

Exploring the Relationship Between Soil Development and Associated Biota: A Comparison of Two Forested Terrestrial Ecosystems in Michigan

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Figure 1 Manistee National Forest. October 2, 2021.

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Abstract

Two forested ecosystems in the Manistee National Forest in northwestern Lower Michigan, Jack Pine (JP) and Northern Hardwood (NH), were examined to gain insight into their composition and function. Field data was recorded at each site, and samples comprised of organic matter and mineral soil were analyzed in a laboratory setting to reveal differences in their physical, chemical, and biological properties. The two ecosystems are located about 20 miles from each other and are similar in parent material and age. However, each site has its own distinct topography, microclimate, and natural disturbance regime, which has influenced soil development and resulted in regional variation in soil properties. Differences in soil texture, moisture, and nutrient deposition influence the plant and microbial communities, and their presence impacts the nutrient status of the soil and provides stability to the ecosystem. Field sample analysis confirmed that both soils have a loamy sand texture, with NH and JP containing 85% and 83.3% sand, respectively. Bulk density (D_b) values were inconsistent. NH soil had a measured D_b of .95 (g/cm^3) and an available water content (AWC) of 26.2%. JP soils had high D_b and AWC values (1.33 g/cm^3 , 54%) which are likely the result of human error. The JP ecosystem was significantly more acidic (pH 3.7) than NH (pH 4.5) when soil acidity was measured in a laboratory setting using .01M CaCl_2 . Consequently, JP soils had approximately five times the exchangeable acidity (1.23 cmol/kg) compared with NH soils (.22 cmol/kg). It was determined that NH soils have a cation exchange capacity (CEC) more than three times the size of JP (6.76 $\text{cmol}(+) \text{kg}^{-1}$, 2.11 $\text{cmol}(+) \text{kg}^{-1}$). Most of the NH CEC is occupied with base cations (97% base saturation), while the JP soil contained a greater abundance of H^+ ions and had a base saturation of 41%. The unique physical properties of each soil and the climatic conditions at each site have impacted the abundance and species composition of above and below-ground biota, and significant differences between the two sites were observed. NH soils contained nearly three times the soil organic matter (SOM) as did JP (92.88 $\text{g C}/\text{m}^2$, 31.76 $\text{g C}/\text{m}^2$), exhibited twice the microbial respiration rate (16.36 $\mu\text{g}/\text{g}/\text{d}$, 8.01 $\mu\text{g}/\text{g}/\text{d}$), and mineralized more N. Bacteria in NH soil are responsible for the small amount of observed nitrification (.06 $\mu\text{g N}/\text{g}/\text{d}$), while the acidic JP soil was incapable of supporting this community. Additionally, overstory biomass was significantly higher in the NH ecosystem (372.39 Mg/ha) compared with JP (74.43 Mg/ha), while biomass on the forest floor was relatively equal (7.33 and 7.24 Mg/ha). JP soil had more total biomass (53.77 Mg/ha) compared with NH (32.52 Mg/ha). All three NH nutrient pools contained significantly more N than JP. Comparative analysis of the field sample data from these two ecosystems reveals that several factors have impacted soil development and the resulting ecological communities that are present at each site.

Introduction

The trajectory of soil development is influenced by soil texture, topography, climate, and natural disturbance. Pedogenic processes determine the abundance and distribution of soil organisms and above-ground biota in forests, and the impact of these species largely dictates ecosystem function. Soil bacteria are immobile and irregularly distributed, and it has been estimated that several billion to over one trillion bacterial species occupy each gram of soil (Brady & Weil, 2002). Fungal diversity in soil has been conservatively estimated at 1.5M total species globally, and several studies have suggested that that figure should be adjusted upwards (Hawksworth, 2001). These incredibly diverse habitats foster relationships that comprise the soil food web and are responsible for the carbon storage capability of soils. Nearly all the net primary production in forested ecosystems accumulates in soil organic matter (SOM) and often remains below ground for long periods of time. These organic compounds are synthesized by the soil microbial community to produce products which are either utilized by plants, leached out of the system, or returned to the atmosphere. Photosynthesis by autotrophs and the decomposition of organic residues by soil organisms are the two major life-generating processes in ecosystems, and serve to maintain their function (Wall et al., 2005).

Soils are dynamic systems that contain air, minerals, water, and life. The soil texture, moisture content, and accumulated organic matter all influence its physical and chemical properties and aeration (Brady & Weil, 2002). Pedogenesis begins with deposition and evolves slowly through time. At its initial state, a soil consists of deposited minerals originating from a parent material and a topography related to the method of deposition. Over time, the influx factors of climate and natural disturbance alter the chemistry and hydrology of the ecosystem, and the product is a site containing a unique soil profile and assemblage of species (Jenny, 1980). Topographic complexity also influences the distribution of plant communities by creating heterogenous nutrient resource availability and microclimates with different levels of solar radiation penetration and hydrologic processes (Rubino and McCarthy, 2003).

Because of these complexities in soil development, soils that are similar in parent material and age but experience different climatic conditions and cycles of natural disturbance can be compared analytically to understand the effects of various environmental factors on soil genesis. Soil texture influences nutrient availability and storage, and texture varies via processes of weathering over time, so similar sites with their own microclimates will contain soils with differing characteristics (Jenny, 1980; Silver et al., 2000).

Soils acidify naturally over time as negatively charged organic compounds accumulate from the incorporation and synthesis of plant, animal, and microbial residues, and acidic rainwater containing carbonic acid enters the system from above. As plant roots extract nutrients from the soil solution they donate hydrogen ions to preserve electroneutrality, and this further contributes to acidification (Nilsson et al., 1982). As soils acidify, exchangeable base cations (Ca^{2+} , Mg^{2+} , K^+ , and Na^+) are released from the CEC into the soil solution. Soils containing calcium carbonate (CaCO_3) are initially capable of buffering against acidification at a pH of 7 by reacting with acids to form CO_2 and H_2O , while depositing positively charged Ca^{2+} ions on the CEC. Soils that do not contain CaCO_3 are buffered by base cations at a pH of 4-5, and when those are depleted, the soil further acidifies (Ulrich & Sumner, 1991). When soils are in this state the pH is low enough to solubilize aluminum ions. The system then equilibrates to an alternate stable state in which H^+ and Al^{3+} ions dominate the CEC binding sites and act as a buffer to keep pH low (Bowman et al., 2008).

Soil biota cycle nutrients and stabilize the system. Autotrophs provide organic compounds to soil organisms via root exudates and are gifted mineralized N from the decay of organic matter. Various plant species influence soil microbial composition by releasing their own nutrient cocktails into the soil, and soil microbial communities indirectly regulate above ground plant community composition through the supply of N (Wardle et al., 2011). The reciprocal relationship between autotrophic flora and the chemoautotrophic bacteria and other organisms that live belowground underscores the importance of

SOM to terrestrial productivity. SOM is a globally important resource that retains more water, nutrients, and C than plants and the atmosphere combined. It is influenced by biotic factors such as the chemical composition of plant inputs and the richness and distribution of organisms that constitute the soil food web. Abiotic factors such as climate, topography, landscape orientation, and natural disturbance are also present (Jackson et al., 2017). SOM accumulation through pedogenesis is therefore dependent on a variety of interconnected factors such as age and development status of the soil, the parent material, and the location of the site within the larger ecosystem context.

The interrelationship between the physical, chemical, and biotic components of soil accounts for the vast diversity of soil types worldwide and the complex ecosystems that they support. In this study, soil samples were collected from sites that were similar in geography but differed in local climate and topography. These site-specific conditions caused them to develop differently, and they contain unique plant and microbial communities as a result. Analysis of the data provides insight into the processes that influence the development of soils and underpin the ecosystems that define our world.

Methods

Site Description

Two forested ecosystems in northern Michigan were sampled for this comparison study on October 2, 2021. The NH samples were retrieved from an east-facing site on the lower slope of an end moraine with a 25% gradient near Wellston, MI. This coarse-textured, ice-contact material is glacial outwash that was reincorporated into another glacier and deposited as a moraine during the most recent glaciation of the region (Figure 2). The overstory vegetation contained *Acer saccharum*, *Fagus grandifolia*, *Tilia americana*, *Quercus rubra*, and *Prunus serotina* trees. Understory vegetation was sparse and includes *Lonicera maackii* and *Sassafras albidum*.

The second site sampled, the JP ecosystem, is located 25 miles west of the NH site. This site is part of a coarse-textured outwash plain with no slope or notable aspect. *Quercus palustris* and *Pinus resinosa* trees were present in the canopy, and the understory consisted of *Vaccinium angustifolium*, *Pinus resinosa*, *Quercus palustris*, *Prunus serotina*, *Comptonia peregrina*, and *Prunus virginiana*.

Because these remote locations share a zip code (49689), mean annual temperature and rainfall data is not available for each site. The annual high and low temperatures of this zip code are 56°F and 34°F, respectively, and the annual rainfall total is 35.58 inches (Weather Averages Wellston, Michigan). However, data collected at these two sites indicates they experience differing climatic conditions, which has resulted in ecological heterogeneity of the landscape.

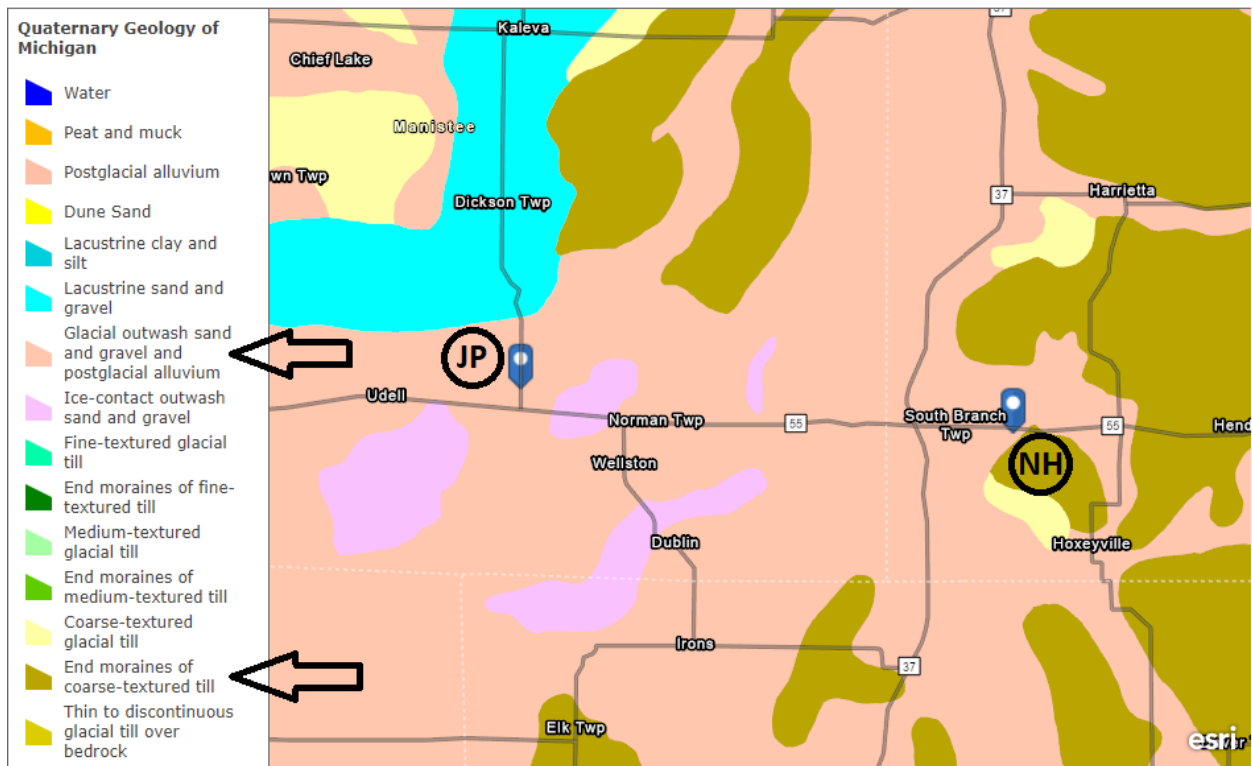


Figure 2. The overlay of feature layer "Quaternary Geology of Michigan" in ArcGIS confirms that the NH site is situated on an end moraine of coarse-textured till, while the JP ecosystem developed on glacial outwash sand and postglacial alluvium.

Field Data Collection

Site selection was determined with guidance from instructors with emphasis on avoiding locations with visible anthropogenic disturbance to the plant community and soil. Each 15m x 30m (0.045 ha) plot was measured with transect tape and its boundaries were marked with flags. The physiography of each site was observed and recorded. Two bulk density (D_b) soil cores were extracted from the surface mineral horizon using the 2-inch soil core tool and a hammer, and were transferred to a plastic whirl back bag. Additional 1-inch soil cores were taken from the same mineral horizon (0-10cm) until a cloth bag was filled to 75% capacity. Two forest floor samples were collected from each plot using a 2809 cm² PVC sampling frame and placed in a paper bag. These contained 100% of the contents of the O_i , O_e , and O_a horizons, and were oven dried to prepare them for laboratory analysis. Soil excavation was accomplished using shovels and hand tools, and one side of each pit was sheared carefully to preserve its horizontal distribution of horizons. This area was wetted with water and colored pins were pressed into the exposed soil profile to indicate horizon boundaries. Samples from each horizon were then analyzed for texture, structure, and pH in the field. Overstory and understory vegetation was also recorded at each site. The diameter at breast height (DBH) of each tree over 10cm was noted, as was species richness of the understory.

Laboratory Analysis of Soil Physical Properties

Soil texture, AWC, and D_b were measured in a laboratory setting. A soil textural analysis was performed by utilizing a hydrometer to measure the rate that particles separated out of an aqueous solution. Each sample was wetted with water in a 250ml Erlenmeyer flask, 100ml of sodium hexametaphosphate was added, and the flask was placed on an orbital shaker for five minutes. This slurry was then homogenized in a blender, transferred to a glass sedimentation cylinder, and filled to 1L with tap water. Each sample was resuspended with a plunger and measured after 40 seconds with a

hydrometer. The solution was then allowed to sit for two hours prior to a second hydrometer reading. Clay particles remained in colloidal suspension indefinitely, while sand and silt particles accumulated at the bottom of the cylinder. Particle size was calculated using Stoke's law, which states that the rate at which a particle falls through a liquid is proportional to the square of its radius. Particles with size greater than 2mm were excluded from this analysis, as they comprise the coarse fraction of soil.

To calculate AWC, two saturated samples of soil from each site were placed within rubber rings on ceramic pressure plates. One sample from each site was then loaded into two pressure chambers for 24 hours to equilibrate to field capacity (.01MPa) and permanent wilting point (1.5MPa). AWC was calculated by subtracting the water content at permanent wilting point from the water content at field capacity. To calculate D_b , subsamples of the soil samples were weighed out, dried overnight in an oven, and an oven-dry/air-dry ratio was calculated for each. D_b was expressed as the oven-dry weight of each sample divided by its volume.

Laboratory Analysis of Soil Chemical Properties

Soil samples were analyzed to observe their pH, exchangeable acidity, exchangeable base cations, CEC size, and base saturation percentage. Soil pH was measured twice by inserting a glass electrode into samples that were saturated in deionized water and separately in a CaCl_2 solution. The pH measurements in deionized water recorded the active acidity in the soil solution, which does not account for the cations bound to the exchange complex. The pH of the samples saturated with the CaCl_2 solution accounted for active acidity as well as exchangeable acidity and is a more accurate representation of what a plant would experience in the soil. SOM was determined via combustion with a LECO TruMac CN analyzer. Samples were heated in this device and the resulting CO_2 was measured using gas chromatography. Because organic matter is approximately 50% carbon, the results from the LECO analysis were multiplied by 2 to obtain the total SOM.

Exchangeable acidity was determined by utilizing the principle of mass action. Soil samples were saturated with 1M KCl and placed on an orbital shaker for 30 minutes so that the base cations were displaced from the CEC and into the soil solution. This was filtered through a Buchner funnel with a Whatman 42 filter and into a side arm flask using the vacuum apparatus attached to the lab bench. Four or five drops of phenolphthalein were added to each sample and titrated with .04M NaOH until a “blushing pink” endpoint was achieved. The amount of NaOH added corresponded with the exchangeable acidity in the soil solution. To correct for the acidity of the KCl, a second titration was performed on 100ml KCl with .04M NaOH, which was used to adjust the data from the first titration.

The relative amounts of base cations in each soil sample were calculated by using a similar procedure. Soil samples were inoculated with 1M NH_4Cl and placed on an orbital shaker for 30 minutes to remove the base cations from the CEC and replace them with NH_4^+ . The same laboratory bench vacuum apparatus was used to filter the sample, and the procedure was repeated once to bring the total volume of the solution to 100ml. Finally, 10ml aliquots of each sample were analyzed using an Inductively Coupled Plasma-Optical Emission Spectrometer (ICP-OES) to measure the abundance of the exchangeable cations the soil samples. The CEC was calculated as the sum of the exchangeable base cations in ($\text{cmol}(+) \text{ kg}^{-1}$). Base Saturation percentage is understood as the percentage of the CEC that contains base cations.

Laboratory Analysis of Soil Biological Properties

The biological properties of the two soil samples that were calculated were microbial biomass and the rates of net N mineralization, nitrification, and microbial respiration. To determine microbial biomass, soil samples were wetted with water and labeled “Control” and “F”. The samples labeled F were fumigated for 20 hours, and then inoculated with 1g of fresh soil of the same sample. These samples were then incubated for 14 days in sealed containers. The resulting CO_2 concentration was a

byproduct of the microbial respiration of the fumigated microbial community and was measured using gas chromatography in units of ($\mu\text{g CO}_2\text{-C mL}^{-1}$). Microbial biomass was calculated by subtracting the CO_2 of the fumigated sample from the atmospheric CO_2 of the control sample and dividing that by a correction factor (K_c) of 0.45.

The accumulated inorganic N present in each sample was determined by extracting the soil from the "Control" samples using a 2:1 ratio of 2M KCl. Samples were transferred to 125ml Erlenmeyer flasks, inoculated with 60ml of 2M KCl, and placed on an orbital shaker for 20 minutes to dissolve the inorganic N in the solution. A small aliquot of each sample was decanted through a filter and into a vial, which was analyzed using a Rapid Flow Analyzer to determine NH_4^+ and NO_3^- concentrations. Unincubated samples of soil from each ecosystem were extracted using the same method to account for the existing N pool in the soil prior to fumigation. The incubated concentrations were subtracted from the initial concentrations and divided by the number of days they were incubated to obtain the net N mineralization of each sample. Net nitrification was determined using a similar equation not including ammonium. The incubated nitrate level was subtracted from the initial nitrate level and divided by the number of incubation days.

Finally, biomass and N pools of each site were calculated for the overstory, forest floor, and the top 10cm of soil. Overstory biomass of stem wood, branch wood, and leaves (Mg ha^{-1}) was estimated using recorded DBH measurements and biomass equations. Biomass of forest floor samples was weighed, and belowground biomass was calculated with another equation using previously calculated organic matter content and D_b values. Aboveground, belowground, and forest floor N content was determined by multiplying the previously calculated biomass by the known percentage of N present in each of these three areas of the plot.

Results

Field Data Results

The mineral fraction of NH soil originated as outwash from a prior glaciation that was reincorporated by a second ice sheet and deposited as an end moraine. It consists of well drained, coarse textured ice contact material. The site observed was on a lower east-facing (25%) slope characterized by end moraine topography. The hilly forest facilitated many smaller microclimates that had varying sunlight and moisture. The soil profile contained Oi/e, A, E, Bhs, Bs, and C horizons and had loamy sand texture until the C horizon, which was sand. The soil was mildly acidic (pH 5.5) in the A horizon and became more acidic in the E horizon (pH 4.5) before adjusting back to mildly acidic in the Bs horizon (pH 6). For detailed information on soil texture and structure, refer to Appendix 1.

The NH overstory contained *Acer saccharum*, *Fagus grandifolia*, *Tilia americana*, *Quercus rubra*, and *Prunus serotina*. Trees present in the understory included *Fraxinus americana*, *Acer saccharum*, *Fagus grandifolia*, and *Sassafras albidum*. *Lonicera maackii* was also present within the boundaries of the site. *Carex pensylvanica* and *Solidago caesia* dominated the ground layer. This site contained many red maples, as indicated by their relative dominance of 61.5%. Red oak and American basswood were present in smaller quantities and there was one small American beech growing in the understory.

Table 1. Basal Area, Relative Dominance, and Total Stand Basal Area of NH overstory species.

Northern Hardwood Overstory Species	Basal Area (total BA/.045) m²	Relative Dominance (%)	Total Stand Basal Area (m²)
<i>Acer saccharum</i>	11.05	61.5	17.95
<i>Fagus grandifolia</i>	0.02	0.128	
<i>Tilia americana</i>	2.78	15.14	
<i>Quercus rubra</i>	4.1	22.85	
<i>Prunus serotina</i>	0.062	0.35	

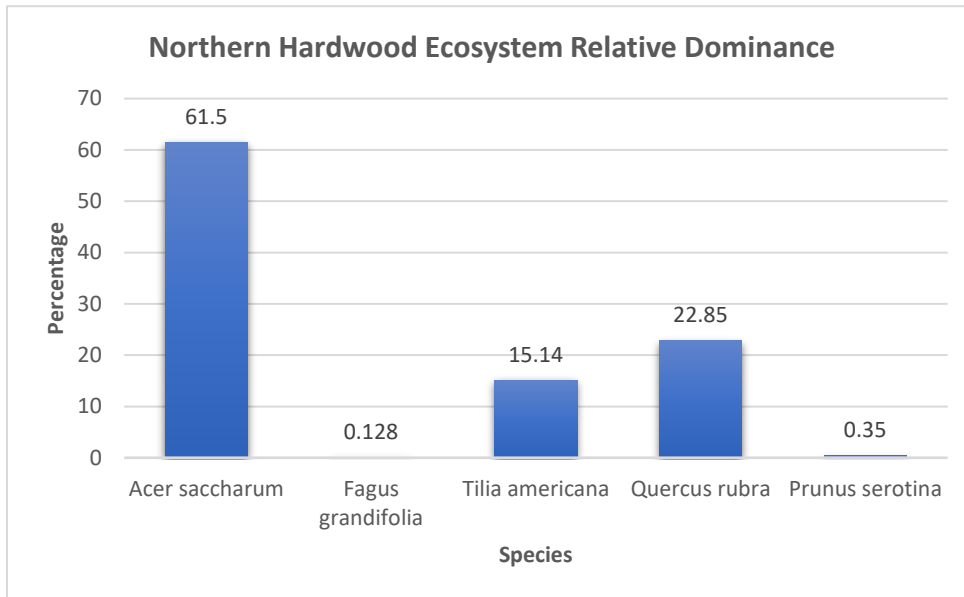


Figure 3. Relative Dominance in the Northern Hardwood ecosystem.

The soils that comprise the JP ecosystem were water-deposited as a sandy glacial outwash plain. The site studied had no slope (0%) or notable aspect. The well-drained soil that has developed on this coarse textured outwash contained Oi/e, A, Bs1, Bs2, and C horizons. The lowest acidity was recorded in the A horizon (pH 4.5), which increased with depth to a pH of 6.5 in the C horizon. Refer to Appendix 2 for a complete account of the soil profile.

Overstory species recorded in the JP ecosystem include *Quercus palustris* and *Pinus resinosa*, with *Vaccinium angustifolium*, *Pinus resinosa*, *Quercus palustris*, *Prunus serotina*, *Comptonia peregrina*, and *Prunus virginiana* present in the understory and ground layer. Red pine was the most common species in the overstory with relative dominance of 71.6%. It was surprising to observe an overstory with so many red pines at this site. An analysis performed in ArcGIS (Figure 5) provided insight into the historical community types present in this area and indicates that the site sampled was historically a Jack Pine-Red Pine Forest, and that it is located within a matrix that was primarily Red Pine-White Pine Forest. This differs from the NH site studied, which was historically located deep within a Beech-Sugar

Maple-Hemlock Forest (Figure 6). The NH ecosystem is reliant on mesic conditions compared to the drier JP ecosystem and has developed in a landscape with higher topographic complexity.

Jack Pine Overstory Species	Basal Area (total BA/.045) m ²	Relative Dominance (%)	Total Stand Basal Area (m ²)
<i>Quercus palustris</i>	2.19	28.4	7.71
<i>Pinus resinosa</i>	5.52	71.6	

Table 2. Basal Area, Relative Dominance, and Total Stand Basal Area of JP overstory species.

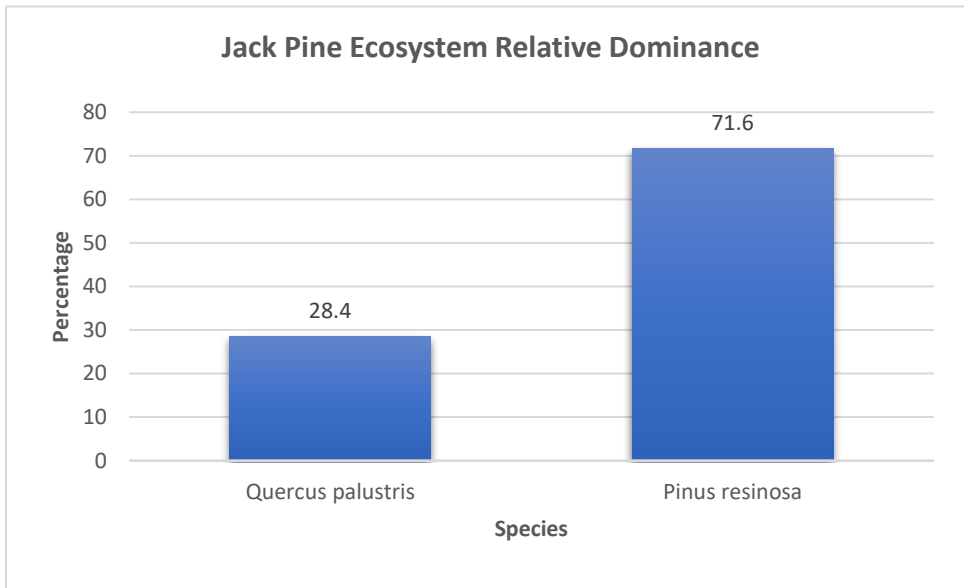


Figure 4. Relative Dominance in the Jack Pine ecosystem.



Figure 5. The overlay of feature layer "Vegetation of Michigan circa 1800s" in ArcGIS reveals that the JP site existed as a peninsula of Jack Pine extending into a Red Pine- White Pine Forest prior to European colonization.

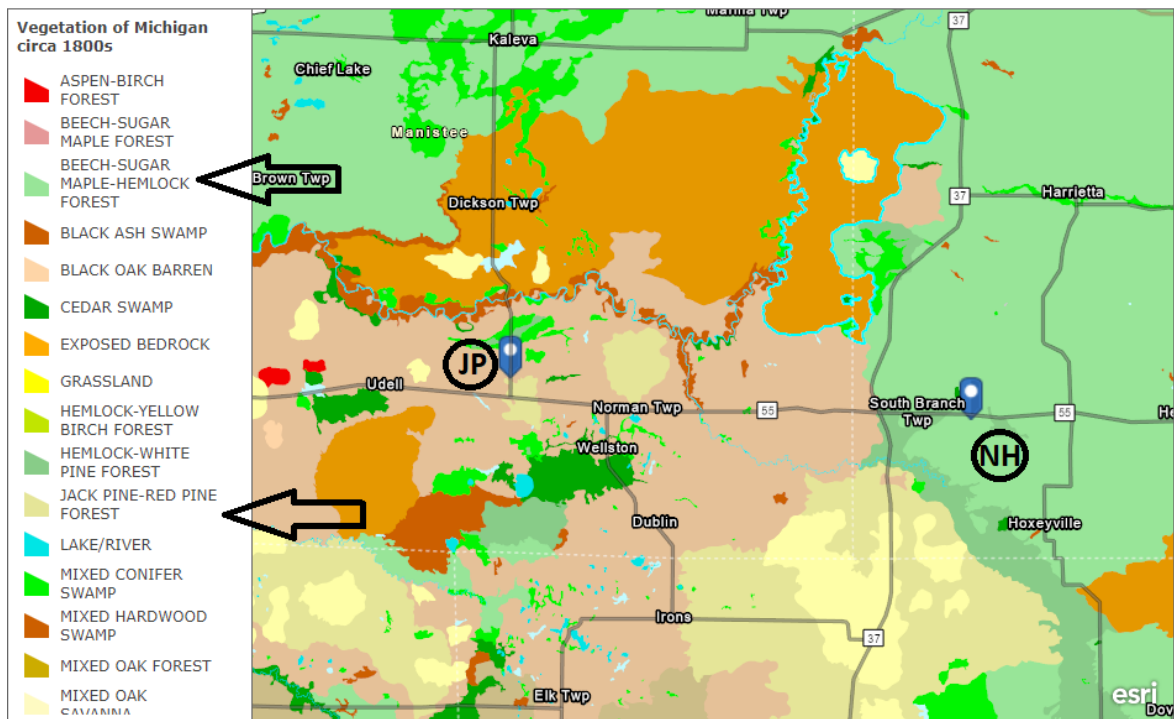


Figure 6. The overlay of feature layer "Vegetation of Michigan circa 1800s" in ArcGIS reveals that the NH site existed historically within a Beech-Sugar Maple-Hemlock Forest prior to European colonization.

Soil Physical Properties

Laboratory analysis determined that both soils are comprised of loamy sand with a similar ratio of sand, silt, and clay (Figure 7). AWC of the NH soil was calculated to be 26 (cm³ H₂O/ cm³ soil) with a D_b of .95 (g/cm³). The AWC and D_b of the JP ecosystem are incorrect due to sampling error in the field. It is believed that a larger volume of soil was collected at this site than the standardized volume that was necessary to perform this analysis. Thus, JP D_b (1.33 g/cm³) and AWC (54%) data values are high and should not be trusted.

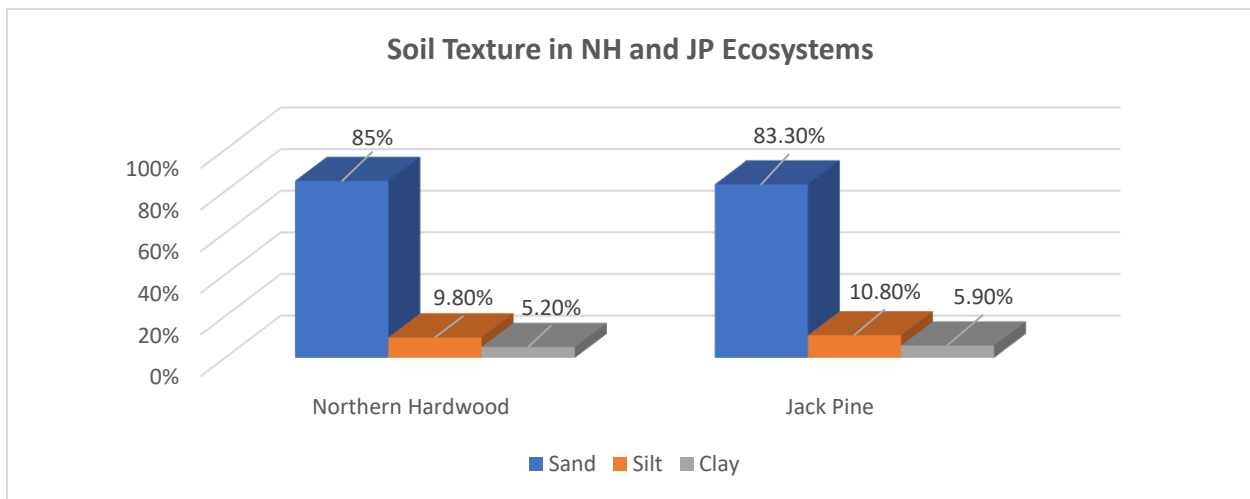


Figure 7. Analysis of NH and JP ecosystem samples indicates that they are similar in composition. Both have relatively equal amounts of sand, silt, and clay, and are understood to have a loamy sand texture.

Table 3. Available Water Content and Bulk Density of NH and JP soils.

	Northern Hardwood	Jack Pine
Available Water Content (AWC) (cm ³ H ₂ O/ cm ³ soil)	26%	54%
Bulk Density (D _b) (g/cm ³)	.95	1.33

Soil Chemical Properties

Field-tested samples of the JP A horizon were more acidic (pH 4.5) than the same test performed at the NH site (pH 5.5). When active acidity was measured with deionized water the JP system was slightly more acidic than NH (pH 4.9, pH 5.3). However, when active and exchangeable acidity were measured together by inoculating samples with CaCl₂, the JP system was significantly more acidic (pH 3.7) than NH (4.5). NH soil contained a CEC over three times the size of JP and was 97% saturated with exchangeable bases. JP soil had just 41% base saturation. Because there were more available locations on the CEC for H⁺ ions to bind in the JP sample, it had a greater exchangeable acidity compared with NH.

Table 4. Field and Laboratory pH measurements for NH and JP ecosystems.

pH	Northern Hardwood	Jack Pine
Field pH	5.5	4.5
Water pH	5.3	4.9
CaCl ₂ pH	4.5	3.7

Table 5. Cation Exchange Capacity, Base Saturation Percentage, and Exchangeable Acidity of NH and JP ecosystems.

	Northern Hardwood	Jack Pine
CEC (cmol(+)kg ⁻¹)	6.76	2.11
Base Saturation (%)	0.968	0.414
Exchangeable Acidity (cmol/kg)	0.22	1.24

Soil Biological Properties

SOM was lower in NH (3.42%) than JP (4.04%), but the NH soil contained almost three times the biomass (92.88 g C/m²) than JP (31.76 g C/m²). The microbial respiration rate was twice as high in NH than in JP. N mineralization and nitrification occurred in NH soil, while the JP soil exhibited a small amount of N mineralization and no nitrification. This is likely due to the acidic conditions of the site.

Most of the biomass in the NH ecosystem is stored in the overstory, while the JP ecosystem had nearly as much belowground biomass as it did above. Both ecosystems had a small amount of biomass located on the forest floor. NH contained over three times the total biomass (412.24 Mg C/ha) compared with JP (136.44 Mg C/ha).

The pool of nitrogen in the overstory of NH (946.65 kg N/ha) was significantly higher than in the JP ecosystem (126.17 kg N/ha). Belowground N content was nearly two times as high in NH as it was in JP and forest floor N content was relatively similar. There is significantly more N in the NH ecosystem (3221.809 kg N/ha) than the JP (1510.47 kg N/ha). It is apparent that the NH ecosystem stores most of its N in the standing biomass of its flora and the JP ecosystem is more reliant on belowground N.

Table 6. Soil Organic Matter Percentage, Microbial Biomass, Microbial Respiration Rate, Net N Mineralization, and Net N Nitrification for NH and JP ecosystems.

	Northern Hardwood	Jack Pine
Soil Organic Matter (%OM)	3.4234	4.0432
Microbial Biomass (g C/m ²)	92.88	31.76
Microbial Respiration Rate (µg/g/d)	16.36	8.01
Net N mineralization (µg N/m ² /d)	0.36	0.19
Net N nitrification (µg N/m ² /d)	0.06	0

Table 7. Calculated Biomass for NH and JP ecosystems.

	Northern Hardwood	Jack Pine
Overstory Biomass (Mg C/ha)	372.39	75.43
Forest Floor Biomass (Mg C/ha)	7.33	7.24
Belowground Biomass (Mg C/ha)	32.52	53.77
Total Biomass (Mg C/ha)	412.24	136.44

Table 8. Calculated N Content values for NH and JP ecosystems.

	Northern Hardwood	Jack Pine
Overstory N Content (kg N/ha)	946.65	126.17
Forest Floor N Content (kg N/ha)	90.159	54.3
Belowground (0-10cm) N Content (kg N/ha)	2185	1330
Total N Content (kg N/ha)	3221.809	1510.47

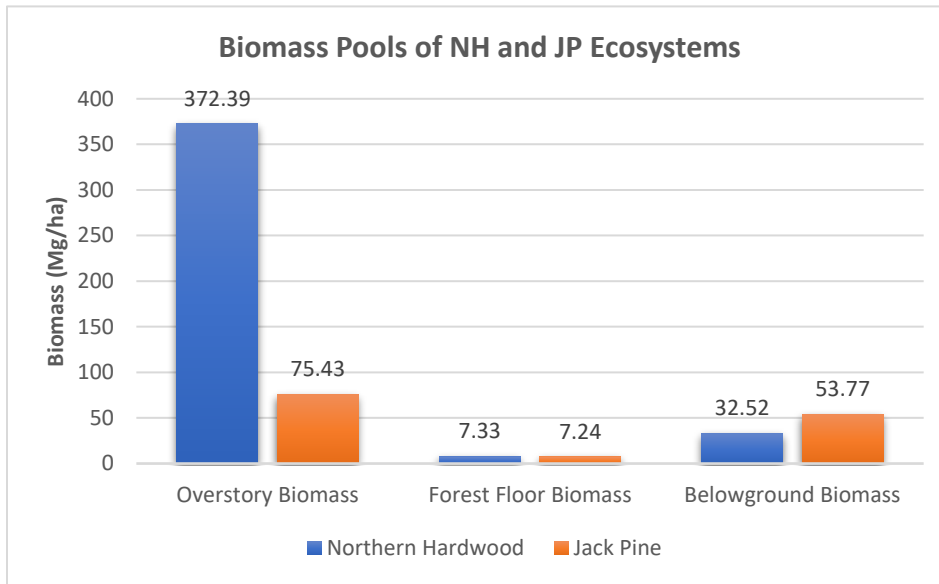


Figure 6. Biomass pools of NH and JP ecosystems.

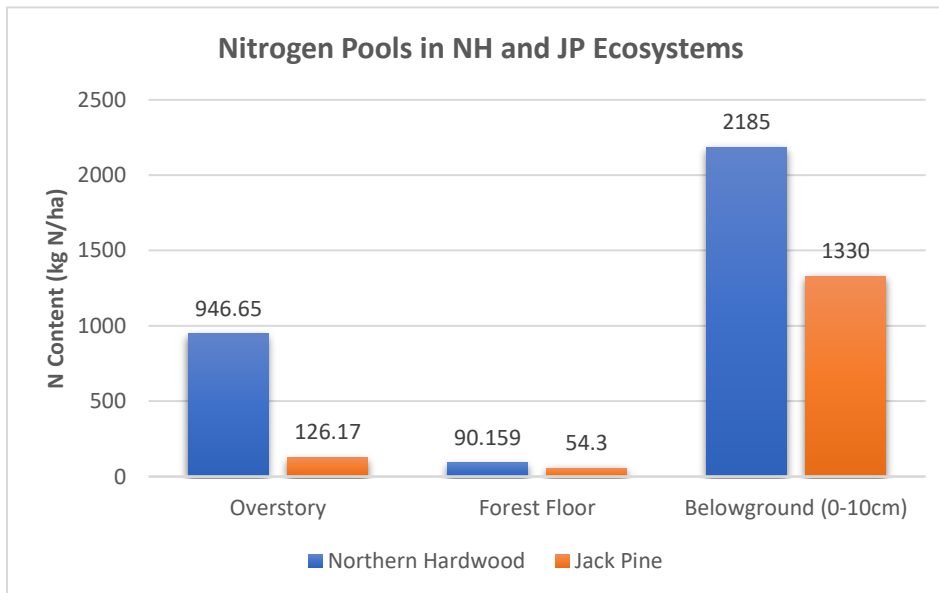


Figure 7. Nitrogen Pools of NH and JP ecosystems.

Discussion

Physical Environment

Varying modes of glacial deposition have characterized the development of these ecosystems. Climatic and topographical conditions impact pedogenic processes and have influenced the physiography of each site. The mineral component of both the NH and JP ecosystems was deposited during the oscillating advance and retreat of the Laurentide ice sheet between 15.5-10ka. The last glacial readvance that reached this portion of lower Michigan was likely approximately 13ka, when ice covered two thirds of the Michigan Basin (Larson and Schaetzl, 2001). Both sites exhibited well drained soil, which is partially facilitated by their coarse texture with little clay. Unfortunately, D_b and AWC data from the JP ecosystem is inaccurate, so a direct comparison of these properties cannot be observed. We theorize that if our calculated JP D_b was accurate, it would be very similar to our NH value of $.95 \text{ g/cm}^3$, and our JP AWC would also be close to our calculated NH AWC of 26%. Neither of these soils contain CaCO_3 from their parent material, so they largely lack the ability to buffer acidity.

The soil in the JP ecosystem originated from sandy sediments deposited by water across an outwash plain, and the NH soil began as sandy outwash from a prior glaciation that was incorporated into a second glacier and subsequently deposited as an end moraine. This endowed the NH ecosystem with topographic heterogeneity and created microclimates with varied light and water inputs, which contributed to soil development. Topography influences soil moisture, as the location of a site affects the amount of solar radiation that can reach its ground layer. Because light and water availability are limiting factors in ecosystems, the slope and aspect of a particular site in the NH ecosystem can influence its development and related plant communities (Coomes and Grubb, 2000; Rubino and McCarthy, 2003).

Increased water availability in an ecosystem will result in higher rates of soil weathering and development, which can be observed in the NH forest by examining the E horizon present in its soil profile. An E horizon develops when there is extensive leaching of nutrients from the A horizon via the percolating of water and is indicative of mesic conditions (Schaetzl et al., 2020; Brady & Weil, 2002). Our NH soil profile (Appendix I) contained a defined E horizon as well as B_hs and B_s horizons below it where leached particles accumulate. These properties are indicative of spodosols; acidic soils with leached surface layers and an accumulation of iron and aluminum oxides in the B horizon (Schaetzl et al., 2020).

Conversely, the JP ecosystem developed without any topographic gradient and lacks the microclimates that define the NH forest. It has been estimated that as much as five times the sunlight reaches the forest floor of this ecosystem as nearby deciduous forests (Coomes and Grubb, 2000). This increases evapotranspiration, which functions as precipitation in reverse and dries the soil (Jenny, 1980). This is apparent in our JP soil profile, which did not contain an E horizon (Appendix II). The JP soils are considerably less developed despite being the same age as NH because they lose water to the atmosphere at a greater rate, and it does not percolate through the soil profile with nutrients. Given their textural similarities and the assumption that they have a similar D_b and AWC it could be theorized that NH and JP ecosystems would have similar species composition. However, the complex physiography of the NH site has resulted in more developed soil that can support broadleaf deciduous trees, which further darken its understory and contribute to a feedback loop that creates microclimates and mesic conditions.

In addition to soil properties, patterns of natural disturbance can have a major impact on the structure, composition, and function of forested ecosystems. Natural disturbance events such as windthrow, disease, and ground fire occur in NH forests. However, because fire has been largely

eliminated from the landscape, fire-intolerant shade species such as *Acer saccharum* are slowly invading these ecosystems (Coomes and Grubb, 2000).

JP ecosystems are characterized by larger natural disturbance events. They contain drought-tolerant, fire-dependent species and rely on cyclical catastrophic fires to maintain their structure and composition. The dominant tree in this ecosystem, *Pinus banksiana*, requires fire to reproduce and grows in dense stands, which are vital nesting grounds of the Kirtland's warbler (*Setophaga kirtlandii*) (Tucker et al., 2016). Historically these fires have occurred on approximately 30-year intervals and have maintained relatively open conditions, preventing the incursion of fire-intolerant mesic tree species and the succession of the landscape. The open conditions allow for more light to penetrate to the soil level, increasing evapotranspiration and decreasing water penetration. This impedes soil development and influences the plant communities that can survive there (Cohen et al., 2015; LeDuc and Rothstein, 2007). Additionally, pine needles that accumulate on the forest floor are highly flammable (Coomes and Grubb, 2000). The combination of dry conditions, flat topography, and dry litter creates the perfect conditions for large fires that can spread across the landscape freely, as opposed to the hilly moraine topography of the NH ecosystem where they would likely be extinguished in the cool, wet valleys. Strangely we did not encounter any *Pinus banksiana* specimens in our JP plot, but we observed *Quercus palustris* and *Pinus resinosa*, which are not uncommon species in this ecosystem.

Chemical Environment

Acidification is a natural weathering process that occurs when there are few base cations remaining to neutralize the constant flux of H⁺ ions entering the soil (Bowman et al., 2008). The measured CaCl₂ pH was low in NH and JP ecosystems (pH 4.5 and 3.7). This is partially due to the lack of CaCO₃ in their parent material, which would have provided a buffering effect on the soil pH (Brady & Weil, 2002). Additionally, NH soil has the properties of a Spodosol and exhibits the effects of

podzolization, a process by which decomposing organic compounds from leaf litter chelate and mobilize Al and Fe cations. Water transports these molecules to the Bh and Bs horizons of the NH soil through percolation and leads to soil development (Schaetzl et al., 2020).

JP soils are less developed and more acidic than NH because the two have evolved divergently due to their physiography and associated plant communities. The topographically induced microclimates of NH are wetter and support hardwood tree species with large biomass pools. This influences the litter composition on the forest floor and allows for the development of the soil profile. The JP ecosystem is dominated by pines, which produce leaf litter that further acidifies the system over time (Burgess-Conforti et al., 2019). Natural disturbance affects soil chemistry in the JP ecosystem because large fires remove biomass and disrupt nutrient cycling (Yermakov and Rothstein, 2006). Because the JP soils are drier, less developed, more acidic, and frequently have nutrient inputs removed from the system via fire, they do not have a CEC as large as the NH soil does. The high quantity of exchangeable bases in the NH forest, deposited annually through organic inputs, buffer the soil pH, and occupy the exchange complex. JP soils have higher quantities of H⁺ ions entering the system and lack these base cations, so the soils acidify faster. Exchangeable acidity is therefore far greater in JP than NH because there are more available binding sites on the JP CEC for H⁺ and Al³⁺ ions to attach.

Biological Environment

Soil organic matter is the substrate that supports the soil food web and underpins productivity in terrestrial ecosystems. Biotic and abiotic factors that influence SOM include the amount of plant inputs and their chemical composition, climate, landscape position, natural disturbance, and geological substrate (Jackson et al., 2017; Jiménez-González et al., 2020). Soil texture greatly influences SOM development, and the lack of clay in the parent material of both the NH and JP ecosystems limits their SOM potential (Silver et al., 2000). In this study, SOM content was found to be higher in JP soil than NH

soil. NH soils are wetter, have high-energy nutrient input fluxes, and thus support microbial communities three times the size of those in JP soils. This would theoretically enable them to build up larger SOM deposits than JP. Leaf litter in JP ecosystems contains more lignin, which provides less energy for microbial growth and builds up on the forest floor over time (Yermakov and Rothstein, 2006). It is possible that the pools of nutrient-rich SOM in the NH ecosystem are synthesized at a greater rate by bacteria, resulting in less total SOM. Additionally, microbial communities are known to play an important role in belowground C stabilization and sequestration. Mycorrhizal symbionts are integral to the development of SOM in nutrient poor, northern forests, and symbiotic ectomycorrhizal fungi store more C in soil over time than ecosystems dominated by arbuscular mycorrhizal fungi. Additionally, JP ecosystems contain vast ectomycorrhizal networks, with at least 56 known species (Visser, 1995; Danielson, 1984). The JP site is nutrient poor and has a low pH, and it is possible that ectomycorrhizal fungal networks facilitate the sequestration of C in this ecosystem, resulting in increased SOM and belowground biomass compared with NH (Clemmensen et al., 2013; Jackson et al., 2017)

Microbial breakdown of SOM is affected by the dry, acidic conditions of the JP ecosystem, and JP soils exhibit half the microbial respiration rate as those of NH. Rates of N mineralization and nitrification are also affected by the physical and chemical differences between the two sites, although both are low. Mineralization allows microorganisms to access energy from organic inputs and sustains their populations in the soil. Moisture, temperature, and the availability and chemical composition of organic inputs largely determine mineralization rates (Kurganova et al., 2012). The higher pH and water content of the NH ecosystem enables populations of bacteria to mineralize SOM. There are also larger pools of organic matter in the NH ecosystem and seasonal fluxes distribute more high energy compounds to the soil surface than in JP. Low rates of mineralization in JP are due to the lack of water and low pH of this soil because high acidity and low moisture availability negatively influence the size

and diversity of soil bacterial communities and their function (Nugroho et al., 2007). This explains the lack of any nitrification in the JP ecosystem.

Because of the large hardwood trees occupying the NH site, our data indicates that the NH ecosystem stores far more biomass in its overstory than JP, as well as twice the N. In fact, the NH ecosystem contained nearly four times the total biomass as JP. Laboratory data reveals that the JP soil contained more biomass than NH. This is due to the slower decomposition rate in JP ecosystems due to lack of surface water and acidity, and the decreased nutrient value of the leaf litter in JP. Natural disturbance also plays a role in this dynamic, as periodic fires in JP forests release nutrients preserved in surface debris and increase N cycling, although the fires are also associated with nutrient loss from the system (Yermakov and Rothstein, 2006). The removal of fire treatments from the JP landscape has eliminated this regenerative process and will have long term consequences as patterns of succession shift to a closed canopy system and mesic tree species increase in abundance.

Conclusion

Soil development is dependent on several physical conditions and environmental factors. In this study, two soils with similar parent material composition and soil texture were comparatively analyzed to elucidate differences in their physical, chemical, and biological properties. The soils in each of these ecosystems differed in their mode of deposition, which impacted the physiography of each site.

Microclimatic conditions developed in the hilly NH forest, which reduced the amount of solar radiation that penetrated to the ground layer and increased water availability. The flat, dry JP ecosystem did not benefit from this topographic heterogeneity in the landscape, and over time multiple factors maintained a feedback loop that slowed soil profile development, effected the loss of base cations, and acidified its soil. Natural disturbance also contributed to the nutrient profile of each ecosystem, as windthrow

events in the NH forest enriched forest floor biomass and periodic, catastrophic fire in JP stands removed organic matter from its ecosystem entirely. The physical and chemical conditions of the soil directly influenced the size and composition of plant, animal, and microbial communities at each site, and these organisms regulate SOM and define the nutrient cycling capabilities of each ecosystem.

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Appendix I: Soil Profile for the Northern Hardwood Forest

This Northern Hardwood Forest is dominated by *Acer saccharum*, *Fagus grandifolia*, *Tilia americana*, *Quercus rubra*, and *Prunus serotina* in the overstory, with an understory including *Fraxinus americana*, *Acer saccharum*, *Fagus grandifolia*. Sparse herbaceous and woody vegetation in the understory included *Lonicera maackii* and *Sassafras albidum*. The site is located on a lower east-facing (25%) slope end moraine topography. The site was originally outwash that was then deposited by a second glacier through direct deposition. The soil is well drained and is developed in coarse textured ice contact material.

- O_{i/e}** 1-0 cm; intact *P. Serotina*, *C. glabra*, and *Q. rubra*, *A. saccharum*, *Q. alba*, leaves; abrupt smooth boundary.
- A** 0-10 cm; very dark grey (7.5YR 3/1) loamy sand, single grain fine structure; strongly acidic; abrupt smooth boundary. pH ~ 5.5
- E** 10-30 cm; very dark greyish brown (10YR 3/2) loamy sand; loamy sand; very strongly acidic; abrupt smooth boundary. pH ~ 4.5
- B_{hs}** 30-42 cm; dark yellowish brown (10YR 3/6) loamy sand; single grain; 0% coarse fragments; strongly acidic; abrupt smooth boundary. pH~5.5
- B_s** 42-65 cm; dark yellowish brown (10YR 4/6) loamy sand; single grain; 0% coarse fragments; moderately acidic; abrupt smooth boundary. pH~6
- C** 65+ cm; brownish yellow (10YR 6/8) sand; fine single grain structure; effervescence not present due to parent material; 0% coarse fragments; slightly acidic, pH ~ 6.5

Appendix II: Soil Profile for the Jack Pine Forest

This Jack pine forest is dominated by *Quercus palustris* and *Pinus resinosa* in the overstory, with an understory including *Vaccinium angustifolium*, *Pinus resinosa*, *Quercus palustris*, *Prunus serotina*, *Comptonia peregrina*, and *Prunus virginiana*. The site is located on a flat (0%) slope with no notable aspect on outwash plain topography. The soil is well drained and is developed in coarse textured outwash.

- O_{i/e}** 1-0 cm; intact *Quercus palustris*, *Pinus resinosa* leaves; abrupt smooth boundary.
- A** 0-15 cm; dark brown (4.5YR 3/4) loamy sand, fine weak granular structure; very strongly acidic; clear smooth boundary. pH ~ 4.5
- Bs1** 15-30 cm; dark brown (7.5YR 3/4) fine granular weak; 0% coarse fragments, loamy sand; medium acidic; abrupt smooth boundary. pH ~ 5
- Bs2** 30-75 cm; dark yellowish brown (10YR 4/6) loamy sand; fine-medium granular weak; 0% coarse fragments; medium acidic; abrupt smooth boundary. pH~5.5
- C** 75+ cm; yellow (10YR 7/8) sand; fine- medium weak granular structure; effervescence not present due to parent material; 0% coarse fragments; slightly acidic, pH ~ 6.5