Gradients in Lake Effect Snowfall and Fire across Northern Lower Michigan Drive Patterns of Soil Development and Carbon Dynamics

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Soils and forest ecosystems vary predictably along a 145-km transect in northern Lower Michigan. In the east, Entisols support open jack pine stands. In the central transect, weak Spodosols have formed under oak–pine–aspen forests. In the Lake Michigan snowbelt on the west, strongly developed Spodosols occur beneath mesic northern hardwoods. We hypothesized that increasing amounts of snowfall, coupled with decreasing fire frequencies, promote soil development and enhance soil C dynamics at western sites. We also hypothesized that enhanced soil development facilitated greater proportions of broadleaf tree establishment, which in turn accelerates snowmelt rates and further facilitates soil development by enhancing deeper C translocation. Along the transect, we described, sampled, and characterized twelve soils. Soil development increases east to west along the transect, changing most rapidly at the inner margins of the snowbelt, near the coniferous–broadleaf forest ecotone. Coincident with strong soil development in the snowbelt is an increase in soil C storage and cycling. Depth profiles of C, ^{13}C, and Fe- and Al-humus complexes all suggest that snowmelt percolation drives these patterns. Hardwoods produce and cycle more C than coniferous stands to the east and have thicker snowpacks. In the snowbelt, late-lying snowpacks limit spring fires, and large pulses of snowmelt water drive the fresh, soluble C from O horizons deeper, enhancing soil development and fostering ecosystem productivity. Although the current snowbelt, climate, and fire patterns across the peninsula might date only to ≈7,000 cal yr BP, they have nonetheless affected pedogenesis to the point that a major Entisol-to-Spodosol continuum has formed. *Key Words: ^{13}C dynamics, ecological feedbacks, Entisols, fire ecology, podzolization.*

沿着下密西根北部的 145 公里横切处, 土壤和森林生态系统的变化是可预测的。在东边, 新成土维系着开放的黑松林场。在中部的横切带, 弱淋淀土在橡树—松树—山杨组成的森林下方生成。在密西根湖雪带的西部, 湿度适中的北方硬木下有着大量生成的淋淀土。我们假设, 增加的降雪量, 以及减少的火灾频率, 促进了西部的土壤发育, 并增进了土壤碳的动态。我们同时假设, 提升的土壤发育, 促进了阔叶木更大比例的生长, 从而加速融雪速率, 并透过促进更深层的碳易位, 进一步增进土壤发育。我们沿着横切带, 对十二种土壤进行描述、采样并分类。土壤的发育, 沿着横切带由东到西增加, 并在雪带的内部边缘中改变最为剧烈, 且接近结毯果—阔叶林的交错群落。在雪带中, 与强健的土壤发育同时而发生的是土壤碳的储存与循环的增加。碳、碳13与铁和铝腐植质的复合体之深度剖面皆指出, 雪带的渗透驱动了这些模 式。越往东边, 硬木相较于结毯果林场, 生产并循环更多的碳, 并拥有较厚的雪被。在雪带中, 较晚沉积的雪被限制了春天的大火, 而大量的雪带水脉驱动了从氧层更深处而来的新鲜且可融的碳, 增进了土 壤发育, 并促进了生态系统的生产力。尽管目前横跨半岛的雪带、气候和火灾模式, 或许只能追溯到校正过后的距今七千年, 它们仍然影响了土壤生成, 直到主要的新成土—淋淀土的连续体形成。 关键词: 碳13动态, 生态反馈, 新成土, 火生态, 灰化作用。

Como era de esperarse, los suelos y los ecosistemas forestales varían a lo largo de un transecto de 145 km en la parte norte de la Baja Míchigan. Al este, los Entisoles permiten el crecimiento de bosques abiertos de pino jack. En el transecto central, los Spodosoles débiles se han formado bajo bosques de roble–pino–álamo. Al oeste, en la franja de nieve del Lago de Míchigan, ocurren Spodosoles muy desarrollados debajo de arbolados norteños de madera dura. Nuestra hipótesis es que el aumento de la cantidad de nieve, junto con una reducción de las frecuencias de incendios forestales, promueven el desarrollo del suelo y fortalecen la dinámica del C en el suelo en sitios localizados al oeste. También formulamos la hipótesis de que el desarrollo realzado del suelo facilitó proporciones más grandes del establecimiento de árboles de hoja ancha, lo que a su vez acelera las tasas de fusión de la nieve facilitando aun más el desarrollo del suelo, al favorecer una translocación más profunda del C. A lo largo del transecto describimos, muestreamos y caracterizamos doce suelos. El desarrollo del suelo se

incrementa de este a oeste, siguiendo el transecto, cambiando de manera más rápida sobre las márgenes interiores de la franja de nieve, cerca del ecotón forestal de coníferas–árboles de hoja ancha. Coincidente con el fuerte desarrollo del suelo en la franja de nieve, ocurre un incremento en el almacenamiento del C en el suelo y en la actividad cíclica. Los perfiles de profundidad del C, el ^{13}C y de los complejos de Fe-humus y Al-humus, en conjunto sugieren que la percolación de la nieve derretida controla estos patrones. Los bosques de madera dura producen y ciclan más C que los arbolados de coníferas hacia el este, y tienen cubiertas de nieve más profundas. En la franja de nieve los relictos tardíos de la cubierta de nieve restringen los incendios de primavera, y los grandes pulsos de agua de fusión de la nieve arrastran a mayor profundidad el fresco y soluble C desde los horizontes O, acentuando el desarrollo del suelo y estimulando la productividad ecosistémica. Aunque la franja de nieve, el clima y los patrones de fuego actuales a través de la península podrían datar solamente de ≈7,000 años cal. AP, si han afectado la pedogénesis, sin embargo, hasta el punto de formar un continuum principal Entisol-a-Spodosol. *Palabras clave: dinámica de ^{13}C, feedbacks ecológicos, Entisoles, ecología del fuego, podzolización.*

One of the most widely used soil development models is Jenny's (1941) functional-factorial (state factor) approach. Studies using this conceptual framework usually examine a suite of soils across the landscape, in which only one factor is allowed to vary. This framework makes it possible to explain changes in pedogenesis and ecosystems at local to regional scales. Although no substitute for pedon-scale, process-based analyses (e.g., Ranger et al. 1991; Schaetzl, Luehmann, and Rothstein 2015) or other types of quantitative pedogenic models (Minasny, McBratney, and Salvador-Blanes 2008), the state factor approach has shown great value in studies of soil distributions and, by association, has helped determine the effects of the various state factors on soil processes (Ponomareva 1958; Phillips 1989, 1998; Schaetzl and Isard 1996; Barrett 1999).

Key to this approach is the ability to hold some of the state factors constant, whereas others are allowed to vary. Over small areas, such a study design can often be easily operationalized (e.g., Cortes and Franzmeier 1972; Parsons and Herriman 1975; Schaetzl 1991, 1992; Egli and Fitze 2001). For regional- or landscape-scale studies, however, holding four state factors constant is challenging, because many of the factors are not invariant over large distances or because of factor covariance. The latter problem is especially pertinent for climosequences, in which only climate varies (Rice, Forman, and Patry 1959; Buntley and Westin 1965; Dahlgren et al. 1997). In all climosequences except at the local scale, vegetation usually covaries with climate. Thus, most climosequences are actually climo-biosequences, as is ours. Although this covariance can have some theoretical disadvantages, our study is set in a region where soil–ecosystem codevelopment has led to interesting and understandable patterns, all of which can help elucidate the interactions among climate, fire, forest composition, and soil

development. Interactions between soils and ecosystems could be better understood through studying climo-biosequences, where some aspect(s) of the regional climate and plant communities change rapidly over a short distance, such as those with lake effect snowbelts (Eichenlaub 1970; Isard and Schaetzl 1995; Scott and Huff 1996; Burnett et al. 2003; Henne, Hu, and Cleland 2007).

As in other Great Lakes snowbelts, a well-known climosequence exists across the northern Lower Peninsula of Michigan. Here, the climate changes from sites in the east that have little snow and are dry (Alpena, Michigan, on the Lake Huron coast, is the driest weather station in the United States east of the Mississippi River; see Figures 1 and 2) to more mesic sites farther west, in the Lake Michigan snowbelt (Braham and Dungey 1984; Norton and Bolsenga 1993; Burnett et al. 2003; Andersen and Winkler 2009; see Figure 2 and Table 1). Soils also change rapidly in character across this climosequence, where pod-
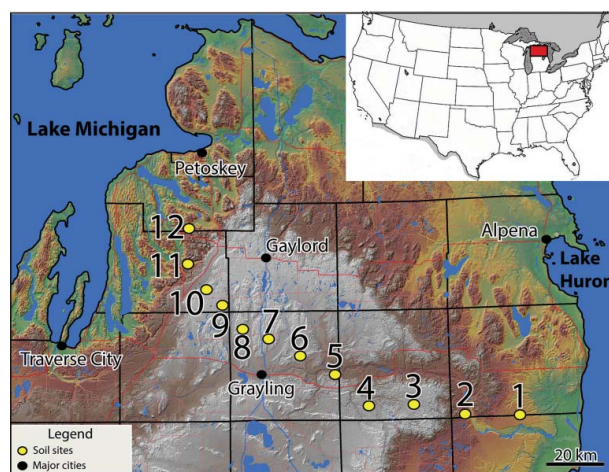
Figure 1. Relief/topography map of the study region, showing the locations of the study sites, by number, as well as county boundaries and major cities. (Color figure available online.)
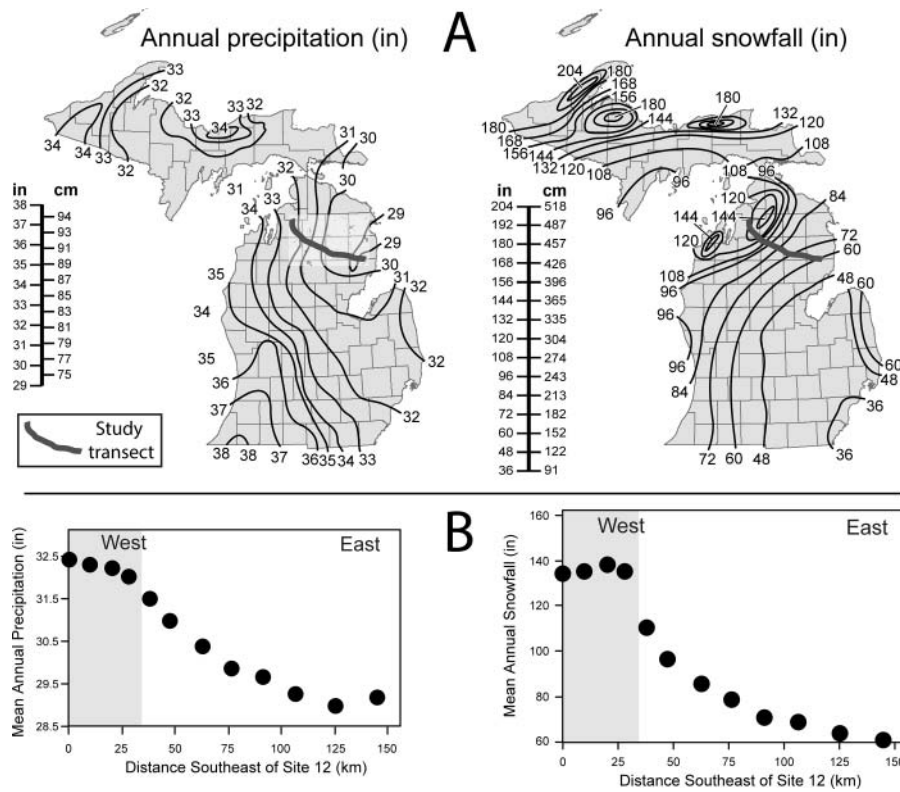
Figure 2. Climatic parameters across the study area. (A) Maps of Michigan's 1971 through 2000 climate normals, showing the location of the transect used in this study. After Andresen and Winkler (2009). (B) Comparable data, interpolated for the twelve study sites. Snowbelt areas are shown in shaded gray.

zolization, leaching, acidification, and cycling of soluble forms of carbon (C) are prominent pedogenic processes (Schaetzl and Isard 1991; Isard, Schaetzl, and Andresen 2007). Moving from the east (drier) to the west (wetter, snowier), soil freezing is also less common, due to thicker, more persistent snowpacks (Isard and Schaetzl 1995, 1998; Isard, Schaetzl, and Andresen 2007; see Table 2). Vegetation composition also changes markedly along this climosequence, from xeric jack pine (*Pinus banksiana*) forests and parklands through mixed coniferous–deciduous forests, to rich, mesic forests of maple (*Acer* spp.), beech (*Fagus grandifolia*), and eastern hemlock (*Tsuga canadensis*; see Table 1 and Figure 3B). Much of this change is mediated by decreasing fire frequencies from east to west (Cleland et al. 2004; see Figure 3C).

Previously, Schaetzl (2002) used the functional-factorial approach to examine soil development in this part of northern Lower Michigan and proposed that the degree of podzolization was controlled by winter climate, specifically total snowfall and snowpack duration. Schaetzl's (2002) winter climate podzolization model emphasized that the depth and speed of hydrologic fluxes are key drivers of podzolization: Soils in

areas of heavy snowfall experience much larger, faster, and deeper fluxes of infiltrating water compared to less snowy areas, which, in turn, determines the depth and development of subsurface illuvial horizons. This earlier study was not concerned with soil C. Nonetheless, increases in podzolization and snowfall or snow cover also coincide with increased illuvial accumulations of organic C at depth. This association is supported by a more recent, process-based study (Schaetzl and Rothstein 2016) documenting the importance of the snowmelt period to the hydrologic transport of surface-generated dissolved organic carbon (DOC) to depth. Thus, we hypothesized that greater hydrologic transport of DOC, associated with deep snowpacks over thousands of years, would lead to greater accumulation of relatively young C deep in the profile and an increase in soil C stocks with increasing snowfall across this gradient.

In this study, we examined soils along a longer (145-km) transect than did Schaetzl (2002), to better understand (1) the role of winter climate as a driver of soil development and (2) how landscape patterns of soil development affect soil C storage. Worldwide, soils contain a tremendous reservoir of C, storing more

Table 1. Environmental aspects of the twelve study sites

Site[a] no.	Dominant overstory vegetation[b] (at time of sampling)	Presettlement vegetation[c] (ca. mid-1800s)	Age of surface[d] (years BP)	Soil freezing activity[e]
1	Red and jack pine, oaks	Jack pine barrens	15,000	Frequent
2	Jack, red, and white Pine; oaks; red maple	Jack pine, red pine forest	15,000	Frequent
3	Jack and red pine, oaks	Jack pine, red pine forest	22,000	Frequent
4	Jack and red pine, oaks	Jack pine, red pine forest	22,000	Frequent
5	Jack and red pine, oaks	Jack pine, red pine forest	21,000	Nominal
6	Jack and red pine, oaks, red maple	Jack pine barrens	21,000	Nominal
7	Aspen, white and red pine	Beech, sugar maple, hemlock forest	21,000	Nominal
8	Sugar maple, basswood, aspen, ironwood	Beech, sugar maple, hemlock forest	21,000	Nominal
9	Sugar maple, yellow birch, ironwood, white birch	Aspen, birch forest	20,000	Nominal
10	Sugar maple, beech, ironwood	Beech, sugar maple, hemlock forest	15,000	Minimal
11	Sugar maple, beech, ironwood	Beech, sugar maple, hemlock forest	14,000	Minimal
12	Sugar maple, hemlock, beech, aspen	Beech, sugar maple, hemlock forest	13,500	Minimal

[a]All sites had generally similar textures and were well drained or drier. Thus, information about the parent material and relief factors is not provided here.
[b]Scientific names: Jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), oak (*Quercus* spp.), white pine (*Pinus strobus*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), basswood (*Tilia americana*), aspen (*Populus* spp., usually *tremuloides*), ironwood (*Ostraya virginiana*), yellow birch (*Betula allegheniensis*), white birch (*Betula papyrifera*), beech (*Fagus grandifolia*), hemlock (*Tsuga canadensis*).
[c]After General land Office survey notes (e.g., Albert and Comer 2008).
[d]Based on best known data, reported in radiocarbon years BP, rounded to nearest thousands of years ago. Important articles used to determine these ages include Schaetzl et al. (2017) and Blewett, Winters, and Rieck (1993).
[e]After Isard and Schaetzl (1998).

than twice the C as the atmosphere and vegetation combined (Falkowski et al. 2000; Intergovernmental Panel on Climate Change 2013), yet it is unclear how soil C responds to environmental perturbations (Eglin et al. 2010; Richter and Houghton 2011). Because well-drained, sandy parent materials of Late Pleistocene age (Table 1) dominate the region, we were generally able to hold the factors of relief, parent material, and time constant, allowing vegetation and climate to covary along the transect. Specifically, all study sites are on flat (or nearly so) upland sites where the water table is well below the solum; that is, they are on well-drained (or drier), geomorphically stable sites. Sandy parent materials dominate each site; details about tex-

**Table 2.** Pedogenic aspects of the soils sampled at the twelve study sites

Site no.	Horizonation[a]	E horizon present?	Profile thickness[b] (cm)	Classification (taxonomic subgroup)	POD Index[c]	E horizon color[d]	Uppermost B horizon color[d]
1	Oi-Oe-A-Bw1-Bw2–2 BC	N	61	Typic Udipsamment	0	—	
2	Oi-Oe-A-Bs1-Bs2-Bs3-BC-C	N	70	Typic Udipsamment	0	—	
3	Oi-Oe-E-Bs1-Bs2-E'-2 Bt	Y	50	Spodic Udipsamment	0	10YR 4/2	7.5YR 4/6
4	Oi-Oe-A-Bs-BC-C	N	45	Typic Udipsamment	0	—	10YR 4/6
5	Oi-Oe-A-Bs1-Bs2-BC-C	N	51	Typic Udipsamment	0	—	7.5YR 4/6
6	Oi-Oe-A-Bs1-Bs2–2 BC-2 C	N	68	Entic Haplorthod	0	—	7.5YR 4/6
7	Oi-A-E-Bs1-Bs2-Bs3	Y	>100	Entic Haplorthod	2	7.5YR 5/2	7.5YR 4/4
8	Oi-A-E/A-EB-Bs1-Bs2-BC	Y	93	Entic Haplorthod	0	10YR 4/3	7.5YR 4/4
9	Oi-Oe-A-E-Bhs-Bs-BC	Y	93	Typic Haplorthod	5	7.5YR 5/2	5YR 3/3
10	Oi-Oe-A-E-Bhs-Bs-BC	Y	90	Typic Haplorthod	2	7.5YR 4/2	5YR 3/3
11	Oi-Oe-E-Bhs-Bs1-Bs2-Bs3	Y	>100	Typic Haplorthod	10	7.5YR 4/2	2.5YR 2.5/3
12	Oi-Oe-A-E-Bhs-Bsm-Bs	Y	>100	Typic Durorthod	18	7.5YR 5/2	2.5YR 2.5/3

[a]All twelve pedons were described and sampled to 1 m depth only.
[b]Measured from soil surface to top of BC or C horizon, whichever is shallower. Includes only horizons formed by podzolization; that is, it excludes the deep Bt horizon in Pedon 3.
[c]After Schaetzl and Mokma (1988). POD Index < 2 typically implies that the soil is an Entisol. POD Index > 6 is typical of strongly developed Spodosols.
[d]Moist Munsell color, as measured in the field.
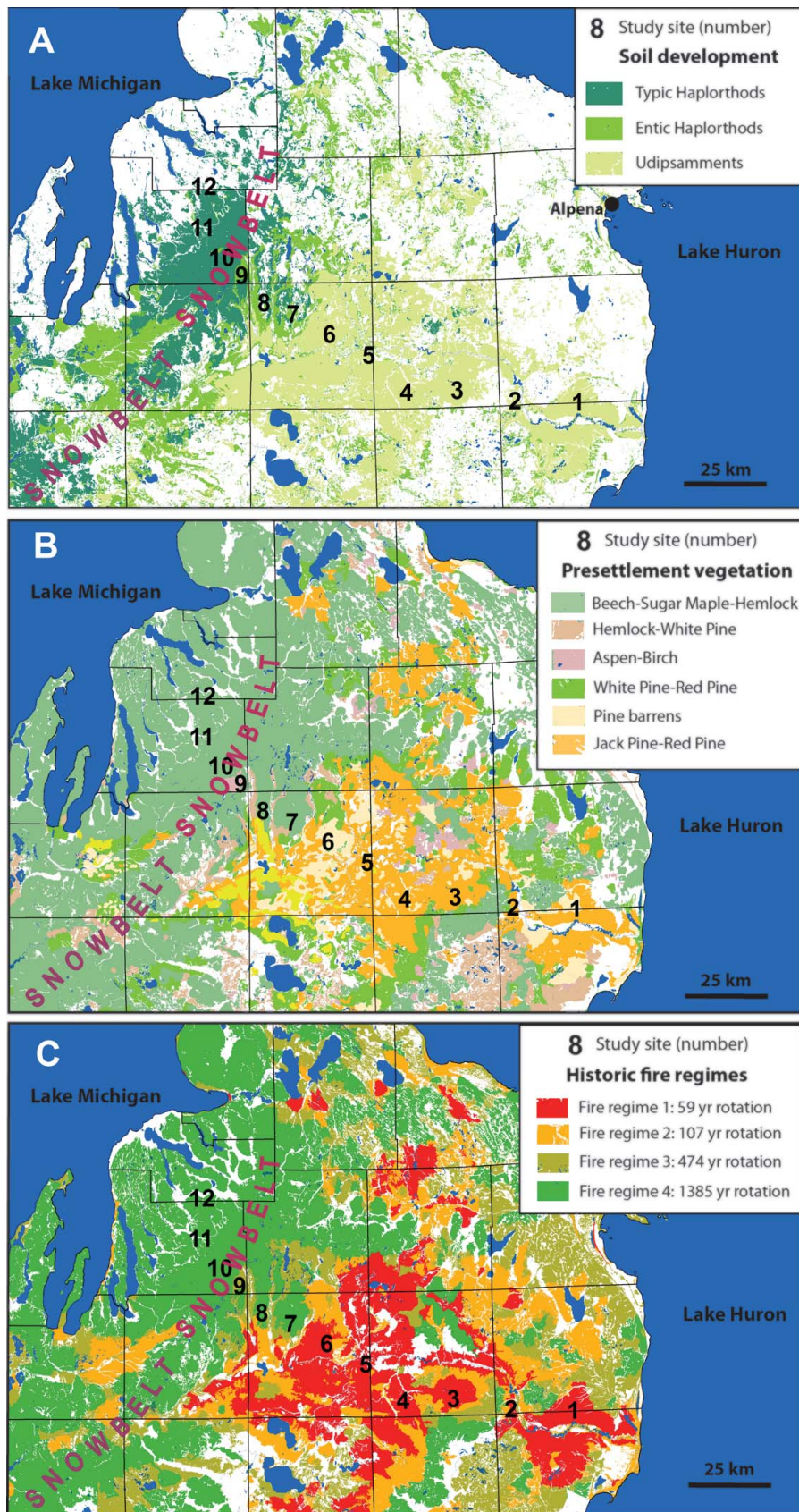
Figure 3. Maps of (A) major soil types, (B) presettlement vegetation (Comer et al. 1995), and (C) historical fire regimes (Cleland et al. 2004) across northern Lower Michigan. White areas in Part C are lowlands. (Color figure available online.)

tures are reported later. Although age of the surfaces does vary between 13,500 and 22,000 years, soils in this region can develop "climatically mature" profiles within 8,000 years or less (Franzmeier and Whiteside 1963; Barrett and Schaetzl 1992). Thus, the soils under study here can be considered pedogenically "mature" for their site. In sum, climate and vegetation are the main factors that vary among the sites.

The purpose of our study is to examine changes in soil development and soil C storage across northern Lower Michigan and to correlate soil development patterns to climatic and vegetative factors. We hypothesized that a soil–vegetation developmental feedback mechanism (involving climate-mediated fire regimes) exists along this transect. Thus, the second focus of our study is to explore this feedback further.

Methods

Study Area Characteristics

The study area spans the northern Lower Peninsula of Michigan (Figure 1). The area is composed of several similar (but mainly sandy) physiographic regions, namely, the Au Sable Delta (Site 1), the Outer Port Huron Plains (Sites 2, 5, and 10), the West Branch Moraine (Site 3), the Houghton Lake Basin (Site 4), the Grayling Fingers (Sites 6–9), and the Northern Lower Peninsula Tunneled Uplands (Sites 11 and 12; Schaetzl et al. 2013). This area has frigid soil temperature and mesic soil moisture regimes (Soil Survey Division Staff 1993). Soils might be slightly warmer in winter in the snowbelt areas to the west, due to the insulating properties of the snow (Isard, Schaetzl, and Andresen 2007); the pedogenic implications of this are discussed later. The region is typified by sandy soils formed in glacial sediment (Schaetzl et al. 2013). Although the last glacier retreated from the region between ≈23,000 and 11,800 cal yr BP (Blewett, Winters, and Rieck 1993; Larson, Lowell, and Ostrom 1994; Schaetzl and Rothstein 2016), most of the study sites are on surfaces that formed between 22,000 and 14,000 cal yr BP (Table 1).

Environmental conditions change markedly from east to west in this region, due primarily to increasing amounts of precipitation and snow (Table 1; Figure 2). Lake effect snowbelts exist in the lee of all five Great Lakes. In northwestern Lower Michigan, the snowbelt is particularly well formed due to orographic uplift on uplands that are 30 to 50 km inland

from the lake. This adds considerably to snowfall totals and therefore enhances snowbelt development (Henne, Hu, and Cleland 2007).

The ecological impacts of lake effect snow in this region are impressive, where it has important influences on forest composition and distribution, as well as on fire frequencies. Henne, Hu, and Cleland (2007) found that snowfall is the most predictive variable for the occurrence of mesic forests within northern Lower Michigan. Forests within the snowbelt are more productive, diverse, and mesic and have lower fire frequencies, whereas outside the snowbelt mesic-type forests are much less common. In the more xeric environments outside the snowbelt, mesic stands are typically only found on fine-textured soils (Henne, Hu, and Cleland 2007). Typically ecosystems in the northeastern Lower Peninsula are characterized by pine and oak forests and barrens, formed on edaphically dry, sandy soils and under lower annual snowfall totals, allowing for more frequent fires (Simard and Blank 1982; Albert 1995; Albert and Comer 2008; see Figures 3B, 3C).

Most soils in the eastern part of the study area are mapped as Udipsamments, with minimal development and A–C profiles (Figures 3A, 4). Ecosystems along the transect become increasingly mesic toward the west, as snowfall totals increase and fire frequencies decline (Table 1). By midtransect, oaks (*Quercus* spp.), red maple (*Acer rubrum*), white birch (*Betula papyrifera*), and the more mesic species of pine (white pine, *Pinus strobus*) all increase in abundance (Mokma and Vance 1989; Schaetzl 2002; see Figure 3B). Many of the soils in the central transect area have weak E horizons and classify as Entic Haplorthods. The western sections of the transect lie in the snowbelt of Lake Michigan and are the most mesic of all of the sites. Here, soils are strongly developed Spodosols with B horizons enriched in C, Al, and Fe compounds (Schaetzl 2002; Figures 3A, 4). Presettlement forests in the snowbelt were dominated by hardwoods such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and basswood (*Tilia americana*), as well as conifers such as hemlock and white pine (Figure 3B). Locally, this forest community has long been referred to as northern hardwoods (Nichols 1935; Bormann and Likens 1979; Schaetzl 1994; Hale, Frelich, and Reich 2006).

The fire season in northern Lower Michigan occurs in late spring or early summer (Simard and Blank 1982; Cardille and Ventura 2001). Fires are uncommon in the snowbelt, mainly due to late-lying snowpacks, more rugged topography, and a greater
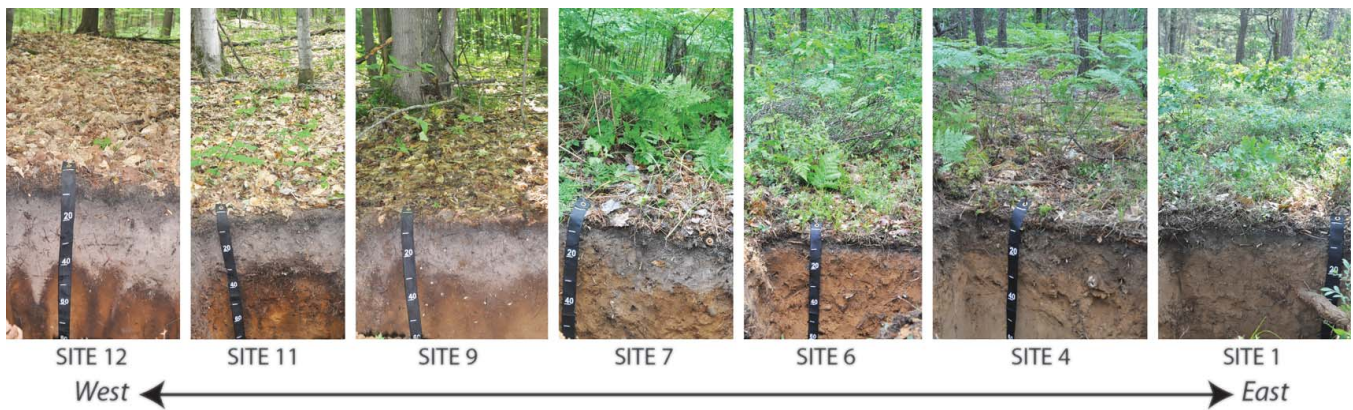
Figure 4. Photos of representative soil profiles and forest cover types along the study area transect. Because morphologies change more rapidly along the western parts of the transect, this section is better represented in the photo collage. (Color figure available online.)

occurrence of wetlands (Cleland et al. 2004; Henne, Hu, and Cleland 2007). In the absence of a snowpack, fire can spread readily across the coarse-textured outwash plains in the east. Due to abundant snowfall, fires do not spread as readily in the west, thereby facilitating the establishment of mesic forests (Figures 3B, 3C). Figure 3C shows generalized historical (presettlement) fire regimes for this region, illustrating the rapid drop-off in fire frequency at about the center of the transect.

Field Methods

We chose twelve forested sites for study, generally uniformly spaced along the 145-km long transect. Each site is on a sandy upland with well-drained (or drier) soils, where evidence of any human interference (save for postsettlement logging operations) has been nil. At each site, we located an area with soils and overstory vegetation that were representative of the region at large and where tree uprooting disturbances were not evident (Schaetzl et al. 1990; Samonil et al. 2013). Preliminary hand augering at each site helped select a representative location for a soil pit. Each ≈130-cm-deep pit was described using standard methods (Schoeneberger et al. 2012). All genetic horizons, including the O horizons, were sampled. To maintain consistency among the sites, all soils were described and sampled only to 100-cm depth. O horizons were sampled using a 30 cm × 30 cm metal sampling frame. Samples for C and ^{13}C analyses were kept separate and immediately placed on ice in a cooler while in the field. Bulk density samples were taken for horizons thicker than about 10 cm, using a thin-walled aluminum ring,

10 cm in diameter, driven into the pit face. Overstory vegetation at each site was described qualitatively.

The degree of spodic development for each profile was quantitatively determined using the POD Index of Schaetzl and Mokma (1988). The POD Index uses the Munsell color hues and values of the E and B subhorizons to assess their relative differences. Larger numbers of B subhorizons, with increasing contrast in color hue and value relative to the E horizon, produce larger POD Index values. This index is especially applicable for soils of the study area, which either are, or are developing toward, Spodosols (Arbogast and Jameson 1988; Schaetzl, Luehmann, and Rothstein 2015).

Laboratory Methods

All mineral soil samples were air dried and passed through a 2-mm sieve. Because all of the soils were sandy, we did not do detailed particle size analysis. Instead, we determined the amount of silt and clay gravimetrically, by dispersing ≈12- to 13-g samples in a weak solution of $(NaPO_3)_{13} \cdot Na_2O$, after shaking for fifteen minutes. The dispersed samples were washed through a 53-μm sieve and the air-dried weight loss was attributed to silt and clay. Soil pH was measured on 1:1 (water:soil) samples (4:1 for organic horizons) using a Mettler MP22 pH meter. Each sample was stirred for thirty seconds and again thirty minutes later. After one hour, three pH readings were recorded; we report only mean data.

Iron (Fe) and aluminum (Al) extractions were conducted on E, Bhs, and Bs horizons, using standard methods. A sodium citrate–dithionite solution was used to extract amorphous and crystalline
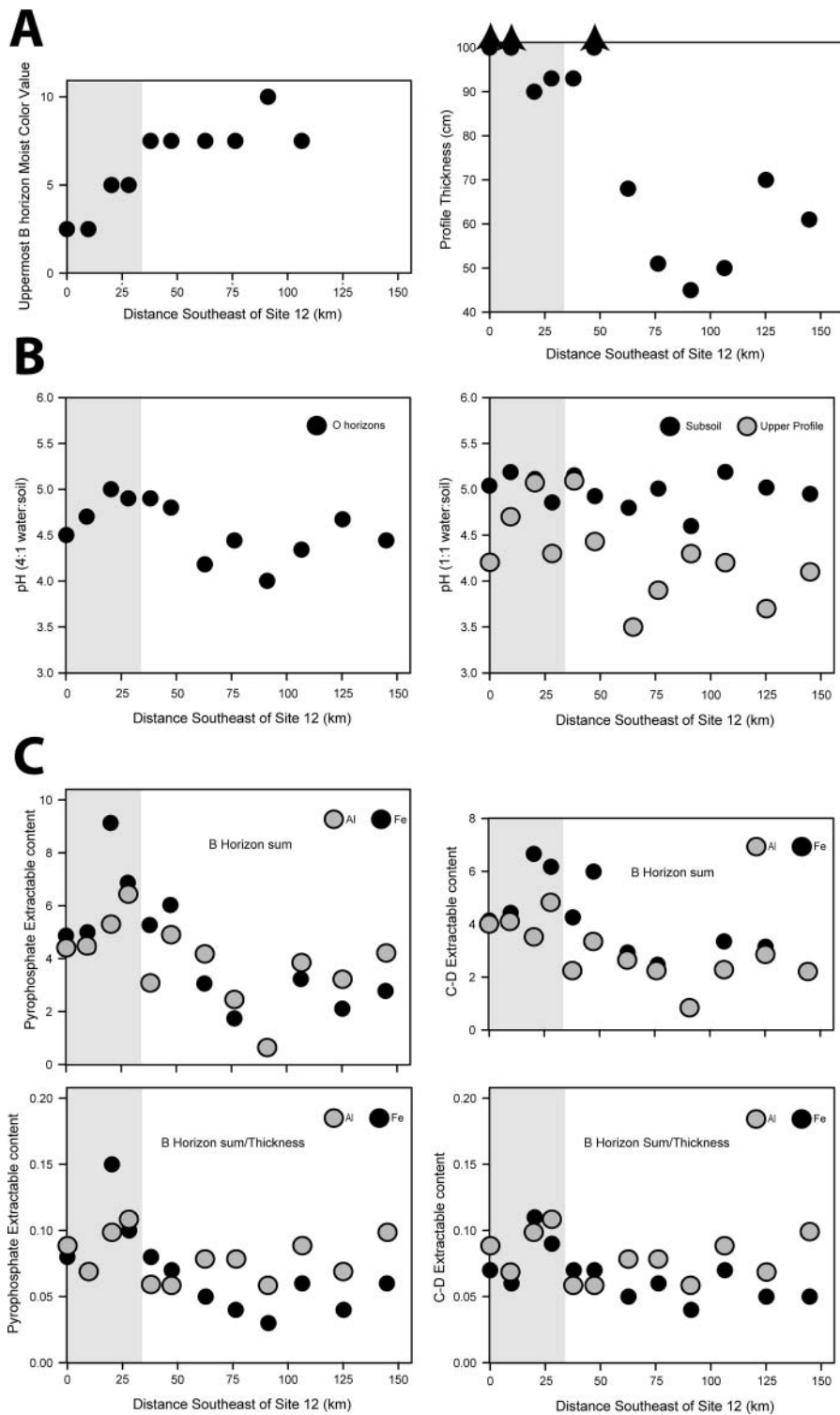
Figure 5. Data for the soils along the transect. (A) Morphologic data. (B) pH data. (C) Chemical data. Arrows in A indicate that profiles were thicker than 100 cm, but data below that depth were not obtained. Thus, the data reported should be considered minimal values.

(commonly referred to as "free") forms of Fe and Al (Mehra and Jackson 1960). Organically bound forms of Fe and Al, which provide a good indicator of the abundance of organo-metallic complexes, were extracted with Na-pyrophosphate (McKeague 1967).

For C analyses, samples were first pulverized in a ball mill to silt size and then analyzed for total C by dry combustion gas chromatography on a Costech ECS 4010 (Costech Analytical Technologies Inc., Valencia, CA) and for naturally abundant ^{13}C using an Elementar Vario EL Cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany), interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd, Cheshire, UK) at the University of California, Davis, Stable Isotope Facility.
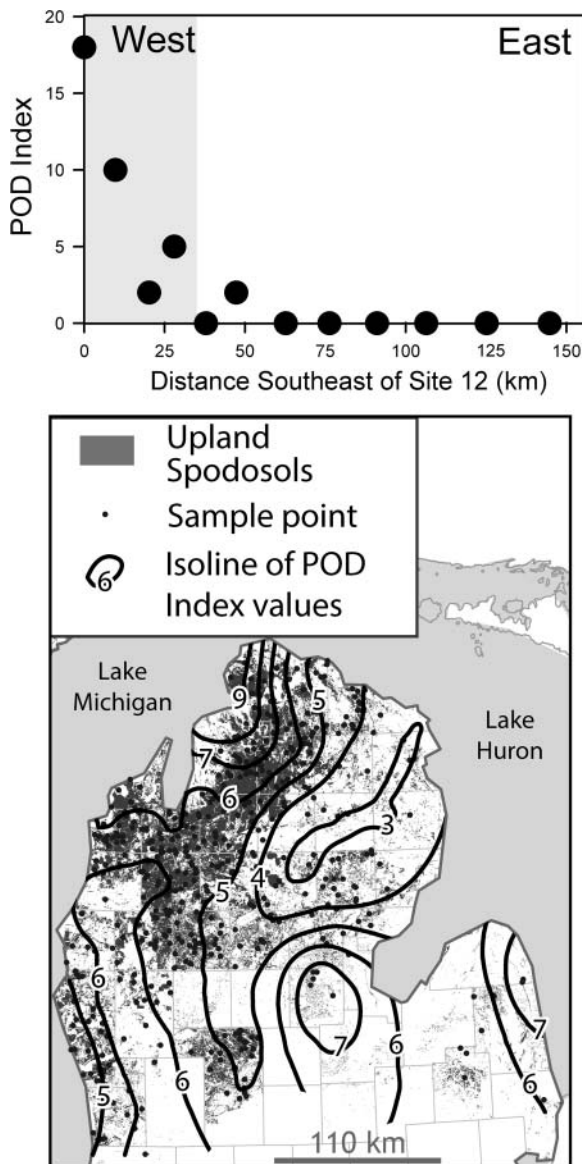
Figure 6. General trends in soil development on sandy, upland sites across the northern Lower Peninsula and at the twelve study sites, as indicated by the POD Index of Schaetzl and Mokma (1988). After Schaetzl, Luehmann, and Rothstein (2015).

Mapping Methods

We used county-level Soil Survey Geographic Database (SSURGO) soils data from the Natural Resources Conservation Service (NRCS), in a geographic information system (GIS), to evaluate soil development as determined by the POD Index. To do this, the SSURGO data for the pertinent counties were combined and rasterized. For each upland Spodosol and Entisol soil series in the region, we determined its POD Index (Schaetzl and Mokma 1988). POD Index data were joined to the attribute table of the soils in a GIS. We next (randomly) assigned ≈2,000 data points across the region. At locations where a data point intersected an upland Spodosol or Psamment map unit, we determined the POD Index from the SSURGO database and kriged the point data to arrive at a smoothed isoline map of POD Index values across the study area.

Results and Discussion

Environmental Characteristics

As shown in Figure 2, the climate changes markedly and predictably across the transect. East-to-west trends include increasing annual precipitation and increased snowfall. Temperature change is minimal across the region, although sites near the lakes typically have lower annual extremes of temperature, due to the moderating influence of the water. Soils freeze most often in the east, where snowpacks are thinnest, and least often in the snowbelt (Isard and Schaetzl 1995, 1998; see Table 2).

General Soil Characteristics

Most samples field-textured as sand or loamy sand (Soil Survey Division Staff 1993). For the sixty-three horizon-based samples, the mean silt and clay content was 7.3 ± 5.0 percent. As all sample sites were on uplands, none of the soils showed indications of wetness or water table influence. Most soils have pH values that fall into the moderately to strongly acidic range, averaging between 4.3 (O horizons) and 5.0 (lower profile; Figure 5). None of the study sites appeared to have had a history of erosion or other types of disturbance.

Regional Soil Development Trends

POD Index data, which incorporate all soils mapped by the NRCS rather than just our study sites, show the east-to-west trends in soil development well (Figure 5). POD Index values for the soils at our study sites show similar trends, with a notable increase within the snowbelt, mirroring the trends observed in the field (Figure 6). The various transect data from our study sites also confirm that, across the northern Lower Peninsula, soil development generally increases from east to west.

All soils have been naturally acidified to the extent that podzolization has been initiated (Figure 5). Nonetheless, soil development has proceeded much farther in soils within the snowbelt than in soils farther east (Figure 4). Soils classify as Typic or Spodic Udipsamments in the east and have thin sola (Table 2). By midtransect (Site 6), most soils classify as Spodosols (i.e., Entic and Typic Haplorthods). The Typic Durorthod at Site 12 has a very thick solum with well-expressed ortstein and a POD Index of eighteen, all suggestive of extreme development (Schaetzl and Mokma 1988).

Morphologic data also indicate that soil development increases near and within the snowbelt; profiles become thicker, E horizons become brighter, and B horizons become darker and redder (Figure 5A). Like POD Index and morphologic data, *summed* extract data (extract concentrations multiplied by horizon thicknesses) for Fe and Al from B horizons show similar east-to-west trends and dramatic increases in the snowbelt (Figure 5B). Concentrations of Fe in B horizons (sums of B horizon extract data, divided by horizon thicknesses; Figure 5B) suggest an increase at snowbelt sites. Al data did not demonstrate a clear trend across the transect.

When examined cumulatively, our suite of data for the twelve study sites confirm that soil development increases across the peninsula from east to west but that the rate of change is not uniform (Table 2; Figure 7). Instead, soils are almost uniformly weakly developed across the eastern third of the transect, with the greatest rate of change occurring at or near the eastern margins of the snowbelt. POD Index values portray this trend quite well; they are zero for Sites 1 through 6, then are between zero and two for Sites 7 through 10, until finally showing large increases at the last two sites (Table 2, Figure 6). Finally, morphologic data show similar trends; E horizons are present in only one soil in the eastern half of the transect
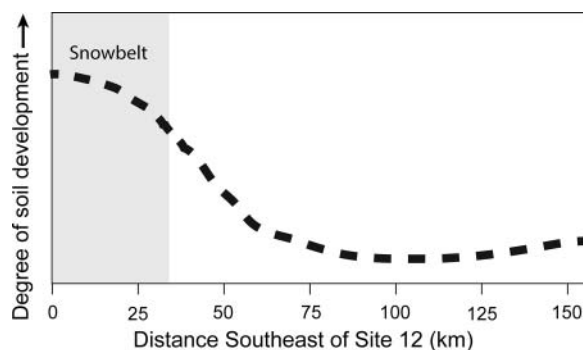
Figure 7. Overall, generalized trend in soil development along the transect, as interpreted from data in Figures 5, 6, and 8.

(Site 3), whereas all soils in the western half have developed E horizons (Table 2). Bhs horizons, indicative of strong podzolic development, are found only at Sites 9 through 12 on the far western end of the transect (Table 2). The soil at Site 12 was an exceptionally well-developed Spodosol, with a POD Index of 18 (Table 2; Figure 4).

Forest diversity and productivity also increased from east to west across the transect (Table 1). Open stands of jack pine and oaks dominate at Sites 1 through 6, where soils all have minimal development (Figure 3B), usually lack E horizons, and have POD Index values of zero, with bright B horizon colors and chromas of 6 (Figure 5A; Table 2). Forests also become more diverse in the central parts of the transect, with increasing amounts of oak, red maple, and aspen (*Populus* spp.) in the overstory. Forests in the western parts of the transect are classical northern hardwoods, with eastern hemlock increasing in importance, especially at Site 12.

Soil Development with Respect to Fire and Snowfall Patterns

Trends in soil development across this region have traditionally been attributed to two main factors: (1) decreased fire frequencies, coupled with (2) increased snowfall and snowmelt percolation, from east to west.

Fires and fire-climax forests were common in the presettlement forests across the eastern part of the transect (Figures 3B, 3C). They were widespread, mainly due to slightly drier summers and lower annual snowfall totals on lower relief, dry, sandy landscapes (Simard and Blank 1982; Abrams, Sprugel, and Dickmann 1985; Cleland et al. 2004; Henne, Hu, and Cleland 2007). Fire can sweep

across these landscapes, often as crown fires, and lead to widespread, even-aged stands of fire-tolerant species, interspersed with open, barrens-like stands of jack pine and oak. Fires burn the litter layer on the forest floor and reduce carbon stocks that could enhance soil development; that is, podzolization (Diebold 1941; Mokma and Vance 1989). Farther west, fire is much less common due to late-lying snowpacks in spring and more rugged topography (Henne, Hu, and Cleland 2007; Figures 1, 3C).

Litter loss from fire also reduces soluble organic compounds on the forest floor; these compounds are requisite for podzolization to occur (Schaetzl 1994; Schaetzl and Harris 2011). Organic compounds can freely translocate into the soils and complex free metal cations, enhancing their solubility. Formation of organo-metallic complexes enables metal cations to be translocated to the lower profile in percolating water, ultimately forming the E–Bs profile that epitomizes Spodosols (Figure 4). Areas outside of the snowbelt, generally in the eastern half of the transect, have thinner O horizons and less developed soils (Table 2); the mean O horizon thicknesses at Sites 1 through 8 and 9 through 12 were 5.5 cm and 7.3 cm, respectively. It is important to note that we only selected mature forests for sampling, which likely overestimate long-term O horizon thicknesses and C stocks (Figure 8) in the fire-prone eastern portion of the transect. In the area around Sites 2 and 3, Rothstein, Yermakov, and Buell (2004) sampled O horizon C stocks along a chronosequence ranging from one to seventy-two years since a wildfire. They found that O horizons were almost entirely consumed by fire and that O-horizon C stocks were negligible ($0.1–0.4 \ kg/m^{-2}$) for the first thirty years of stand development, and then increased rapidly toward an asymptotic value of $\sim 1.2 \ kg/m^{-2}$. The average presettlement fire-return interval for this area is about sixty years (Cleland et al. 2004), which implies that O horizon C stocks are normally lower than those we measured in the mature stands we studied. Thus, the transect-wide differences in O horizon C stocks shown in Figure 8 might have been larger if we had not avoided sampling recently burned sites.

A second line of explanation for the dramatic increases in soil development across the region, particularly in the west, is increased snowfall and snowpack thicknesses (Schaetzl and Isard 1991, 1996; Schaetzl 2002; Figure 2). The Lake Michigan snowbelt is best developed about 10 to 50 km inland (Eichenlaub 1970; Norton and Bolsenga 1993; Burnett et al. 2003; Andresen and Winkler 2009; Figure 2). Here, thick
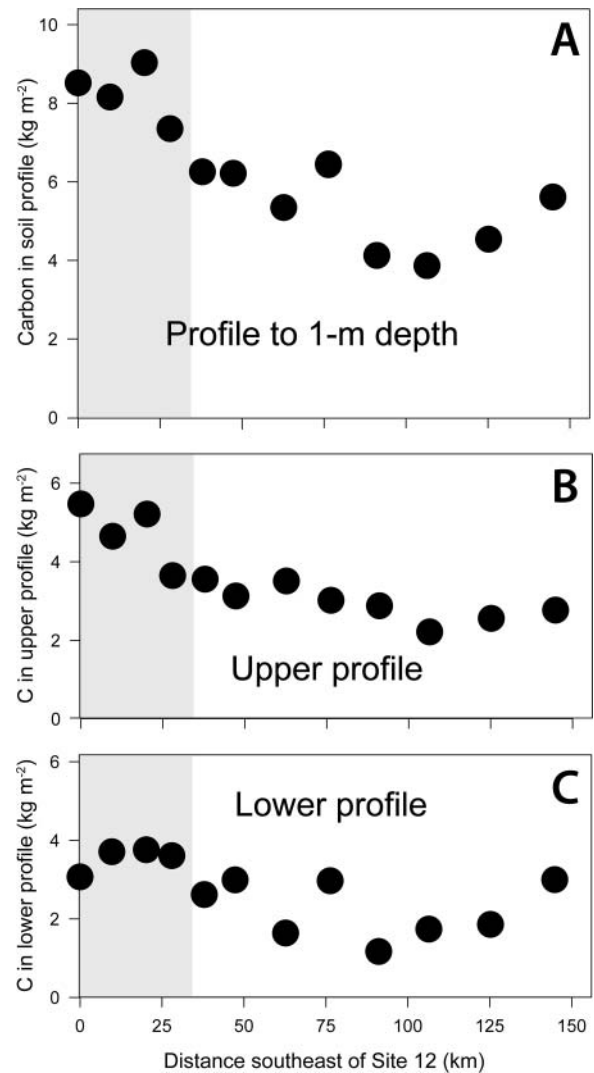
Figure 8. Soil C stocks sites along the transect, including (A) the entire profile to 1-m depth; (B) the upper profile including O, A, and E horizons; and (C) only B horizons in the lower profile.

snowpacks accumulate early, inhibit soil freezing, and keep the soil and litter layers warmer than in areas further east, where snowfall is less reliable and snowpacks are thinner (Isard and Schaetzl 1995, 1998; Isard, Schaetzl, and Andresen 2007; Figure 2). Soils in snowbelt areas are more likely to remain unfrozen and permeable throughout the winter. This allows large "pulses" of snowmelt water to freely infiltrate, often as nearly continuous, days-long wetting events (Schaetzl and Isard 1991, 1996; Schaetzl, Luehmann, and Rothstein 2015; Schaetzl and Rothstein 2016). The deep snowpacks of the snowbelt also insulate the litter layer and facilitate decomposition throughout the winter, thereby promoting the production of soluble organic acids (Taylor and Jones 1990). Long, steady pulses of snowmelt water are therefore able to drive soluble
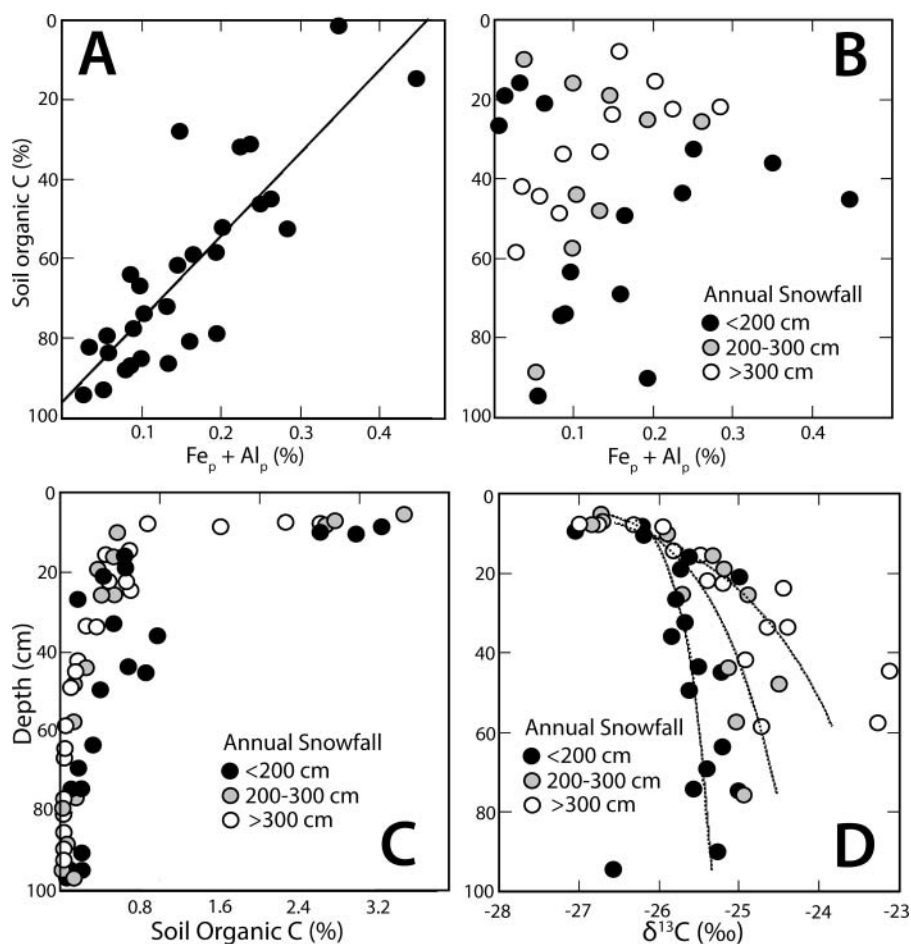
Figure 9. Soil organic carbon chemistry, as it varies by depth and amount of snowfall. (A) Relationship between soil organic C concentration and the concentration of pyrophosphate-extractable (organically bound) Fe and Al ($Fe_p + Al_p$) across all B horizon samples, showing the best-fit linear regression line. (B) $Fe_p + Al_p$ concentrations with depth, split according to snowfall: sites receiving 100 to 200 cm y^{-1} of snow (Sites 1–5), sites receiving 200 to 300 cm y^{-1} of snow (Sites 6–8), and sites receiving > 300 cm y^{-1} of snow (Sites 9–12). (C) Distributions of soil organic C concentrations by depth and according to snowfall, as in (B). (D) Distributions of ^{13}C natural abundance in soil organic matter and according to snowfall, as in (B). The lines shown in part (D) represent best-fit linear-log regressions.

organic acids (and any metals they might have complexed) to the deep subsoil, where they are retained in C-rich Bhs and Bs horizons (Schaetzl and Rothstein 2016).

Litter in snowbelt areas also stays wetter longer into spring, which is the main fire season in the Great Lakes area (Henne, Hu, and Cleland 2007). Thus, the litter layer is burned less frequently in snowbelt areas, maintaining the source of organic acids and, hence, potentially enhancing soil development. Growth and reproduction of mesic, fire-intolerant species such as sugar maple, beech, basswood, and yellow birch are also promoted in this type of ecosystem. In summary, in the snowbelt areas, where soils are most strongly developed, fire has traditionally been less prevalent and, hence, litter is thicker and the production of organic acids is greater. Due to the thick snowpacks,

soil frost is less likely, enhancing soil permeability during snowmelt. Thus, spring snowmelt percolation events are larger and longer, leading to greater soil water storage and, ultimately, enhanced ecosystem productivity.

Soil Carbon Storage across the Transect

As hypothesized, soil C stocks increased with increasing soil development, east to west across the transect (Figure 8). They ranged from a low of 3.9 kg C/m^{-2} at Site 3 to a high of 9.0 kg C/m^{-2} at Site 10 within the snowbelt. Although the general pattern of increasing C stocks from east to west was clearly evident, a few sites appeared to deviate from the overall trend. In areas outside of the snow belt, to the east,

Sites 1 and 5 had larger total C stocks than any of the surrounding sites, and in both cases these higher stocks were driven by higher contents of C in the B horizon (Figure 8C). Higher B horizon C contents at Sites 1 and 5 were not associated with higher concentrations of Fe and Al hydrous oxides (Figure 5B), nor were they associated with greater silt and clay contents (data not shown); therefore, it is unclear what might explain these elevated C stocks, other than natural landscape variability. Site 10 had an A horizon that was thicker and had higher C concentrations than soils at the other snowbelt sites but had O and B horizon C contents similar to soils at Sites 9 and 11. It is also important to note that the data shown in Figure 8 underestimate total profile C contents for Sites 7, 11, and especially 12, because those profiles extended below the 1-m limit of sampling.

The 50 mg C/ha^{-1} change in soil C storage we observed across this climosequence is approximately the same magnitude as the difference expected in C storage for above-ground biomass. Zak and Pregitzer (1990) found that mature sugar maple–dominated forests in snowbelt areas of northwestern Lower Michigan stored 90 to 100 mg C/ha^{-1} in above-ground biomass. In contrast, Rothstein, Yermakov, and Buell (2004), working in the area at the eastern end of our transect, found that mature jack pine forests store at most 50 mg C/ha^{-1} in above-ground biomass. This large difference in soil C storage is noteworthy because parent material was held constant across the transect. Soil parent material properties, particularly geochemistry and soil texture, are thought to be major drivers of the capacity of soils to store organic carbon (Parton et al.

1987; Six et al. 2002; Heckman et al. 2009; McFarlane et al. 2013), but our work shows that climate and vegetation factors can lead to a greater than twofold difference in C storage for soils, even on similar parent materials. These findings concur with other recent studies where vegetation and climate factors were found to be much stronger predictors of soil C stocks than geochemical properties of the parent material (De Vos et al. 2015; Johnson, Xing, and Scatena 2015).

Our hypothesis that soil C storage increases with increasing snowfall was based on the idea that illuvial transport of Fe, Al, and DOC is greater during snowmelt periods (Schaetzl and Rothstein 2016). Ultimately, this would build larger organic C stocks in the B horizon over time for soils in snowbelt areas. The importance of illuvial accumulations of Fe- and Al-humus complexes for deep soil C storage is validated by the strong relationship between pyrophosphate-extractable Fe and Al (Fe$_p$ + Al$_p$) and soil C concentrations in B horizon soil samples across the gradient (SOC(percent) = 2.087 * (Fe$_p$ + Al$_p$) + 0.037; R^2 = 0.714; see Figure 9A). Distributions of Fe$_p$ + Al$_p$ with depth also change predictably across the gradient (Figure 9B). At sites in the east, where snowfall is <200 cm/y^{-1}, the highest Fe$_p$ + Al$_p$ concentrations occur at around 20 cm and then decline rapidly with depth. As annual snowfall totals increase, however, peak concentrations of Fe$_p$ + Al$_p$ occur deeper in the soil and then decline more gradually with depth (Figure 9B). Depth gradients in total soil organic carbon (SOC) are also consistent with the mechanism of increasing illuvial accumulation of C with increasing snowfall. Note that subsoil SOC concentrations are higher in the snowbelt sites (>300 cm annual snowfall), and at these sites these data show slow declines with depth (Figure 9C).

In an attempt to better evaluate the importance of hydrologic transport and cycling of surface-derived DOC vis-à-vis deep soil C storage, we examined depth gradients of ^{13}C natural abundance across the transect. Soil ^{13}C contents typically become enriched with depth, which is thought to result from kinetic fractionation against ^{13}C during decomposition (Wynn, Harden, and Fries 2006) or increased contributions of ^{13}C-enriched microbial C (Boström, Comstedt, and Ekblad 2007). Thus, ^{13}C-enriched C at depth is older, more recalcitrant, and primarily of microbial origin, compared to ^{13}C-depleted carbon in O horizons; C in O horizons is more representative of relatively modern, recent plant litter. Because DOC in O horizons has a

Figure 10. Ecosystem interconnections and feedbacks in northern Lower Michigan, as informed by data from this study. A key feedback is shown in italics.

depleted ^{13}C signature (Sanderman, Baldock, and Amundson 2008; Kaiser and Kalbitz 2012), we reasoned that the decline in ^{13}C values in these soils would be gradual, due to enhanced snowmelt-driven percolation of surface-derived C.

Theory suggests that soils in snowbelt areas experience deeper and more frequent percolation, driving soluble compounds, including SOC, deeper into illuvial horizons. This theory is clearly supported by the ^{13}C data (Figure 9). Soils in the snowbelt have more depleted SO[13]C values at depth relative to those farther east (Figure 9D), which receive less snow and more frequently lose much of their O horizon C to fire. The key takeaway from these data is that C is translocated to greater depths in the snowbelt, as compared to sites to the east. Because the ^{13}C depth trends change in accordance with snowfall (Figure 9D), snowmelt and deep percolation appear to be major drivers of rapid C cycling in these soils. This finding supports existing podzolization theory (Schaetzl and Isard 1991, 1996; Schaetzl, Luehmann, and Rothstein 2015; Schaetzl and Rothstein 2016) by providing evidence of the deep percolation of "fresh" C in snowbelt soils, whereas soils formed under lower snowfall and more frequent fire regimes are dominated by older, microbial-derived C and have less C overall.

Ecological Feedbacks and Thresholds

Using the information discussed already, we developed a flowchart for the soil and forest ecosystems in northern Lower Michigan (Figure 10), where conditions on uplands favor podzolization on sandy parent materials (Schaetzl and Isard 1991, 1996; Schaetzl 2002). These conditions, along with topography, affect soil development by affecting (1) fire frequencies (Mokma and Vance 1989; Cleland

et al. 2004) and (2) leaching and deep percolation during snowmelt. Key to this system is the feedback that leads to the codevelopment of northern hardwood ecosystems on Spodosols.

We interpret feedbacks within this soil–vegetation system as follows (Figure 10). Fire leads to thinner litter layers, particularly in the east, where jack pine barrens were common in presettlement times (Table 2; Figure 3B) and where such forests continue to dominate the modern-day landscape. Thinner litter layers lead to diminished soil development (and lower C stocks) because podzolization is driven by soluble C derived largely from the litter. Our research on podzolization in soils from the eastern Upper Peninsula (UP) of Michigan, based on soil solution data recovered in situ, has shown the importance of autumn rains and spring snowmelt to podzolization and to the processes that translocate C to the lower profile (Schaetzl, Luehmann, and Rothstein 2015; Schaetzl and Rothstein 2016). Rains strip labile C from fresh litter and facilitate a pulse of C into the mineral soil in late autumn and early winter. Autumn precipitation totals are slightly higher in the snowbelt than at sites farther east. As a result, a stronger but more temporally compressed pulse of C into the mineral soil occurs during snowmelt (Schaetzl and Isard 1991). This C has been largely stripped from litter that has undergone decomposition beneath the snowpack. Soluble C, translocated in percolating water, complexes with Fe and Al ions that have been released through weathering, rendering them mobile in solution and facilitating their translocation to the lower profile. B horizons become enriched in C, Fe, and Al. E horizons, impoverished in these compounds, develop above. This suite of processes is the essence of podzolization (Franzmeier and Whiteside 1963; DeConinck 1980; Evans 1980; Buurman and van Reeuwijk 1984; Sauer et al.
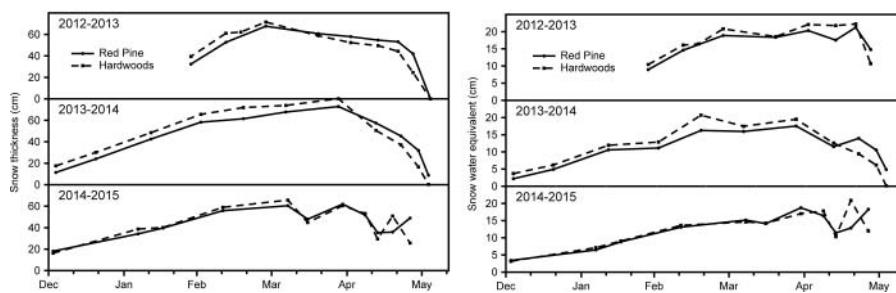
Figure 11. Comparative data on mean snowpack thickness and snow-water equivalents for six forest sites in the Upper Peninsula of Michigan for the winters of 2012 through 2015. Shown are values for three sites in pine and three in hardwoods.

2007; Sanborn, Lamontagne, and Hendershot 2011; Schaetzl and Rothstein 2016).

In sum, thinner litter layers lead to weaker soil development, both because there is less C in the litter to translocate into the mineral soil and because soils with less organic matter foster less productive ecosystems; that is, a feedback (Figure 10). In essence, less developed soils provide a feedback for the above-ground ecosystem, as they tend to support coniferous communities that have lower above-ground biomass and productivity than the northern hardwood forests on the western margins of the transect (e.g., Grigal and Ohmann 1992). In the west, soils have more organic matter at the surface and at depth (Figure 8) and thus are capable of retaining more water and nutrients, leading to increased ecosystem productivity and, in turn, greater C production and cycling (Figure 9).

The rapid rate of change in soil development within the western third of the transect (Figures 4, 7) provides additional insight into other factors at play within this soil system. In the past, such changes have been ascribed primarily to rapidly increasing amounts of snowfall and thicker snowpacks, which lead to enhanced snowmelt infiltration (Schaetzl and Isard 1991, 1996). Data gleaned from research in the UP, however, show that other factors are also in play. In the UP, we have been monitoring snowpack thicknesses and sampling soil water at six research sites, three under red pine and three under northern hardwoods (Schaetzl, Luehmann, and Rothstein 2015). Like previous research has shown (Gelfan, Pomeroy, and Kuchment 2004; Mahat and Tarboton 2013), less snow reaches the ground under the conifers, due to increased canopy interception (Figure 11). Indeed, for the period leading up to snowmelt, snowpacks are 93 percent as thick and have only about 90 percent as much snow–water equivalent (SWE), on average. Despite being thicker, snowpacks under hardwoods melt more rapidly than beneath the dense conifer canopies (Figure 11). Thus, as soils at western snowbelt sites become better developed and as ecosystems become more productive (more hardwoods), snowpacks might become thicker and the pulse of snowmelt water might become larger and more temporally contracted. Theory states that a shorter, more intense pulse of snowmelt water drives C to greater depths, where it is less likely to decompose. ^{13}C data for the snowbelt soils support this conclusion (Figure 9C, 9D).

Historical Aspects of the Soil–Vegetation System

The importance of the snowbelt to this system is evident, but it might have only been present for half the time that soils have been developing in this region. Indeed, the comparatively short length of time that this soil–vegetation feedback system has been operating, relative to the geologic age of the landscapes (Table 1), makes the soil–ecosystem linkages particularly intriguing.

In a key article, Henne and Hu (2010) examined oxygen isotopes in sediment from two northern Lower Michigan lakes, one within the snowbelt ($\approx$19 km east of our Site 12) and the other outside the snowbelt ($\approx$13 km north of our Site 2). Currently, groundwater inflows to the lake within the snowbelt are depleted in ^{18}O by 2.3 percent, relative to the lake outside of the snowbelt, because snowfall is depleted in ^{18}O, relative to rainfall (Machavaram and Krishnamurthy 1992; Delcourt et al. 2002).

To determine when the lake effect snowbelt became established, Henne and Hu (2010) compared ^{18}O profiles from calcite in lake bottom sediment spanning the past 11,500 years. Sediment from the eastern lake (outside the snowbelt) became enriched in ^{18}O by the early Holocene, coincident with ^{18}O-depletion of groundwater in snowbelt lakes. Based on these data, they argued that the lake effect snowbelt did not form until about 9,500 cal yr BP, with the largest increase in lake effect snow occurring around and after 7,000 cal yr BP. This finding matches the geological record, which has documented a small, very low-level lake (Lake Chippewa) within the Lake Michigan basin, starting about 11,500 cal yr BP (Hansel et al. 1985; Larson and Schaetzl 2001; Booth, Jackson, and Thompson 2002; Lewis et al. 2007; Kincare and Larson 2009; Lewis 2016). This small lake would have generated little lake effect snowfall. Water levels of Lake Chippewa slowly rose throughout its history, during a period known as the Nipissing Transgression (Booth, Jackson, and Thompson 2002). The lake reached maximum heights (and, hence, maximum lake areal expanse) between 6,300 and 4,500 cal yr BP (Thompson and Baedke 1997; Booth, Jackson, and Thompson 2002). Thus, a significant lake effect snowbelt could only have been established later, after the lake became larger and wider.

Adding to the timing of snowbelt development was a climatic trend toward increasingly mesic conditions that began between 4,000 and 6,000 years ago, which increased sharply in recent millennia at locations within

lake effect snowbelts (Davis et al. 2000). This change to increased precipitation might have facilitated the rapid expansion of hemlock across the study area between 7,000 and 5,500 cal yr BP, coincident with a decline in $\delta^{18}O$ values and leading to the establishment of mesic forests on preferred sites by 4,000 years cal yr BP (Davis et al. 1986; Davis et al. 2000; Booth, Jackson, and Thompson 2002; Jackson and Booth 2002; Brugam, Owen, and Kolesa 2004; Henne 2006). ^{18}O data from lake sediment in the eastern UP suggest that lake effect snowfall there also increased sharply after 3,000 yr BP (Delcourt et al. 2002).

In sum, if the lake effect snowbelt had only been occurring for the past 7,000 years and was strongest during the past few millennia, then the soils we report on might have only diverged morphologically over the past 7,000 years; most of the change might actually have occurred in the past 4,000 years. As shown in Table 1, most of the soils in the study area are between 12,000 and 15,000 years old, suggesting that the lake effect east-to-west "disparity" in climate and (potentially) forest ecosystems might have existed for only about half of the potential soil-forming interval. Thus, the system feedbacks we report on must indeed be quite robust and tightly interconnected to have caused such pedogenic changes over such a short time frame.

Summary and Conclusions

The soil–vegetation system in northern Lower Michigan, as shown in Figure 10, is perhaps best described and evaluated on a geologic timescale. By about 15,000 to 13,000 cal yr BP, the climate had remained cool and precipitation was only slightly lower than modern values (Davis et al. 2000). Forest vegetation, dominated by pine and spruce, was slowly invading the region (Hupy and Yansa 2009). The small size of Lake Chippewa in the Lake Michigan basin precluded any significant amounts of lake effect snowfall across the region, particularly in the northern sections of the lake (northwest of the study transect), where the lake was relatively shallow and narrow (J. A. Clark, Zylstra, and Befus 2007). Thus, the lake effect snowbelt, as we know it today, did not exist (Henne and Hu 2010). These conditions led to general uniformity among the soil-forming factors across the region, suggesting that soils at all twelve sites along the transect were developing similarly but slowly, assisted in part by slowly increasing annual temperatures. Data from Henne and Hu (2010) confirmed that lake effect snowfall began to develop by 9,500 cal yr BP, with the greatest increase of

lake-effect snowfall at ca. 7,000 cal yr BP. By about 7,000 to 6,000 cal yr BP, Lake Chippewa had risen to levels comparable to those of modern Lake Michigan and, thus, the lake effect climate system was fully in place (Hansel et al. 1985; Henne and Hu 2010). Isotopic data from Henne and Hu (2010) also point to a regional shift to moister, snowier winters and perhaps cooler conditions between 7,000 and 4,000 cal yr BP, which led to an expansion of mesic species (Henne 2006) and facilitated rising lake levels at inland sites (Booth, Jackson, and Thompson 2002; Brugam, Owen, and Kolesa 2004). Enhanced regional moisture likely set up a feedback (i.e., a wetter regional climate led to rising Great Lakes levels), which in turn led to a strengthening of the snowbelt. By 4,000 cal yr BP, wintertime precipitation was increasing across the entire region and podzolization processes were accelerating but most rapidly within the snowbelt. Changes in Great Lakes levels and regional climate have been minimal over the past 2,000 to 4,000 years, suggesting that the patterns established in the soil–vegetation system by the mid-Holocene have remained relatively unchanged since that time.

As the snowbelt began to emerge and strengthen during the early to mid-Holocene, several environmental factors might have converged to facilitate podzolization there: (1) declining fire frequencies, which in turn (2) facilitated the expansion of fire-intolerant species such as hemlock, yellow birch, basswood, and sugar maple. The increased dominance of deciduous species in the forests within the snowbelt reduced canopy interception loss of snow, which led to thicker snowpacks with larger SWEs. The more open canopy beneath the hardwoods also facilitated more rapid melting of snowpacks in spring. This trend occurred simultaneously with increased snowfall in the snowbelt due to rising lake levels in the Lake Michigan basin, associated with the Nipissing Transgression, and region-wide trends toward increased precipitation. The increased snowfall and thicker snowpacks in snowbelt areas limited soil freezing and enhanced deep percolation of meltwater in spring, which further facilitated soil development (Schaetzl, Luehmann, and Rothstein 2015; Schaetzl and Rothstein 2016) and drove soil C into the subsoil, where it was more readily sequestered.

Lowered incidence of soil freezing and overall moister soil conditions also tend to favor sugar maple over hemlock (Henne, Hu, and Cleland 2007); hemlock seedlings are the more drought tolerant. Alternatively, sugar maple can respond to moist conditions by growing rapidly when water availability is high (Schreeg, Kobe, and Walters

2005). In short, hemlock is competitively superior on drought-prone soils, whereas sugar maple thrives on soils with abundant early season moisture, such as within the snowbelt. These conditions led to the establishment of northern hardwood stands within the snowbelt, where sugar maple is currently abundant. Nonetheless, these stands retain a hemlock component. The broadleaf + hemlock character of these forests significantly enhances podzolization, as discussed earlier; the hemlock component is important because its litter is highly acidic (Bockheim 1997; Finzi, Van Breemen, and Canham 1998).

In sum, as the snowbelt formed, fire frequencies declined and rates of soil development increased. The better developed soils, with greater and deeper C stocks, promoted ecosystem productivity and ultimately led to increased representation of hardwoods in the canopy. This in turn led to (1) thicker snowpacks, which (2) stored more water over winter, which then (3) promoted the feedback toward better soil development and increased C sequestration, at the same time (4) acting to reduce fire frequencies.

Acknowledgments

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