *Tsuga canadensis - Betula alleghaniensis / Ilex verticillata / Sphagnum* spp. Forest; Eastern Hemlock - Yellow Birch / Common Winterberry / Peatmoss species Forest; Hemlock – Hardwood Swamp

I.B.2.N.g; *Fraxinus nigra - Acer rubrum* Saturated Forest Alliance; *Acer rubrum - Fraxinus nigra - (Tsuga canadensis) / Tiarella cordifolia* Forest; Red Maple - Black Ash - (Eastern Hemlock) / Heartleaf Foamflower Forest; Northern Hardwood – Hemlock Seepage Swamp

I.B.2.N.g; *Fraxinus nigra - Acer rubrum* Saturated Forest Alliance; *Acer rubrum - Fraxinus* spp. - *Betula papyrifera / Cornus canadensis* Forest; Red Maple - Ash species - Paper Birch / Canadian Bunchberry Forest; Red Maple – Ash – Birch Swamp Forest

I.B.2.N.g; *Fraxinus nigra - Acer rubrum* Saturated Forest Alliance; *Fraxinus nigra* - Mixed Hardwoods - Conifers */ Cornus sericea / Carex* spp. Forest; Black Ash - Mixed Hardwoods - Conifers / Red-osier Dogwood / Sedge species Forest; Black Ash – Mixed Hardwood Swamp

I.C.3.N.d; *Pinus strobus - (Acer rubrum)* Saturated Forest Alliance; *Pinus strobus - (Acer rubrum) / Osmunda* spp. Forest; Eastern White Pine - (Red Maple) / Royal Fern species Forest; White Pine – Red Maple Swamp

I.C.3.N.d; *Tsuga canadensis - Acer rubrum* Saturated Forest Alliance; *Betula alleghaniensis - Acer rubrum - (Tsuga canadensis, Abies balsamea) / Osmunda cinnamomea* Forest; Yellow Birch - Red Maple - (Eastern Hemlock, Balsam Fir) / Cinnamon Fern Forest; Hardwood – Conifer Seepage Forest

I.C.3.N.d; *Thuja occidentalis - Acer rubrum* Saturated Forest Alliance; *Thuja occidentalis - Fraxinus nigra* Forest; Northern White-cedar - Black Ash Forest; White-cedar – Black Ash Swamp

Michigan Resource Information Systems (MIRIS): 423 (conifer swamp): 4237 (hemlock, yellow birch), 4238 (hemlock), 4239 (white pine); 432 (lowland hardwoods & conifer): 4322 (white pine, tamarack, red maple, yellow birch, black ash, cedar, [&/or hemlock]), 4322 (hemlock, yellow birch)

Other states and Canadian provinces (natural community types with significant overlap with Michigan hardwood-conifer swamp indicated in *italics*):

MN: Northern wet cedar forest; Northern wet ash swamp; Northern very wet ash swamp (Minnesota Department of Natural Resources 2003)

WI: *White pine – red maple swamp* (Epstein et al. 2002)

ON: *White pine – hemlock mineral coniferous swamp ecosite*; White cedar mineral coniferous swamp ecosite; White cedar mineral mixed swamp ecosite; Maple mineral mixed swamp ecosite; Birch – poplar mineral mixed swamp ecosite; White cedar organic mixed swamp ecosite; Maple organic mixed swamp ecosite; Birch – poplar organic mixed swamp ecosite; *Fresh – moist hemlock coniferous forest ecosite*; *Fresh – moist hemlock mixed* *forest ecosite*; *Fresh – moist white cedar coniferous forest ecosite*; *Fresh – moist white cedar – hardwood mixed forest ecosite*; Fresh – moist poplar – white birch mixed forest ecosite (Lee et al. 1998)

OH: *Hemlock – hardwood swamp* (Schneider and Cochrane 1998)

PA: *Hemlock palustrine forest*; *Hemlock – mixed hardwood palustrine forest*; Red maple – highbush blueberry palustrine woodland; Red maple – sedge palustrine woodland; red maple – mixed shrub palustrine woodland (Fike 1999)

NY: *Hemlock – hardwood swamp*; *Rich hemlock – hardwood peat swamp* (Edinger et al. 2002)

MA: *Hemlock – hardwood swamp*; Red maple swamp; Black ash swamp (Swain and Kearsley 2001)

VT: *Red maple – white pine – huckleberry swamp*; Spruce – fir – tamarack swamp; *Hemlock swamp*; *Hemlock – hardwood swamp*; Red maple – black ash swamp; Red maple – northern white cedar swamp; (Thompson and Sorenson 2000)

NH: *Northern hardwood – black ash – conifer swamp*; *Northern white cedar – hemlock swamp*; *Hemlock – cinnamon fern forest* (Sperduto and Nichols 2004)

ME: *Hemlock – hardwood pocket swamp*; Hardwood seepage forest; Red maple – sensitive fern swamp (Gawler and Cutko 2004)

Related Abstracts: rich conifer swamp, rich tamarack swamp, poor conifer swamp, northern hardwood swamp, floodplain forest, wooded dune and swale complex, Cooper's hawk, northern goshawk, spike-lip crater, red-shouldered hawk, Blanding's turtle, wood turtle, rapids clubtail, eastern massasauga, osprey, eastern box turtle, great blue heron rookery, goldenseal, Michigan monkey-flower, painted trillium, large toothwort, calypso, ram's head lady's-slipper.

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Photo by Bradford S. Slaughter

White pine and red maple dominate a hardwood-conifer swamp in Newaygo County.

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