Journal of Ecology 2007
95, 517–529

Lake-effect snow as the dominant control of mesic-forest distribution in Michigan, USA

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Summary

1 Recent studies demonstrated the sensitivity of northern forest ecosystems to changes in the amount and duration of snow cover at annual to decadal time scales. However, the consequences of snowfall variability remain uncertain for ecological variables operating at longer time scales, especially the distributions of forest communities.

2 The Great Lakes region of North America offers a unique setting to examine the long-term effects of variable snowfall on forest communities. Lake-effect snow produces a three-fold gradient in annual snowfall over tens of kilometres, and dramatic edaphic variations occur among landform types resulting from Quaternary glaciations. We tested the hypothesis that these factors interact to control the distributions of mesic (dominated by *Acer saccharum*, *Tsuga canadensis* and *Fagus grandifolia*) and xeric forests (dominated by *Pinus* and *Quercus* spp.) in northern Lower Michigan.

3 We compiled pre-European-settlement vegetation data and overlaid these data with records of climate, water balance and soil, onto Landtype Association polygons in a geographical information system. We then used multivariate adaptive regression splines to model the abundance of mesic vegetation in relation to environmental controls.

4 Snowfall is the most predictive among five variables retained by our model, and it affects model performance 29% more than soil texture, the second most important variable. The abundance of mesic trees is high on fine-textured soils regardless of snowfall, but it increases with snowfall on coarse-textured substrates. Lake-effect snowfall also determines the species composition within mesic forests. The weighted importance of *A. saccharum* is significantly greater than of *T. canadensis* or *F. grandifolia* within the lake-effect snowbelt, whereas *T. canadensis* is more plentiful outside the snowbelt. These patterns are probably driven by the influence of snowfall on soil moisture, nutrient availability and fire return intervals.

5 Our results imply that a key factor dictating the spatio-temporal patterns of forest communities in the vast region around the Great Lakes is how the lake-effect snowfall regime responds to global change. Snowfall reductions will probably cause a major decrease in the abundance of ecologically and economically important species, such as *A. saccharum*.

Key-words: lake-effect snow, landscape ecosystems, MARS, sugar maple, winter ecology

Journal of Ecology (2007) **95**, 517–529
doi: 10.1111/j.1365-2745.2007.01220.x

Introduction

Ecological processes that control the function and structure of northern temperate ecosystems are sensitive to variations in the amount and duration of snow cover. For example, deep (> 20 cm), persistent snowpacks insulate soils, prevent freeze–thaw cycles and promote podzolization (Hardy *et al*. 2001; Schaetzl 2002; Decker *et al*. 2003). In snow-insulated soils, respiration is stimulated by elevated microbial activity and by reduced microbial and fine-root mortality (Tierney

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et al. 2003; Schimel *et al*. 2004; Monson *et al*. 2006). In the absence of snowpacks, soil freezing increases the mobilization and leaching of nitrate, contributing to soil acidification (Fitzhugh *et al*. 2003a,b). Snowpacks also provide critical recharge to plant-available water deep in the soil profile, thereby increasing ecosystem productivity especially where growing-season moisture is limiting (Chimner & Welker 2005; Grippa *et al*. 2005). However, the long-term consequences of snowfall variability for specific ecological variables (e.g. vegetational distributions) remain uncertain because of the complex interactions between snowfall and other factors affecting ecosystem dynamics at local to regional scales.

In the Great Lakes region of North America, snowfall varies sharply on the scale of tens of kilometres because of the occurrence of lake-effect snow downwind of the Great Lakes (Norton & Bolsenga 1993; Scott & Huff 1996). Underlying the pronounced snowfall gradient are dramatic geomorphological and edaphic variations resulting from Pleistocene glaciation. Adjacent landform types often support functionally and structurally different forest communities with separate successional pathways (Host *et al*. 1987; Host & Pregitzer 1992). For example, when compared with nearby outwash features, morainal landforms generally support forest ecosystems with a higher abundance of mesic plant species (e.g. *Acer saccharum* Marsh.) in all age classes, greater primary productivity, greater nutrient availability and longer fire return intervals (Host *et al*. 1988; Zak *et al*. 1989; Cleland *et al*. 2004). In addition, vegetational and edaphic responses to long-term climatic change in the region vary greatly among different landforms (Brubaker 1975; Ewing 2002). Thus, the Great Lakes region provides a unique opportunity to examine the long-term interactive effects of snowfall and geological substrate upon forest communities.

In this paper we examine the relationship between the abundance of mesic tree species and lake-effect snow on a heterogeneous landscape. We hypothesize (i) that the abundance of mesic species increases with annual snowfall and (ii) that the influence of snowfall on the abundance of mesic vegetation is moderated by geological substrate. We test these hypotheses in northern Lower Michigan (Fig. 1), an area that allows us to compare the abundance of mesic vegetation among repeatable landscape units over a snowfall gradient. Within this area we overlay a suite of ecological factors in a geographical information system (GIS) and model their importance as predictors of mesic-species abundance.

Methods

STUDY AREA

Our analyses were focused on a 1.3 million ha transect in northern Lower Michigan (Fig. 1). We chose the area for its sharp east–west gradient in average annual snowfall, variable glacial landforms and diverse upland forest communities (Albert 1995).

We assume that our entire study area experiences similar synoptic-scale circulation patterns and that climatic variations within the study area result from mesoscale interactions with the Great Lakes (Braham & Dungey 1984; Scott & Huff 1996). For example, extratropical cyclones often deliver copious snowfall to Michigan, and although such events have marked interannual variation, their effect is equal across the entire transect. By contrast, lake-effect moderation of cold continental air masses consistently produces abundant snowfall only in the lee of the Great Lakes (Fig. 1) (Braham & Dungey 1984; Norton & Bolsenga 1993). Lake-effect snow (or rain if temperature is > 0 °C) is common within a ‘snowbelt’, the area located within approximately 80 km of the Great Lakes shorelines (Scott & Huff 1996). Lake-effect storms often develop without antecedent moisture when synoptic-scale circulation would lead to clear and dry conditions in the absence of lake moderation (Ellis & Leathers 1996). The heaviest snowfall often occurs some distance inland, especially in areas such as north-west Lower Michigan where orographic uplift enhances snowfall production (Stromen & Harman 1978; Hjelmfelt 1992) (Fig. 1).

Mean annual precipitation ranges from 72 to 92 cm across our transect, and it is most abundant within the snowbelt (Daly & Taylor 2000). Snowfall accounts for much of the spatial variability, but lake-effect rain that occurs mainly during the autumn months also contributes to this difference (Miner & Fritsch 1997). By contrast, summer rain tends to dampen this pattern. During summer months, when the atmosphere is warmer than the lake surface, the Great Lakes stabilize overlying air masses, reducing convective precipitation near the shoreline (Scott & Huff 1996).

The Great Lakes also moderate the temperature of the study area year-round, and the strongest influence occurs when the lakes are warmer than the atmosphere (Scott & Huff 1996). Mean annual temperature ranges from 4.7 to 7.8 °C across our study transect. The most continental conditions (largest annual variation) occur in the interior of the transect, the most moderate along the Lake Michigan shoreline, and a strong gradient exists ~25–50 km inland (Scott & Huff 1996). Mean temperatures remain below 0 °C from December through March throughout the study area (Daly & Taylor 2000). However, periods with temperatures above freezing are common, and snowpacks are often of sufficient depth to persist during winter thaws within but not outside the snowbelt (Schaetzl 2002). For example, the weather stations at Gaylord (within snowbelt) and Mio (outside snowbelt) (Fig. 1) experience similar winter temperatures (January mean 1961–90 = –8.2 °C and –8.5 °C, respectively). However, during the same period, Gaylord averaged 98 days per winter with a snow depth of > 20 cm, while Mio averaged only 55 days (http://www.ncdc.noaa.gov).

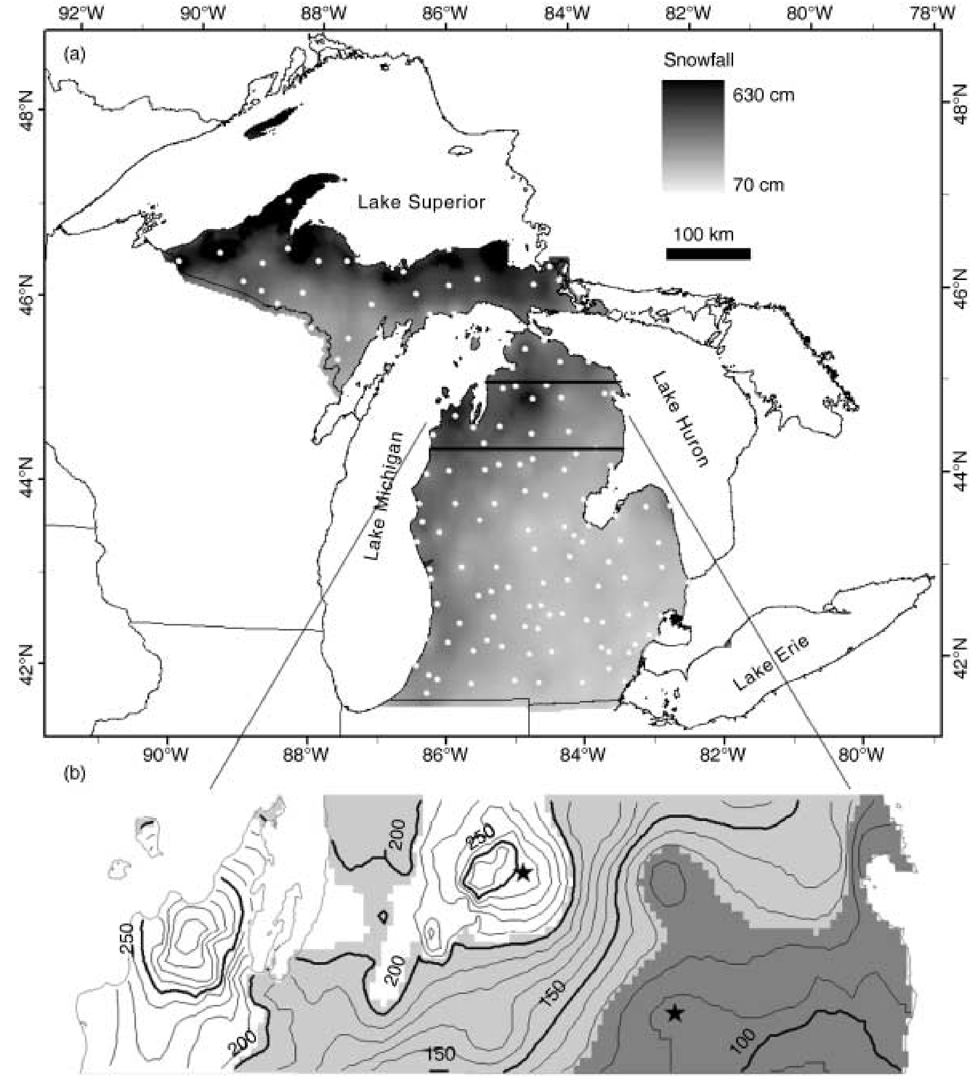

Fig. 1 (a) Western Great Lakes region and average annual snowfall in Michigan. Dark lines outline study area, white dots denote National Weather Service Cooperative stations used in snowfall interpolation (Daly & Taylor 2000). (b) Average annual snowfall (cm) in study area during months with an average temperature < 0 °C (December–March); stars denote weather stations at Gaylord (snowbelt) and Mio (outside snowbelt).

Repeated glacial advances and retreats during the Pleistocene created diverse landforms in northern Lower Michigan (Blewett & Winters 1995; Schaetzl *et al.* 2000; Schaetzl & Welsenborn 2004). Glacial drift underlying the region is generally very thick (up to 300 m) and sandy (Rieck & Winters 1993). Landform types include glacial outwash, terminal and ground moraines, ice-contact terrain, and glacial lake plains (Fig. 2a; Leverett & Taylor 1915; Albert 1995; Corner *et al.* 1999).

Upland forest communities exhibit marked variation in ecological characteristics (e.g. species composition, productivity) at the scale of tens of kilometres within our study area (Host *et al.* 1988; Zak *et al.* 1989; Host & Pregitzer 1992). On the most mesic sites, forest communities are characterized by the high abundance of sugar maple, American beech (*Fagus grandifolia* Ehrh.) and eastern hemlock (*Tsuga canadensis* L.). Red pine (*Pinus resinosa* Ait.), jack pine (*P. banksiana* Lamb.) and northern pin oak (*Quercus ellipsoidalis* E.J. Hill) dominate the most xeric communities, whereas white pine (*P. strobus* L.) and northern red oak (*Q. rubra* L.) are typical of intermediate sites (Albert 1995). Early-successional species (e.g. *Populus* spp.) are abundant across the region, a result of extensive 19th-century land clearing and subsequent fires (Whitney 1987).

LANDSCAPE CLASSIFICATION AND IDENTIFICATION OF THE STUDY UNIT

We obtained data of soil attributes and climatic variables thought to explain the distribution of forest communities in Michigan (Denton & Barnes 1987; Iverson & Prasad 1998). These data and a record of pre-European-settlement vegetation were overlaid onto our chosen unit of comparison, landtype associations (LTAs) (Corner *et al.* 1999), for modelling the abundance of mesic tree species. LTAs are based on hierarchical ecosystem classification that has been used extensively in the

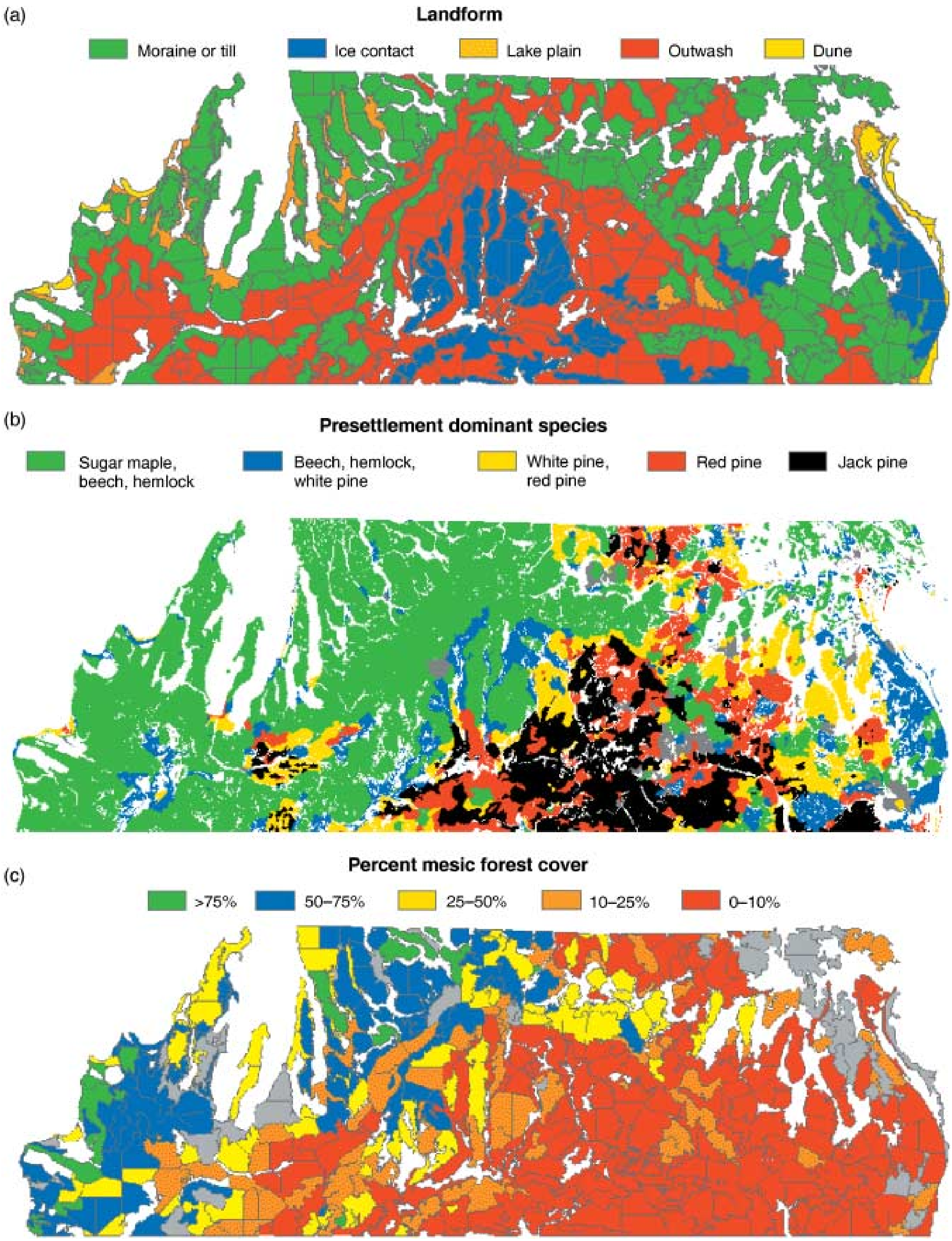

Fig. 2 (a) General landform types in the study area. Moraine and till landforms occupy 45% of the study area, outwash 27%, ice contact 23%, lake plain 4% and dunes 1%. (b) Qualitative description of upland forest communities around 1860 (Comer *et al*. 1995). Sugar maple, beech, hemlock communities occupy 53% of the study area; beech, hemlock, white pine 11%; white pine, red pine 11%, red pine 11%, and jack pine 14%. Other upland forest types (e.g. aspen communities) are indicated in grey and occupy 2% of the study area. Wetland communities occupy 270 000 ha in this transect of northern Lower Michigan, but are not included in the study area. (c) Percentage of LTA occupied by northern hardwood forest cover type (i.e. sugar maple, beech, hemlock communities) *c*. 2000 (adapted from MDNR 2001). Grey areas have less than 25% forest cover. (d) Quantification of abundance of mesic tree species around 1860 using a mesic importance value (MIV), (e) MIV predicted by MARS model and (f) clusters of high and low MIV with statistical significance ($P < 0.05$) determined using Moran's *I*.

Lake States region for the delineation and comparison of repeatable landscape units (e.g. Barnes *et al*. 1982; Albert 1995). The LTA data set for northern Lower Michigan was developed by grouping similar landtypes on the basis of landform, lake density, topography, soil texture and soil drainage. Because separation of LTAs relies upon these abiotic factors, rather than pre-settlement vegetation or vegetation potential (Cleland *et al*. 2004), LTAs provide a useful unit for evaluating the relationships between snowfall and forest composition on

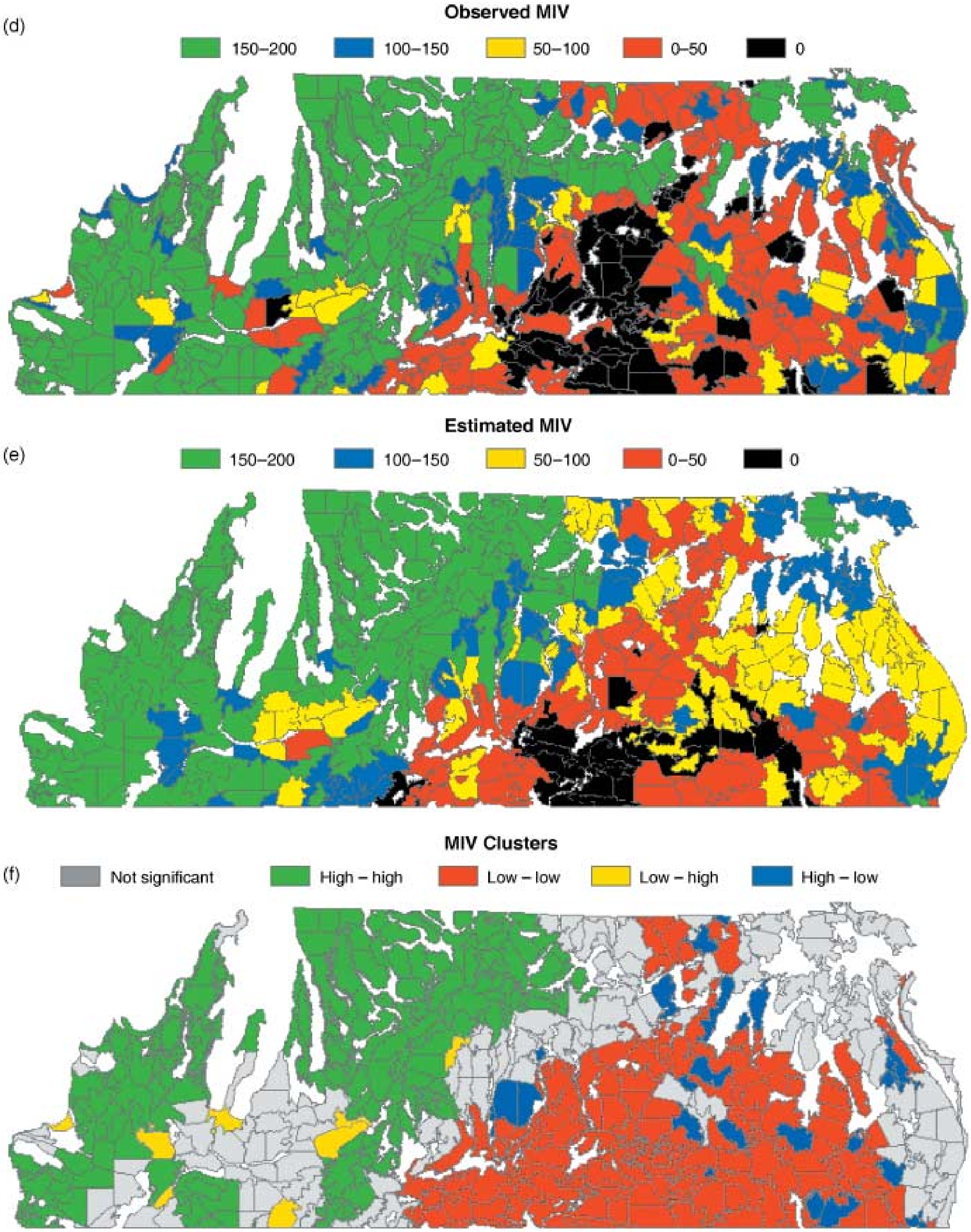

Fig. 2 *continued*

similar substrates. Although LTAs were delineated with the goal of attaining similar edaphic conditions, a large LTA polygon can contain considerable variation. Therefore, we divided large (> 50 000-ha) polygons on the basis of topography prior to associating soil attributes with LTAs. In addition, because large LTA polygons often extend over significant climatic gradients, we further divided long and/or large (> 7000 ha) polygons near their centre point prior to overlaying climatic and vegetational attributes. However, most LTAs are < 2000 ha and did not require subdivision.

CLIMATIC FACTORS

We obtained gridded normals of precipitation, snowfall and temperature for the period 1961–90 that were generated by the PRISM climate mapping project (Daly *et al.* 2000). PRISM is a regression model that incorporates the influences of elevation and large water bodies. These data were interpolated from weather stations to a 2.5′ resolution and then smoothed to a 1.25′ (~2 km^2) grid. Snowfall estimates are based on interpolated depth of freshly fallen snow (Daly *et al.*

2000). We focused our analyses on snowfall that contributes to the formation of snowpacks by including only mean snowfall during months with an average temperature of < 0 °C. For each LTA polygon, we assigned the average value of the PRISM grids it intersects by using the join function in ArcMap 9.0 (ESRI Inc. 2004). We estimated potential evapotranspiration (PET) and actual evapotranspiration (AET) using monthly mean temperature, precipitation and soil-available water capacity as inputs to a water balance model (Willmott *et al*. 1985; Gavin & Hu 2005).

SOIL FACTORS

We assigned to each LTA polygon soil characteristics based on SSURGO digital soil data bases (http://soildatamart.nrcs.usda.gov). Because these county-level soil surveys were undertaken at varying intensity over different time periods, unrealistic differences exist among survey areas. However, by associating soil variables with LTA polygons instead of political boundaries, we reduced the effect of this problem. For each SSURGO polygon, we calculated an average value for the soil variables weighted by depth (upper 150 cm) and area (percentage composition of soil type). To focus exclusively on upland forest communities, we excluded hydric soils from our calculations. We created a raster coverage of the study area with 1-ha grid cells for each variable, and used the spatial analysis zonal statistics function in ArcMap 9.0 (ESRI Inc. 2004) to generate a spatially weighted average for each LTA polygon. SSURGO soils maps were available for all but one (Benzie County) of the 12 counties in the study area. Where polygons within Benzie County extended significantly into adjacent counties, we assigned the attributes of the adjacent county to the entire polygon. For those LTA polygons entirely or nearly entirely within Benzie County, we assigned the soil variables of the nearest similar LTA in an adjacent county.

CLASSIFICATION OF FOREST COMMUNITIES

We evaluated the importance of mesic trees within each LTA using ArcInfo point coverages developed from General Land Office (GLO) surveyor records of line-tree data (D.T. Cleland, unpublished data). This data set provides the location, diameter and species of 'line trees' that were encountered along a grid of section lines delineated by 19th-century surveyors (Table 1). Line trees were recorded separately from the witness trees established at the corners where section lines met and at halfway points along the 1.6-km section lines. Whereas surveyors received instructions to select witness trees that would serve as long-term markers, no such limitations were associated with line trees. Therefore, line-tree data are not prone to biases in species and diameter that are inherent to witness trees, and provide the best available record of species composition and diameter distributions of pre-European-settlement forests in northern Lower Michigan. The GLO tree-line data set also holds distinct advantages over modern forest cover data sets available for northern Lower Michigan. For example, the line-tree record has broader areal coverage than modern mensurational data (e.g. Forest Inventory and Analysis data), and includes landtypes that largely lack forest cover today (e.g. abandoned and extant agricultural lands on morainal landforms). Line-tree data also provide tree species distribution and abundance information not available from LandSat imagery.

Table 1 Excerpt transcribed from GLO surveyor notes. Surveyors recorded details regarding (1) timber, soils and ecosystem type; (2) the location, species and diameter of line trees (indicated in bold type); and (3) established witness trees at corners where section lines met, and halfway points along section lines. Georeferenced line-tree data were used to calculate a mesic importance value for each landtype association polygon

	Town 14 North Range 15 West
(1)	79.90 Intersected East boundary 13lks north – Land rolling west of river over sandy soil. Hemlock Pine Beech and Maple – East of River 2nd rate Sugar Beech
	West corrected between sec 25 & 36
(2)	**28.74 sugar 12 inches in diameter**
	39.95 set quarter section west in river
(3)	elm 10 s9w 1.14 lynn 8 s8e 1.16
(2)	**57.87 hemlock 18 inches in diameter**
	79.90 sect cor

Our approach, using pre-settlement vegetation to examine the ecological influence of snowfall, has limitations when applied to present and future conditions. These data provide only a snapshot of vegetation, and they do not necessarily reflect the long-term dynamics of forest ecosystems. For example, a decline in fire recurrence since European settlement has changed the drivers that created the forest mosaic observed by 19th-century surveyors (Leahy & Pregitzer 2003; Cleland *et al*. 2004). However, palaeorecords suggest that the gradient in lake-effect snowfall influenced the distribution of mesic trees long before the historical record, and provide robust evidence for a long-standing relationship between snowfall and mesic forest communities in this region (Davis *et al*. 2000; Delcourt *et al*. 2002; Schaetzl 2002).

Prior to quantifying vegetation for each LTA polygon, we removed species typical of wetlands (e.g. *Thuja occidentalis*) from the line-tree data and separated upland trees into two groups: mesic and other (Barnes & Wagner 1981) (Table 2). We calculated a mesic importance value (MIV; Iverson & Prasad, 1998) for each LTA polygon by overlaying the LTA polygons with line-tree data, and summing the percentage dominance [(number of mesic trees/number of all upland trees) × 100] and relative dominance [(basal area of mesic trees/basal area of all upland trees) × 100] of mesic species. We used MIV as a dependent variable for modelling the

Table 2 Common and scientific names, category (mesic or other) and abundance of trees recorded by GLO surveyors within the study area

Tree	Mesic	Abundance
Sugar maple* (*Acer saccharum*)	yes	7148 (22.9%)
Eastern hemlock (*Tsuga canadensis*)	yes	4883 (15.7%)
American beech (*Fagus grandifolia*)	yes	4836 (15.5%)
Elm (*Ulmus* spp.)	yes	702 (2.2%)
Basswood (*Tilia americana*)	yes	476 (1.5%)
Yellow birch (*Betula alleghaniensis*)	yes	288 (0.9%)
Hop-hornbeam (*Ostrya virginiana*)	yes	124 (0.3%)
White ash (*Fraxinus americana*)	yes	34 (0.1%)
Jack pine (*Pinus banksiana*)	no	3778 (12.1%)
Red pine (*Pinus resinosa*)	no	3250 (10.4%)
White pine (*Pinus strobus*)	no	2446 (7.8%)
Pine (*Pinus* spp.)	no	977 (3.0%)
Aspen (*Populus* spp.)	no	935 (3.0%)
Paper birch† (*Betula papyrifera*)	no	694 (2.2%)
Oak‡ (*Quercus* spp.)	no	508 (1.5%)
Red maple (*Acer rubrum*)	no	38 (0.1%)
Other	no	46 (0.1%)

*Includes trees recorded in GLO notes as 'maple'.
†Includes 'birch and white birch'.
‡Includes 'red oak, white oak, scrub oak, jack oak, bur oak, and oak'.

Table 3 Environmental variables evaluated as predictors of MIV. Key predictor variables included in the final MARS model are indicated in bold type

Precipitation variables
Mean annual snowfall (mm)
July–August precipitation (mm)
Mean annual precipitation (mm)
October–March precipitation (mm)
April–September precipitation (mm)
September–November precipitation (mm)
May–August precipitation (mm)
Water balance and temperature variables
Mean annual PET (cm)
Mean annual AET (cm)
Mean annual AET/PET
July–August AET (cm)
July–August PET (cm)
July–August AET/PET
Mean annual temperature (°C)
Mean temperature coldest month (°C)
Mean minimum temperature coldest month (°C)
Extreme minimum temperature (°C)
Mean temperature warmest month (°C)
Mean maximum temperature warmest month (°C)
Growing degree days (base 5 °C)
Annual mean temperature range (°C)
Annual extreme temperature range (°C)
Soil and topographic variables
Percentage sand
Percent passing sieve number 10 (coarse fragment abundance)
Percentage passing sieve number 4
Percentage passing sieve number 40
Percentage passing sieve number 200
Total available water capacity (cm, to 150 cm)
Soil erodibility factor
Percentage clay
Soil drainage class
Mean slope
Elevation (m)

distribution of mesic forest communities over the gradient in lake-effect snow. To evaluate how the distribution of individual mesic tree species relates to the gradient in snowfall, we calculated importance values for each of the three dominant mesic species in the region: sugar maple, beech and hemlock. Polygons with fewer than five upland trees were excluded from this analysis. We verified our quantification of mesic importance by comparison with a qualitative classification of pre-settlement forest communities (Fig. 2b; Comer *et al*. 1995). In addition, because present and future vegetational distributions are also contingent upon interactions with anthropogenic disturbances, we validated the relevance of our classification by comparison to vegetation of *c*. 2000 (Fig. 2c). We constructed this vegetation layer by overlaying the LTA polygons with a landcover classification developed from LandSat imagery and calculating the percentage of forest cover inside each polygon classified as northern hardwood association (MDNR 2001).

MODEL

We expected that the relationships between the environmental variables and forest communities would vary across the snowfall gradient in our study area. Therefore, we developed a model flexible enough to identify changes in the influence of each variable on the abundance of mesic vegetation. Specifically, we applied multivariate adaptive regression splines (MARS) (Friedman 1991) using the software package MARS 2.0 (http://www.salford-systems.com). MARS is a non-parametric regression procedure that uses local adaptation to partition highly dimensional data. A MARS model splits the training data into sections termed basis functions. Each function is locally responsive because the slope of the regression can change within a single input variable, and between input variables (Friedman 1991). The complexity of the final model is minimized by applying a penalty to each basis function added to the model.

Recent modelling studies have demonstrated the utility of MARS for predicting forest characteristics (e.g. biomass per acre, percentage cover) (Moisen & Frescino 2002), plant distributions (Munoz & Felicisimo 2004) and soil temperatures (Yang *et al*. 2004). Comparisons of various techniques commonly used for vegetational modelling (e.g. generalized linear models, classification and regression trees) indicated superior performance and greater interpretability of MARS for highly dimensional data (Moisen & Frescino 2002; Munoz & Felicisimo 2004).

We evaluated 33 environmental variables as predictors of MIV in exploratory MARS runs (Table 3).

Table 4 MARS importance values and ANOVA decomposition

Variable(s)	Importance value	SD	Cost of omission	No. of basis functions
Snow	1.00	0.66	0.34	2
Percentage sand	0.71	0.31	0.23	1
Snow × percentage sand	NA	0.27	0.21	3
PET	0.21	0.22	0.19	2
July–August precipitation	0.10	0.12	0.17	1
Coarse fragment abundance	0.07	0.10	0.16	1

In the final model, we narrowed the field to five key predictors by dropping variables that did not enter the MARS model on preliminary model runs, and by eliminating highly redundant variables via correlation analysis. For example, although we evaluated several annual and seasonal precipitation variables (e.g. growing season precipitation, annual precipitation), only average snowfall and precipitation during July and August contributed to model performance.

Results

The spatial patterns of MIV are consistent with a previous qualitative classification of the presettlement forest communities in our study area (Fig. 2b,d; Comer *et al*. 1995). This similarity is expected because both are based upon vegetational data recorded by 19th-century surveyors. Nonetheless, this agreement demonstrates that our quantification using LTA polygons captures landscape-level changes in forest communities and thus that LTA is an appropriate unit of comparison. Furthermore, the distribution of LTA polygons with high MIV is consistent with that of modern mesic upland forest communities, although mesic species are less abundant on the modern landscape, and oak- and aspen-dominated forest communities are more prevalent (Fig. 2c; Leahy & Pregitzer 2003). Comer *et al*. (1995) delineated forest communities on the basis of dominant overstorey species. Our LTAs with an MIV > 1.5 correspond to communities classified as beech, sugar maple and yellow birch. LTAs with moderate MIV (1.0–1.5) correspond to communities dominated by beech and hemlock, hemlock and white pine, and hemlock, beech and red maple. LTAs with MIV values of 0.5–1.0 and < 0.5 have similar distributions to communities identified as red pine and white pine, and jack pine and red pine, respectively. Because our classification relies upon the abundance and dominance of mesic species, it misses some variation among the most xeric community types.

The distribution of forest community types exhibits significant spatial autocorrelation ($P = 0.01$, Moran's $I = 0.68$, with 1 = high spatial autocorrelation and −1 = random distribution; Fig. 2f). Communities dominated by mesic species are clustered along the western portion of the transect within the snowbelt. In this region, polygons with MIV > 1.5 occur on every category of LTA, and polygons with MIV < 1.0 occur only on very coarse-textured substrates. By contrast, outside the snowbelt, polygons with high MIV (> 1.0) occur only on LTAs with fine-textured soils.

Preliminary MARS runs indicated that annual snowfall and percentage sand were the most predictive variables for MIV. We allowed the model to develop an interaction term between these critical variables because we expected that the relationship between soils and MIV would vary with the amount of snowfall. To maximize interpretability of the model, we disallowed interactions among the remaining variables. Our final MARS model for MIV captures the spatial variation in forest communities ($R^2 = 0.75$; Fig. 2e). Among the five variables, annual snowfall has the largest influence on model performance (Table 4). Removing it reduces model performance 29% more than removing percentage sand, the next most important variable. Two basis functions directly relate the influence of annual snowfall to MIV, breaking the data into three regions. Below 127 cm, snowfall does not directly enter the model. Between 127 and 204 cm, snowfall and MIV are positively related. Above 204 cm, the influence on MIV declines but remains positive.

One basis function directly relates percentage sand to MIV. Percentage sand is strongly correlated with several variables related to soil texture, including available water capacity and percentage clay (Pearson correlation coefficient = −0.93 and −0.92, respectively). Soils containing greater than 90% sand (i.e. coarse-textured soils) have a negative influence on MIV, whereas sand abundance does not directly enter the model in LTAs with finer-textured soils. However, soil texture also interacts with snowfall to control MIV (Table 4). When percentage sand is less than 90% and snowfall greater than 127 cm, a decrease in percentage sand or an increase in average snowfall has a positive impact on MIV (Fig. 3). Soils with less than 86% sand have a strong positive influence on MIV at all levels of snowfall abundance, and annual snowfall greater than 204 cm interacts strongly with all soil textures.

Two basis functions divide annual PET into three regions. PET positively correlates with several temperature variables, including growing degree days (0.99), annual average temperature (0.97), average July maximum temperature (0.93) and average January minimum temperature (0.89). It negatively correlates with the annual temperature range (−0.81). An increase in PET has a positive impact on MIV where PET is less than

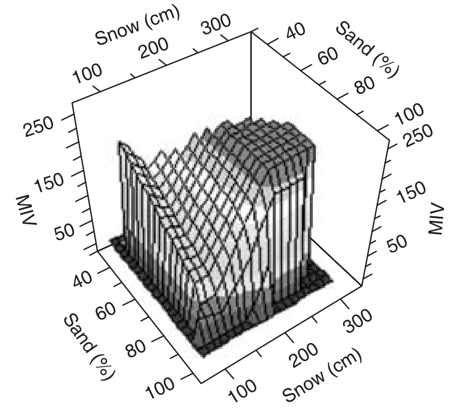

Fig. 3 MARS basis functions for the interaction between annual snowfall and percentage sand.

552 cm (i.e. lowest annual average temperatures). However, where PET is greater than 552 cm, it has a negative impact. Average annual July–August precipitation, the fourth most important variable, has one basis function. Above 15.3 cm, July–August precipitation is negatively related to MIV, and below 15.3 cm, there is no relationship. Percentage of soil passing through a number 10 (2 mm) screen (i.e. coarse fragment abundance), the final variable retained in the model, has one basis function. Low values (typical of moraines) make no contribution to the model, and high values (typical of outwash) have a negative influence on MIV.

On sites dominated by mesic species (MIV > 1.0), the importance of the three dominant mesic forest species (sugar maple, American beech and eastern hemlock) differs among the three snowfall regimes identified by MARS. At low annual snowfall (< 127 cm), the importance values are significantly greater ($P < 0.0001$) for hemlock than for sugar maple and beech and are similar ($P = 0.22$) between the latter two (Fig. 4). At moderate annual snowfall (127–204 cm), sugar maple increases and hemlock declines in importance, and both species are significantly more important than beech ($P = 0.0015$ and $P < 0.0001$, respectively). Hemlock retains a greater mean importance value than sugar maple, although the difference is only marginally significant ($P = 0.07$). At high annual snowfall (> 204 cm), sugar maple is significantly more important than either hemlock or beech ($P < 0.0001$), and hemlock is more important than beech ($P = 0.02$).

Discussion

Our results identify snowfall abundance as the most predictive variable for the occurrence of mesic forest communities within our study area. This finding probably reflects the influence of snowfall on (i) soil moisture availability, (ii) nutrient availability and (iii) fire history. These three factors also control the relative abundance of the dominant species within the mesic forest communities.

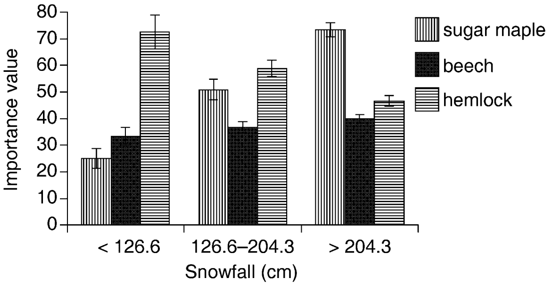

Fig. 4 Importance values of sugar maple, beech and hemlock, under different snowfall regimes in LTA dominated by mesic species (i.e. MIV > 100). Error bars are 1 standard error.

SPATIAL DISTRIBUTION OF MESIC FOREST COMMUNITIES IN RELATION TO LAKE-EFFECT SNOW

Snowfall directly affects the distribution of forest species by changing soil moisture availability. In northern Michigan, the amount of spring soil moisture varies among the three snowfall regimes identified by our MARS model (Figs 1b & 3a) because the average duration of snow cover corresponds to the abundance of lake-effect snow. Where lake-effect snow is rare or absent (i.e. the low snowfall regime), snow cover rarely persists through the winter. In these areas, soils enter the growing season drier, leading to earlier development of water deficits (Hardy *et al.* 2001; Schaetzl 2002). Conversely, where lake-effect snowfall is most abundant, snowpacks most probably persist through the winter to provide ample spring moisture in soils. Thus, increased snowfall in these areas influences moisture availability only slightly. Areas with moderate lake-effect snow (i.e. where snowfall has the largest influence on the MARS model) are most sensitive to changes in snowfall abundance. Elevated snowfall there means an increased probability that snow cover will persist through the winter to provide spring soil moisture.

Early season soil moisture may be especially important for the establishment of mesic tree species. For example, sugar maple and beech saplings have poor growth and high mortality in xeric soils (Caspersen & Kobe 2001; Kobe 2006). These species dominate fine-textured soils throughout the study area, but they are abundant on coarse-textured soils only within the snowbelt. This pattern reflects the fact that fine-textured soils retain moisture during spring and well into the growing season, thus favouring the establishment of mesic vegetation regardless of snowfall. By contrast, coarse-textured soils retain little water, and springtime meltwater from lake-effect snow is critical to the establishment and recruitment of mesic species.

Soil water from snowmelt is a more important constraint on mesic vegetation than summer precipitation. Although modelled water-balance data indicate soil water deficits (i.e. PET > AET) throughout the study area during July and August, especially on coarse-textured soils, the distribution of mesic vegetation does not correspond to the abundance of July and August rain. In fact, mesic vegetation is clustered near the lakeshore where July and August precipitation is lowest. Furthermore, our results reveal that at high values, July–August rainfall negatively influences MIV. This relationship probably reflects the negative correlation between summer and winter precipitation, instead of the effects of July–August precipitation on vegetation *per se*. Lake-effect rain increases annual precipitation in the snowbelt from September to November, and it is possibly an important source of soil moisture. Because snowfall is positively correlated (Pearson correlation coefficient = 0.92) with precipitation in these months, we are unable to separate definitively the influence of autumn precipitation from snowfall in our model. However, lake-effect snow can be retained on the landscape until spring, and thus it is probably more relevant to plant growth than autumn precipitation.

Nutrient availability in relation to snow cover and soil-freezing disturbance may also contribute to the spatial patterns of mesic vegetation across our study transect. Soils at snowbelt sites with deep, persistent snowpacks often remain unfrozen throughout the winter, whereas non-snowbelt sites have thin and ephemeral snowpacks with a greater occurrence of soil-freezing disturbance (Isard & Schaetzl 1998; Schaetzl *et al*. 2005). Soil freezing causes fine-root and microbial mortality, reduces root–soil–microbe interactions, and can lead to increased nitrate leaching (Fitzhugh *et al*. 2003a; Tierney *et al*. 2003; Monson *et al*. 2006). Snow-insulated ecosystems are therefore better able to immobilize and assimilate nitrogen, especially during spring when nutrient availability is highest (Brooks & Williams 1999; Fitzhugh *et al*. 2003b). Mesic species exhibit competitive superiority where soil resources (e.g. mineral nutrients) are abundant and low survivorship where soil nutrients are limiting (Walters & Reich 1997; Schreeg *et al*. 2005). Because persistent snowpacks promote nutrient retention, lake-effect snow favours the establishment and recruitment of mesic vegetation.

Lake-effect snow may also control the frequency and spread of wildfire to affect the composition of plant communities. The trees classified as mesic in this study (e.g. sugar maple, hemlock) are late-successional, fire-intolerant species (Barnes & Wagner 1981). Wildfires in the lake states are most common during two periods, early spring before plants flush out and mid-summer when soil water deficits develop, but the vast majority of wildfires (> 80%) occur during March–May (Simard & Blank 1982; Cardille & Ventura 2001). Snowpacks or meltwater can reduce the flammability of the forest floor during this critical period of the fire season. Thus, fewer spring fires occur in snowbelt areas where snowpacks persist through March and even into April, favouring the dominance of mesic, late-successional species. Furthermore, mesic forest communities, especially those dominated by sugar maple, have a negative reciprocal association with fire because their standing biomass and forest floor have low flammability in comparison with pine- and oak-dominated ecosystems (Cleland *et al*. 2004). Thus, longer fire rotations in the snowbelt favour the establishment of fire-resistant, late-successional mesic species, which in turn further reduce the likelihood of fire.

Fire may be particularly effective at creating and maintaining the spatial autocorrelation of vegetational types (Fig. 2f). Fire regimes in the Great Lakes region vary with physiography and soil texture (Cleland *et al*. 2004; Schulte & Mladenoff 2005). For example, flat, coarse-textured outwash sites tend to support fire-prone communities (e.g. jack pine barrens) that have shorter fire cycles and produce more extensive fires than adjacent finer-textured landforms. Although fire-prone, pine-dominated communities (i.e. low MIV) occur on edaphically restricted landforms throughout the study area, such communities form significant clusters only outside the snowbelt. By contrast, pine forests clustered with mesic forests (i.e. high MIV) and mesic forests clustered with mesic forests occur only within the snowbelt. In the absence of snowpacks, fire can spread readily from the most fire-prone areas (e.g. jack pine barrens on coarse-textured outwash plains) to adjacent landforms. Conversely, fires do not spread far where snowfall is abundant, allowing the establishment of mesic forest clusters.

INTERACTIONS OF DOMINANT MESIC SPECIES IN RELATION TO LAKE-EFFECT SNOW

By moderating soil moisture, nutrient availability and fire history, lake-effect snow affects not only the distribution of mesic forest communities, but also the interactions among the dominant mesic species within these communities (Fig. 4). Although sugar maple, hemlock and beech co-dominate mesic forests, they exhibit different mortality and growth in response to drought and nutrient limitation. In general, hemlock is more tolerant of low soil-resource (e.g. mineral nutrients, water) availability than sugar maple, and beech is of intermediate tolerance. For example, among these species, hemlock seedlings are the most drought-tolerant, and they allocate the greatest proportion of resources to root development (Caspersen & Kobe 2001; Templer & Dawson 2004). Sugar maple has a plastic response to soil conditions, and exhibits rapid growth when water availability is high (Schreeg *et al*. 2005). Therefore, hemlock is competitively superior on drought-prone spring soils, and sugar maple on soils with abundant early season moisture.

Differences in nutrient dynamics may also exist between snowbelt and non-snowbelt areas that contribute to variation in the relative abundance of mesic tree species across our study transect. Of the three dominant mesic species, sugar maple is most susceptible to nitrate and base-cation leaching associated with soil-freezing disturbance (Boutin & Robitaille 1995; Lovett *et al*. 2004; Fujinuma *et al*. 2005; Templer *et al*. 2005). Thus, winter soil insulation by lake-effect snow favours sugar maple.

Because hemlock seedlings have lower mortality than sugar maple or beech in acidic and nutrient-poor soils (Frelich *et al*. 1993; Catovsky & Bazzaz 2002), they are better adapted to frequent soil-freezing disturbance outside the snowbelt. In addition, sugar maple may be more sensitive to physical damage from frost than hemlock or beech. For example, episodic sugar maple decline has been attributed to high root mortality during winters with sparse snow cover (Bauce & Allen 1991; Payette *et al*. 1996).

Fire regimes also affect the relative abundance of sugar maple, beech and hemlock. Although these three species are all sensitive to fire damage, hemlock readily establishes following fire, and historically it was a dominant species on sites with moderate fire rotations (~500 years) (Cleland *et al*. 2004). Thus, shorter fire rotations outside the snowbelt favour the dominance of hemlock over beech and sugar maple on the most mesic sites. However, repeated fire can remove hemlock from the landscape (Leahy & Pregitzer 2003).

Conclusions and implications

Our findings that lake-effect snow is important for mesic vegetation by no means contradict the numerous studies that indicate that vegetational composition and ecological processes (e.g. response to climatic change, successional pathway, N cycling) vary with glacial landforms (Host *et al*. 1987; Zak *et al*. 1989; Ewing 2002). Instead, our results demonstrate that snowfall abundance constrains the influence of landforms on vegetational composition. Fine-textured soils typical of glacial till support mesic vegetation throughout the study area, although mesic species are less abundant under low snowfall even on fertile soils with high available water capacity. Coarse-textured soils typical of glacial outwash support mesic forests only where snowfall is abundant. For example, forests dominated by mesic species on soils with greater than 90% sand covered 170 000 ha in the snowbelt (12% of total study area), but do not exist on such soils outside the snowbelt. However, on the coarsest soils mesic species are rare, and *Pinus* spp. dominate forest communities regardless of snowfall. Thus, snowfall has the largest influence on forest communities developing on soils with intermediate fertility and water-holding capacity, and the edaphic requirements to support mesic forest communities decrease with increasing annual snowfall.

Because of the importance of lake-effect snow for mesic tree species, future plant communities of the Great Lakes region will depend on how the lake-effect snow regime responds to global change. Lake-effect snowfall increased during the 20th century, a possible response to rising average lake-surface temperatures (Burnett *et al*. 2003). However, individual lake-effect snowstorms require favourable (< 0 °C) air temperatures, and snowy years result from below average winter temperatures (Braham & Dungey 1984; Norton & Bolsenga 1993). Therefore, the trend of increasing lake-effect snow can only continue as long as the frequency of winter incursions of frigid arctic air over the Great Lakes remains similar (or increases). General circulation models predict an average increase of 2.7–4.4 °C in winter air temperatures in the Great Lakes region and a reduction in the occurrence of below-freezing days (Kutzbach *et al*. 2005). Such a situation would reduce lake-effect snowfall and increase lake-effect rain (Kunkel *et al*. 2002). Furthermore, higher winter and early spring temperatures would reduce the duration of snow cover. These changes, along with other pervasive human disturbances (e.g. invasive species), can have severe implications for the Upper Great Lakes region where mesic forests on sandy, well-drained soils abound.

Acknowledgements

We thank D. Gavin for the water balance data, and R. Fitzhugh and D. Kristovich for helpful discussion. M. Chipman, G. Clarke, B. Clegg, D. Gavin, A. Henderson, D. Nelson, K. Wolfe and two anonymous referees helped improve earlier drafts of the manuscript. Support came from the University of Illinois Graduate College and Program in Ecology and Evolutionary Biology, and the Centre for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory. The Joint Fire Science Program funded development of the GLO data.

References

Albert, D.A. (1995) *Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification*. Rep. No. Gen. Tech. Rep. NC-178. USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN.

Barnes, B.V., Pregitzer, K.S., Spies, T.A. & Spooner, V.H. (1982) Ecological forest site classification. *Journal of Forestry*, **80**, 493–498.

Barnes, B.V. & Wagner, W.H. (1981) *Michigan Trees*. University of Michigan Press, Ann Arbor.

Bauce, E. & Allen, D.C. (1991) Etiology of a sugar maple decline. *Canadian Journal of Forest Research*, **21**, 686–693.

Blewett, W.L. & Winters, H.A. (1995) The importance of glaciofluvial features within Michigan Port Huron Moraine. *Annals of the Association of American Geographers*, **85**, 306–319.

Boutin, R. & Robitaille, G. (1995) Increased soil nitrate losses under mature sugar maple trees affected by experimentally-induced deep frost. *Canadian Journal of Forest Research*, **25**, 588–602.

Braham, R.R. & Dungey, M.J. (1984) Quantitative estimates of the effect of Lake-Michigan on snowfall. *Journal of Climate and Applied Meteorology*, **23**, 940–949.

Brooks, P.D. & Williams, M.W. (1999) Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. *Hydrological Processes*, **13**, 2177–2190.

Brubaker, L.B. (1975) Postglacial forest patterns associated with till and outwash in North Central Upper Michigan. *Quaternary Research*, **5**, 499–527.

Burnett, A.W., Kirby, M.E., Mullins, H.T. & Patterson, W.P. (2003) Increasing Great Lake-effect snowfall during the twentieth century: a regional response to global warming? *Journal of Climate*, **16**, 3535–3542.

Cardille, J.A. & Ventura, S.J. (2001) Occurrence of wildfire in the northern Great Lakes Region: effects of land cover and land ownership assessed at multiple scales. *International Journal of Wildland Fire*, **10**, 145–154.

Caspersen, J.P. & Kobe, R.K. (2001) Interspecific variation in sapling mortality in relation to growth and soil moisture. *Oikos*, **92**, 160–168.

Catovsky, S. & Bazzaz, F.A. (2002) Feedbacks between canopy composition and seedling regeneration in mixed conifer broad-leaved forests. *Oikos*, **98**, 403–420.

Chimner, R.A. & Welker, J.M. (2005) Ecosystem respiration responses to experimental manipulations of winter and summer precipitation in a Mixedgrass Prairie, WY, USA. *Biogeochemistry*, **73**, 257–270.

Cleland, D.T., Crow, T.R., Saunders, S.C., Dickmann, D.I., Maclean, A.L., Jordan, J.K., Watson, R.L., Sloan, A.M. & Brosofske, K.D. (2004) Characterizing historical and modern fire regimes in Michigan (USA): a landscape ecosystem approach. *Landscape Ecology*, **19**, 311–325.

Comer, P., Albert, D.A., Wells, H.A., Hart, B.L., Raab, J.B., Price, D.L., Karshian, D.M., Corner, R.A., Schuen, D.W., Leibfreid, T.R., Austin, M.B., DeLain, C.J., Prange-Gregory, L., Scrimger, L.J. & Sprtzley, J.G. (1995) *Michigan's Presettlement Vegetation, as Interpreted from the General Land Office surveys 1816–1856*. Michigan Natural Features Inventory, Lansing, MI.

Corner, R.A., Albert, D.A., DeLain, C.J. & Austin, M.B. (1999) *Landtype Associations of Northern Lower Michigan*. Report no 1999-02–1999-07 prepared for the Northern Lower Michigan Ecosystem Management Project. Michigan Natural Features Inventory, Lansing, MI.

Daly, C. & Taylor, G. (2000) *United States Average Monthly or Annual Precipitation, 1961–90*. Spatial Climate Analysis Service, Oregon State University, Corvallis, OR.

Daly, C., Taylor, G.H., Gibson, W.P., Parzybok, T.W., Johnson, G.L. & Pasteris, P.A. (2000) High-quality spatial climate data sets for the United States and beyond. *Transactions of the ASAE*, **43**, 1957–1962.

Davis, M., Douglas, C., Calcote, R., Cole, K.L., Winkler, M.G. & Flakne, R. (2000) Holocene climate in the western Great Lakes national parks and lakeshores: implications for future climate change. *Conservation Biology*, **14**, 968–983.

Decker, K.L.M., Wang, D., Waite, C. & Scherbatskoy, T. (2003) Snow removal and ambient air temperature effects on forest soil temperatures in Northern Vermont. *Soil Science Society of America Journal*, **67**, 1234–1242.

Delcourt, P.A., Nester, P.L., Delcourt, H.R., Mora, C.I. & Orvis, K.H. (2002) Holocene lake-effect precipitation in northern Michigan. *Quaternary Research*, **57**, 225–233.

Denton, S.R. & Barnes, B.V. (1987) Tree species distributions related to climatic patterns in Michigan. *Canadian Journal of Forest Research*, **17**, 613–629.

Ellis, A.W. & Leathers, D.J. (1996) A synoptic climatological approach to the analysis of lake-effect snowfall: potential forecasting applications. *Weather and Forecasting*, **11**, 216–229.

Ewing, H.A. (2002) The influence of substrate on vegetation history and ecosystem development. *Ecology*, **83**, 2766–2781.

Fitzhugh, R.D., Driscoll, C.T., Groffman, P.M., Tierney, G.L., Fahey, T.J. & Hardy, J.P. (2003a) Soil freezing and the acid–base chemistry of soil solutions in a northern hardwood forest. *Soil Science Society of America Journal*, **67**, 1897–1908.

Fitzhugh, R.D., Likens, G.E., Driscoll, C.T., Mitchell, M.J., Groffman, P.M., Fahey, T.J. & Hardy, J.P. (2003b) Role of soil freezing events in interannual patterns of stream chemistry at the Hubbard Brook experimental forest, New Hampshire. *Environmental Science and Technology*, **37**, 1575–1580.

Frelich, L.E., Calcote, R.R., Davis, M.B. & Pastor, J. (1993) Patch formation and maintenance in an old-growth hemlock–hardwood forest. *Ecology*, **74**, 513–527.

Friedman, J.H. (1991) Multivariate adaptive regression splines. *Annals of Statistics*, **19**, 1–67.

Fujinuma, R., Bockheim, J. & Balster, N. (2005) Base-cation cycling by individual tree species in old-growth forests of Upper Michigan, USA. *Biogeochemistry*, **74**, 357–376.

Gavin, D.G. & Hu, F.S. (2005) Bioclimatic modelling using Gaussian mixture distributions and multiscale segmentation. *Global Ecology and Biogeography*, **14**, 491–501.

Grippa, M., Kergoat, L., Le Toan, T., Mognard, N.M., Delbart, N., L'Hermitte, J. & Vicente-Serrano, S.M. (2005) The impact of snow depth and snowmelt on the vegetation variability over central Siberia. *Geophysical Research Letters*, **32**, L21412.

Hardy, J.P., Groffman, P.M., Fitzhugh, R.D., Henry, K.S., Welman, A.T., Demers, J.D., Fahey, T.J., Driscoll, C.T., Tierney, G.L. & Nolan, S. (2001) Snow depth manipulation and its influence on soil frost and water dynamics in a northern hardwood forest. *Biogeochemistry*, **56**, 151–174.

Hjelmfelt, M.R. (1992) Orographic effects in simulated lake-effect snowstorms over Lake-Michigan. *Monthly Weather Review*, **120**, 373–377.

Host, G.E. & Pregitzer, K.S. (1992) Geomorphic influences on ground-flora and overstory composition in upland forests of northwestern Lower Michigan. *Canadian Journal of Forest Research*, **22**, 1547–1555.

Host, G.E., Pregitzer, K.S., Ramm, C.W., Hart, J.B. & Cleland, D.T. (1987) Landform-mediated differences in successional pathways among upland forest ecosystems in northwestern Lower Michigan. *Forest Science*, **33**, 445–457.

Host, G.E., Pregitzer, K.S., Ramm, C.W., Lusch, D.P. & Cleland, D.T. (1988) Variation in overstory biomass among glacial landforms and ecological land units in northwestern Lower Michigan. *Canadian Journal of Forest Research*, **18**, 659–668.

Isard, S.A. & Schaetzl, R.J. (1998) Effects of winter weather conditions on soil freezing in southern Michigan. *Physical Geography*, **19**, 71–94.

Iverson, L.R. & Prasad, A.M. (1998) Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs*, **68**, 465–485.

Kobe, R.K. (2006) Sapling growth as a function of light and landscape-level variation in soil water and foliar nitrogen in northern Michigan. *Oecologia*, **147**, 119–133.

Kunkel, K.E., Westcott, N.E. & Kristovich, D.A.R. (2002) Assessment of potential effects of climate change on heavy lake-effect snowstorms near Lake Erie. *Journal of Great Lakes Research*, **28**, 521–536.

Kutzbach, J.E., Williams, J.W. & Vavrus, S.J. (2005) Simulated 21st century changes in regional water balance of the Great Lakes region and links to changes in global temperature and poleward moisture transport. *Geophysical Research Letters*, **32**, L17707.

Leahy, M.J. & Pregitzer, K.S. (2003) A comparison of presettlement and present-day forests in northeastern lower Michigan. *American Midland Naturalist*, **149**, 71–89.

Leverett, F. & Taylor, F. (1915) *The Pleistocene of Indiana and Michigan and the History of the Great Lakes*. Report no. 53. United States Geological History, Washington, DC.

Lovett, G.M., Weathers, K.C., Arthur, M.A. & Schultz, J.C. (2004) Nitrogen cycling in a northern hardwood forest: do species matter? *Biogeochemistry*, **67**, 289–308.

MDNR (2001) *IFMAP Southern Michigan Land Cover*. Michigan Department of Natural Resources, Lansing, MI.

Miner, T.J. & Fritsch, J.M. (1997) Lake-effect rain events. *Monthly Weather Review*, **125**, 3231–3248.

Moisen, G.G. & Frescino, T.S. (2002) Comparing five modelling techniques for predicting forest characteristics. *Ecological Modelling*, **157**, 209–225.

Monson, R.K., Lipson, D.L., Burns, S.P., Turnipseed, A.A., Delany, A.C., Williams, M.W. & Schmidt, S.K. (2006)

Winter forest soil respiration controlled by climate and microbial community composition. *Nature*, **439**, 711–714.

Munoz, J. & Felicisimo, A.M. (2004) Comparison of statistical methods commonly used in predictive modelling. *Journal of Vegetation Science*, **15**, 285–292.

Norton, D.C. & Bolsenga, S.J. (1993) Spatiotemporal trends in lake effect and continental snowfall in the Laurentian Great-Lakes, 1951–1980. *Journal of Climate*, **6**, 1943–1956.

Payette, S., Fortin, M.J. & Morneau, C. (1996) The recent sugar maple decline in southern Quebec: probable causes deduced from tree rings. *Canadian Journal of Forest Research*, **26**, 1069–1078.

Rieck, R.L. & Winters, H.A. (1993) Drift volume in the southern peninsula of Michigan – a prodigious Pleistocene endowment. *Physical Geography*, **14**, 478–493.

Schaetzl, R.J. (2002) A spodosol–entisol transition in northern Michigan. *Soil Science Society of America Journal*, **66**, 1272–1284.

Schaetzl, R.J., Knapp, B.D. & Isard, S.A. (2005) Modeling soil temperatures and the mesic–frigid boundary in the central great lakes region, 1951–2000. *Soil Science Society of America Journal*, **69**, 2033–2040.

Schaetzl, R.J., Krist, F.J., Rindfleisch, P.R., Liebens, J. & Williams, T.E. (2000) Postglacial landscape evolution of northeastern lower Michigan, interpreted from soils and sediments. *Annals of the Association of American Geographers*, **90**, 443–466.

Schaetzl, R.J. & Welsenborn, B.N. (2004) The Grayling Fingers region of Michigan: soils, sedimentology, stratigraphy and geomorphic development. *Geomorphology*, **61**, 251–274.

Schimel, J.P., Bilbrough, C. & Welker, J.A. (2004) Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry*, **36**, 217–227.

Schreeg, L.A., Kobe, R.K. & Walters, M.B. (2005) Tree seedling growth, survival, and morphology in response to landscape-level variation in soil resource availability in northern Michigan. *Canadian Journal of Forest Research*, **35**, 263–273.

Schulte, L.A. & Mladenoff, D.J. (2005) Severe wind and fire regimes in northern forests: historical variability at the regional scale. *Ecology*, **86**, 431–445.

Scott, R.W. & Huff, F.A. (1996) Impacts of the Great Lakes on regional climate conditions. *Journal of Great Lakes Research*, **22**, 845–863.

Simard, A.J. & Blank, R.W. (1982) Fire history of Michigan jack pine forest. *Michigan Academician*, **15**, 59–71.

Stromen, N.D. & Harman, J.R. (1978) Seasonally changing patterns of lake-effect snowfall in western lower Michigan. *Monthly Weather Review*, **106**, 504–509.

Templer, P.H. & Dawson, T.E. (2004) Nitrogen uptake by four tree species of the Catskill Mountains, New York: implications for forest N dynamics. *Plant and Soil*, **262**, 251–261.

Templer, P.H., Lovett, G.M., Weathers, K.C., Findlay, S.E. & Dawson, T.E. (2005) Influence of tree species on forest nitrogen retention in the Catskill Mountains, New York, USA. *Ecosystems*, **8**, 1–16.

Tierney, G.L., Fahey, T.J., Groffman, P.M., Hardy, J.P., Fitzhugh, R.D., Driscoll, C.T. & Yavitt, J.B. (2003) Environmental control of fine root dynamics in a northern hardwood forest. *Global Change Biology*, **9**, 670–679.

Walters, M.B. & Reich, P.B. (1997) Growth of *Acer saccharum* seedlings in deeply shaded understories of northern Wisconsin: effects of nitrogen and water availability. *Canadian Journal of Forest Research*, **27**, 237–247.

Whitney, G.G. (1987) An ecological history of the Great-Lakes forest of Michigan. *Journal of Ecology*, **75**, 667–684.

Willmott, C.J., Rowe, C.M. & Mintz, Y. (1985) Climatology of the terrestrial seasonal water cycle. *Journal of Climatology*, **5**, 589–606.

Yang, C.C., Prasher, S.O., Lacroix, R. & Kim, S.H. (2004) Application of multivariate adaptive regression splines (Mars) to simulate soil temperature. *Transactions of the ASAE*, **47**, 881–887.

Zak, D.R., Host, G.E. & Pregitzer, K.S. (1989) Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern Lower Michigan. *Canadian Journal of Forest Research*, **19**, 1521–1526.

Received 2 December 2006
revision accepted 22 December 2006
Handling Editor: Jonathan Newman