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# Are Ecotonal Systems More Sensitive to Climate Change? Past Ecotonal Dynamics and Rates of Vegetation Change in Michigan

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## ABSTRACT

**Aim:** Ecotones are expected to be sensitive to climate change, but supporting evidence is scarce. Here we test the ecotonal sensitivity hypothesis by reconstructing past movements of a major temperature-governed forest ecotone (the Tension Zone, separating temperate deciduous forests and northern mixed hardwood-conifer forests) and comparing the variability of ecotone-proximal and distal vegetation.

**Location:** Michigan, United States.

**Time Period:** Holocene.

**Major Taxa Studied:** Temperate tree taxa in north-central U.S.

**Methods:** We apply non-metric multidimensional scaling (NMDS) and empirical Bayesian Kriging (EBK) to a new pollen record from Sunrise Lake, MI located in the Tension Zone and 19 extant fossil pollen datasets from the Neotoma Paleoecology Database to track movements of the Tension Zone during the Holocene and use the *R-Ratepol* package to measure compositional variability.

**Results:** NMDS Axis 2 clusters southern hardwoods from northern mixed forest, and so can be used to indicate Tension Zone position, while Axis 4 captures shifts in mesic versus xeric taxa, Axis 1 captures the early Holocene decline of *Picea* woodlands and Axis 3 captures the rise of *Ambrosia*-dominated assemblages after Euro-American settlement. At Sunrise Lake, which is within the Tension Zone, major changes include expansions of *Tsuga canadensis* populations at 6.7 ka and *Fagus grandifolia* at 6.3 ka BP. The Tension Zone shifted northwards by approximately 150 km from 11 and 6 ka during a 3.5°$C_{TJuly}$ warming, then retreated southwards, reaching its current position by 2 ka. Sites close to the Tension Zone ecotone show more compositional variability than distal sites, suggesting that ecotonal populations in Michigan were more sensitive to Holocene climate variability. This relationship varied over time and strengthened after 6 ka.

**Main Conclusions:** These findings support the ecotonal sensitivity hypothesis, constrain estimates of climate-driven forest ecotonal movement, and reinforce concerns about the sensitivity of ecotonal ecosystems to anthropogenic global warming.

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## 1 | Introduction

Identifying which species and ecosystems are most sensitive to climate change (known as climate or ecoclimate sensitivity) is a major question in global change ecology (Charney et al. 2016; Seddon et al. 2016; Seidl et al. 2020; Williams et al. 2022) with implications for how to allocate management resources to climate adaptation (Crausbay et al. 2022). One standard hypothesis is that sensitivity to climate change is higher in ecotonal regions (Gosz and Sharpe 1989; Gosz 1991; Neilson 1993; Allen and Breshears 1998) than in distal areas. This expectation that regional- to continental-scale ecotones have a high climate sensitivity, called here the ecotonal sensitivity hypothesis, remains widely assumed but rarely tested, because few regions have observational networks of sufficient spatiotemporal extent and sampling to study climate-driven ecotonal dynamics. At present, alpine treelines have been the most studied ecotones (Smith et al. 2009; Davis et al. 2020) and trees are encroaching upslope due to 20th and 21st-century temperature rises (Körner and Hiltbrunner 2024), albeit with trends complicated in places by land use (Ameztegui et al. 2016). Here we seek to test the ecotonal sensitivity hypothesis by reconstructing past shifts in the position of a major forest ecotone in eastern North America while also assessing whether ecotone-proximal sites have higher compositional variation than ecotonal-distal sites. Our case study focuses on the gradient between temperate broadleaf deciduous forests and northern mixed hardwood-conifer forests, called the Tension Zone, in Michigan over the past 12,000 years.

Ecotones exist across a wide range of scales (Holland et al. 1991), with various processes governing the persistence and dynamics of ecotonal boundaries. Broad-scale terrestrial ecotones often correspond to mapped biome boundaries and are regarded as climate-regulated (Woodward 1987; Loehle 2000) although controlling processes vary by scale and, at regional to local scales, factors such as soil characteristics and fire regime can co-regulate ecotonal position and dynamics (McCann 1979; Grimm 1984; Nelson et al. 2006; Gregory and Van Thomas-Gundy 2021; Shea et al. 2022). Ecotones can represent gradients of high community turnover (Shea et al. 2020) or confluences of range limits, which are believed to be loci of species sensitivity to climate change (Sagarin et al. 2006). Conservationists have called for the prioritisation of ecotonal ecosystems, to protect climate-adaptive genotypic variation (Smith et al. 2001), although others have countered that ecotonal populations should be deprioritized because they are marginal populations depending on other parts of the metacommunity to persist (Kark and van Rensburg 2006).

A major compositional and structural ecotone in North America is the gradient between temperate broadleaf deciduous forests and northern mixed hardwood-conifer forests. This ecotone, called the Tension Zone, extends from Minnesota to New England (Curtis 1959; Cogbill et al. 2002; Andersen 2005; Shea et al. 2022) and is a boundary between EPA Level 1 ecoregions (Cleland et al. 2007). The Tension Zone is primarily temperature-regulated at a continental scale, with growing degree days a strong predictor (Curtis 1959; McCann 1979; Woodward 1987), and with soil characteristics, soil water availability, and fire history determining forest composition at stand to landscape scales (Gregory and Van Thomas-Gundy 2021; Shea et al. 2022). The Tension Zone is well expressed in Michigan, where the Michigan Tension Zone (MTZ) is characterised both as a change in dominant taxa (Potzger 1948) and by the northern range limit of many southern species (McCann 1979). Prior to Euro-American settlement, southern Lower Michigan (i.e., the 'mitten' portion of Michigan) largely consisted of *Fagus grandifolia* and *Acer saccharum* forest with substantial patches of *Quercus* savanna and *Quercus-Carya* forest, while northern Lower Michigan consisted of *F. grandifolia*, *A. saccharum*, and *Tsuga canadensis* forests; stands of *T. canadensis* and *Pinus strobus*; and mixed-*Pinus* forests (Comer et al. 1995). Respectively, these southern hardwoods comprise part of the Midwest broadleaf forest province, while the northern hardwoods and conifers represent the Laurentian mixed forest province (Cleland et al. 2007). Water availability, mediated by soil texture and east–west gradients in lake-effect snow, exerts an important second-order influence on tree distributions in Michigan (Henne et al. 2007), particularly for mesic taxa such as *F. grandifolia* and *T. canadensis*.

Because forest changes often develop over centuries to millennia, paleoecological approaches are well-suited for studying ecotonal dynamics in areas of sufficient site density. Rapid ecotonal shifts in the mid- to late-Holocene are well documented throughout eastern North America (ENA). The prairie-forest ecotone is particularly well studied (Webb et al. 1983; Williams et al. 2009; Danz et al. 2013) and is regulated by water availability and fire, with high spatial heterogeneity (Grimm 1984; Nelson and Hu 2008; Schlenker et al. 2024). In other regions, however, paleoecological approaches have found limited evidence for the ecotonal sensitivity hypothesis, because they demonstrate widespread climate-driven compositional change (Gajewski 1987; Shuman et al. 2004, 2009; Williams et al. 2004).

Prior studies of MTZ dynamics show that this ecotone formed at the beginning of the Holocene and advanced northwards until 6 ka, then retreated southwards (Webb et al. 1983; Hupy 2012). These shifts can be linked to regional warming during the early to middle Holocene and subsequent cooling (Salonen et al. 2025), with changes in moisture availability and fire also potential contributors. A prior reconstruction suggests dramatic changes in MTZ position (Hupy 2012), with northward expansion of southern hardwood forests to occupy all of Lower Michigan at 6 ka and the consequent effective disappearance of the Tension Zone from Lower Michigan. If correct, these changes would suggest a very high sensitivity of ecotonal position and forest composition to small temperature variations. However, this reconstruction by Hupy (2012) is inconsistent with individual sites that suggest persistence of northern Laurentian hardwoods and pine forest throughout the Holocene in northern Michigan (Henne and Hu 2010). More precise reconstructions of past ecotonal dynamics are now possible, with the approximate doubling of the number of Holocene pollen records in Michigan (Booth and Jackson 2003; Henne 2006; Booth, Brewer, et al. 2012; Kettle 2015) in the Neotoma Paleoecology Database (Williams et al. 2018), relative to prior efforts (Webb et al. 1983; Hupy 2012). Hence, the time is ripe for a new mapping of shifts in the MTZ during the Holocene and to sharpen our understanding of the sensitivity of this temperate forested ecotone to climate change.

Here we seek to (1) better constrain the ecoclimatic sensitivity of the Tension Zone by better constraining the extent of its latitudinal shifts during the Holocene and (2) use the MTZ as a case

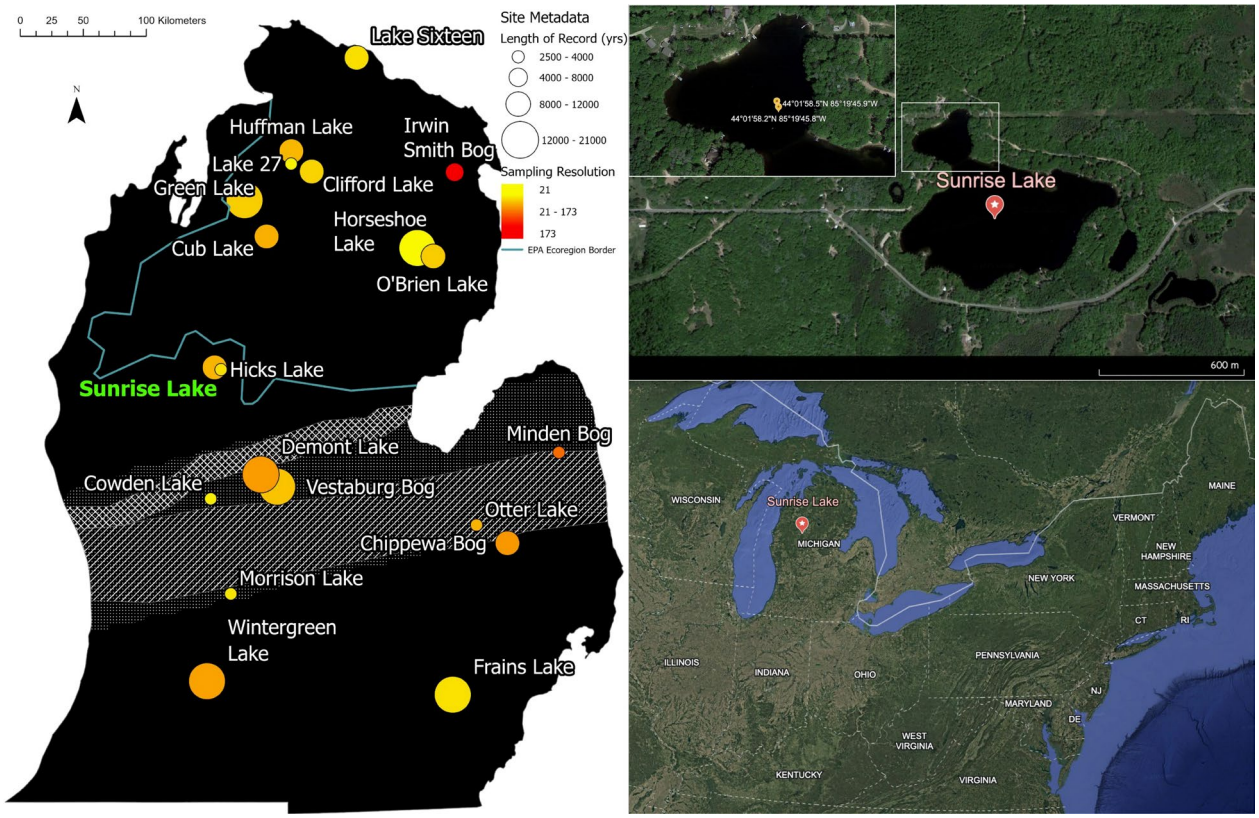



**FIGURE 1** | (A) Locations of Lower Michigan fossil pollen records used here, with circle size indicating length of record and circle colour indicating average sampling resolution. Prior efforts to map the Michigan Tension Zone are included here, represented by the cross-hatched (Hupy 2012), striped (Andersen 2005, 200), and dotted (McCann 1979) zones. Additionally, the border between the Eastern temperate forests and Northern forests ecoregions as defined by the EPA is indicated in blue (Cleland et al. 2007). (B) Google Earth map of Sunrise Lake, MI, with coring locations in the northern bay indicated by orange location markers in the inset map. (C) Google Earth map of eastern North America, with a red pin marking the location of Sunrise Lake, MI.

study to test the ecotonal sensitivity hypothesis. If the ecotonal sensitivity hypothesis holds, we expect that ecotonal sites should show higher rates of compositional change throughout the Holocene than distal sites. To achieve these goals, we present a new full-Holocene pollen record from Sunrise Lake, located near the MTZ, and conduct a spatiotemporal analysis of Sunrise and 19 other records (Figure 1) from Neotoma (Williams et al. 2018). We ordinate these data via non-metric multidimensional scaling (NMDS) and spatially interpolate ordination scores through empirical Bayesian Kriging (EBK). We test whether sites closer to the MTZ have a higher average rate of compositional change, using *R-Ratepol* (Mottl et al. 2021). This work is designed to contribute new insights into temperature-driven ecotonal vegetation dynamics, test the ecotonal sensitivity hypothesis, and inform conservation strategies by identifying regions of high ecoclimate sensitivity (Williams et al. 2022) that can be targets for focused climate-adaptation interventions (Lynch et al. 2021; Crausbay et al. 2022).

## 2 | Material and Methods

### 2.1 | Ecotonal Data Analyses and Mapping

All pollen data were retrieved from Neotoma (Williams et al. 2018) except for our new record from Sunrise Lake (Section 2.2). Taxa were filtered to retain trees and shrubs and upland herbs. All sites were taxonomically harmonised using the *mutate* function from *dplyr* (Wickham et al. 2023). We retained the 20 most frequent taxa, defined as the number of pollen assemblages across all sites that contained these taxa. Proportional abundances were calculated relative to the sum of these 20 taxa.

NMDS (Shepard 1962; Kruskal 1964) for all 20 sites (Table S2) was performed using the *vegan* R package (Oksanen et al. 2022). NMDS was selected because its rank-ordering makes weaker assumptions of linearity, which minimises distortions when analysing complex ecological gradients (Pielou 1984). We ran the *metaMDS* function for the pollen dataset with all pollen abundances expressed as proportional abundance and using a four-dimension Chi-squared dissimilarity index without automatic transformation. Chi-squared dissimilarity is a signal-to-noise metric that has been shown to have high skill in discriminating vegetation types relative to other palynological dissimilarity metrics (Overpeck et al. 1985; Gavin et al. 2003).

Analyses indicated that NMDS Axis 2 best captured the north–south compositional gradient that includes the MTZ (Results). Hence, to map past MTZ movements, NMDS Axis 2 scores were averaged by site across all samples within 1000-year bins and then spatially interpolated for each 1000-year period, weighting equally all sites with samples for that interval and

using Empirical Bayesian Kriging (EBK) (Krivoruchko and Gribov 2019) in ArcGIS (Johnston et al. 2001). EBK accounts for spatial autocorrelation, does not require prior parameter specification, and is more accurate than other kriging methods for small, spatially autocorrelated, and unevenly distributed datasets (Krivoruchko and Gribov 2019). EBK was run using a K-Bessel detrended semivariogram (Guinness and Fuentes 2016) with an empirical data transform (Gribov and Krivoruchko 2012).

The resulting interpolated NMDS Axis 2 scores were categorised as isobands using a geometrical interval classification scheme and representing nine classes of ordination scores. We defined the MTZ to correspond to the isoband located within the steepest spatial gradient of the interpolated Axis 2 scores for the 0–1 ka interval, which was isoband 6 (Section 3). We then mapped for each 1000-year time window the position of isoband 6 (see Table S4 for midline values of isoband 6 for each time period), to represent movements in ecotonal position over time (main text), with an alternative mapping based on a fixed NMDS value of 0.244, which is the midline contour for the isoband for the 0–1 ka interval (Supporting Information).

### 2.2 | Sunrise Lake: Site Description, Field and Lab Methods

Sunrise Lake (44.03283° N, 85.32938° W, 380 m elevation) is a 33 ha kettle lake in Osceola County, Michigan in central Michigan, near the Tension Zone (Figure 1). The lake sits atop sandstone and shale from the Pennsylvanian Saginaw Formation (Milstein 1987). The substrate consists of end moraines of coarse-textured till underneath well-drained, sandy, acidic spodosols. The surrounding vegetation is classified as the Northern Lower Peninsula section of the Laurentian Mixed Forest Province (Cleland et al. 2007). The vegetation surrounding Sunrise Lake is forested with low-density residential development and roads, with common trees including *Fagus grandifolia*, *Acer saccharum*, *A. rubrum*, *Pinus strobus*, *Nyssa sylvatica*, and *Betula papyrifera*.

Four centre-basin cores were extracted from the northern bay of Sunrise Lake (44.032833° N, 85.329383° W) in September 2021 at 12 m water depth (Figure 1B) and composited (Supporting Information). The total length of the composite core was 568 cm, with one stratigraphic gap at 506–507 cm. The composite core was divided into 1-cm cross-sections and subsampled for pollen, charcoal, and loss-on-ignition (LOI) (Supporting Information). Sixteen terrestrial plant macrofossils were sent to the Keck Carbon Cycle Accelerator Mass Spectrometer Facility for radiocarbon dating. Radiocarbon dates were calibrated using the IntCal20 Northern Hemisphere curve (Reimer et al. 2020) in the *Bchron* package (Parnell et al. 2008). All ages are reported relative to 1950 CE. The *Bchron* age-depth model is based on these $^{14}$C dates, the pre-settlement horizon, placed at 4.5 cm based on the *Ambrosia* rise and estimated at 1870 ± 15 CE (Whitney 1987), and a core top prescribed as 2020 ± 15 CE (Table S1). Pollen analyses followed standard methods (Supporting Information), and pollen data were stratigraphically clustered using CONISS (Grimm 1987).

### 2.3 | Data Analyses: Community Variability and Rates of Change

To assess community variability for each site-level pollen record, we calculated the mean and maximum rate of compositional change (RoC) between 11.0 and 0.3 ka, using *R-Ratepol* (Mottl et al. 2021). Spatiotemporal variations in pollen assemblage composition are indicators of vegetation compositional changes (Solomon and Webb 1985; Dawson et al. 2016). The time bounds were chosen to focus on Holocene community variation and avoid Euro-American land clearance (McAndrews 1988). RoC scores for each record were calculated using a Shepard's 5-term smoothing filter and a Chi-squared dissimilarity coefficient across 500-year moving windows. Site-level means and maxima of the sample-level RoC scores were calculated and mapped. The spatial distance to the Holocene-average position of the MTZ was calculated for each site by calculating for each 1 ka interval the distance from the site to the nearest point on the MTZ at that time interval. We then analysed mean and maximum RoC as a function of average distance to the MTZ, using a general additive model (GAM) and LOESS curve for the site-level RoC means and maxima, respectively, to test the hypothesis that sites nearer to the ecotone had higher rates of compositional variability during Holocene climate change.

## 3 | Results

### 3.1 | NMDS Ordination of Holocene Vegetation

*metaMDS* solutions well describe the variance ($R^2 = 0.995$) in the pollen dataset, with a stress value of 0.0682 (Figure S1). In the resulting four-dimensional ordination (Figure 2), NMDS Axis 1 captures the well-known Pleistocene–Holocene decline in *Picea* and *Artemisia* that marks the widespread decline of no-modern-analogue mixed parklands across the Upper Midwest (Wright Jr. et al. 1963; Williams and Jackson 2007) and a secondary late-Holocene increase in *Picea* that has been linked to cooling climates in eastern North America (Gajewski 2019; Oswald et al. 2020) (Figure S6), with the *Picea-Artemisia* cluster clearly differentiated from other groups (Figure 2).

Axis 2 captures the latitudinal gradients of vegetation in Michigan during the Holocene, and the region of maximum steepness in the spatial gradient for Axis 2 is a good indicator of the MTZ. Several lines of evidence support this inference. First, Axis 2 differentiates temperate hardwoods found in southern Michigan (*Quercus*, *Carya*) from cool-temperate and northern conifers (*Pinus*, *Tsuga*), with *Ulmus*, *Ostrya*/*Carpinus*, *Fagus*, *Tilia*, *Alnus*, and *Betula* in intermediate positions (Figure 2). Axis 2 when plotted and interpolated spatially follows a north–south gradient (Figure 3) that well matches the historic gradient of tree taxa distributions from southern to northern Michigan (Webb 1974; Comer et al. 1995; Paciorek et al. 2021). The spatial pattern and ecological ordination for NMDS Axis 2 also match well to PCA Axis 1 of pollen and vegetation data in Michigan, which was also interpreted to indicate the north–south gradient in Michigan vegetation and Tension Zone (Webb 1974). The area of maximum steepness for Axis 2 for 0–1 ka corresponds to Isoband 6 (Figure 3), and this area of maximum steepness corresponds well to other mappings of the MTZ (Figure 1). Hence, in all subsequent analyses we use Axis 2 scores as the primary indicator of the past position of the MTZ,

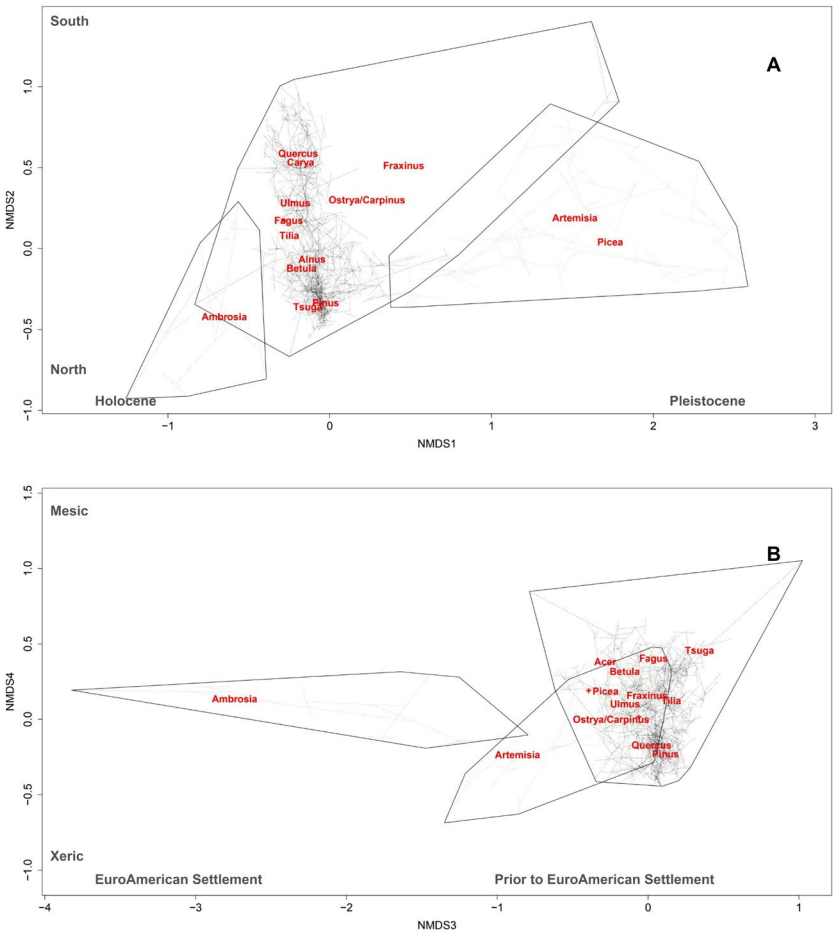



**FIGURE 2** | NMDS biplots for all samples in the Lower Michigan pollen dataset and the position of taxa relative to these ordination axes. In panel (A), NMDS Axis 1 differentiates late-Pleistocene assemblages from Holocene assemblages, while NMDS Axis 2 differentiates southern hardwoods from the northern mixed coniferous forests in the Holocene vegetation of Michigan. In panel (B), NMDS Axis 3 differentiates all other pollen assemblages from the *Ambrosia*-dominated pollen assemblages of the EuroAmerican land clearance period. NMDS Axis 4 captures hydroclimate sensitivity of tree taxa, with mesic taxa such as *Tsuga*, *Fagus*, and *Acer* clustered at one end and xeric taxa such as *Quercus* and *Pinus* at the other.

and employ two alternative representations of the MTZ based on Axis 2: (1) Isoband 6, with the NMDS values for Isoband 6 allowed to vary between time periods and (2) NMDS = 0.244, which is the midline contour for Isoband 6 for 0–1 ka (Table S4).

NMDS Axis 3 captures the vegetation changes caused by Euro-American land use (Figure 2, Figure S6). *Ambrosia (ragweed)*, which is a disturbance taxon closely associated with EuroAmerican land clearance (McAndrews 1988), is strongly differentiated from all taxa, with *Artemisa* also receiving high scores, while all other taxa are clustered at right (Figure 2). NMDS Axis 4 clusters *Tsuga*, *Fagus*, *Acer*, and *Betula* on one side, and *Quercus* and *Pinus* on the other. NMDS Axis 4 thus appears to differentiate tree taxa by hydrological sensitivity and shade-tolerance (Burns and Honkala 1990). Plant distributions represented by NMDS Axis 4 may be shaped by east–west gradients in lake-effect snow and water availability (Henne et al. 2007).

### 3.2 | Vegetation Changes and Ecotonal Dynamics Over Time at Sunrise Lake

The age-depth model for Sunrise Lake is well constrained by the 18 radiocarbon dates and other age controls, and sediment rates are approximately linear (Figure S3). However, the interval between 350 and 500 cm (ca. 5 to 10 ka) lacked datable terrestrial plant macrofossils and the timing of events in this interval is more uncertain than for other portions of the record (Figure S3). This area of heightened uncertainty is noted in Figure 4.

Zonation of the Sunrise record reveals five zones of vegetation composition (Figure 4). The early-mid Holocene vegetation, represented by Zone A from 10.9 to ca. 6.5 ka, represents a northern mixed forest. Changes within Zone A are consistent with increasing elements of southern tree taxa and a northward shift of the MTZ, as indicated by increasing abundances of *Quercus*, *Acer*, *Ostrya*/*Carpinus*, and, at the end, *Tsuga canadensis*. *Pinus* abundances initially were moderate to high, mostly consisting of *P. strobus* and secondarily *P. banksiana*/*resinosa*. During this period of *Pinus* dominance, negative NMDS Axis 2 scores (Figures 2 and 4) indicate that the MTZ was south of Sunrise Lake. NMDS Axis 2 scores rise after ca. 7.5 ka, associated with rises in *Quercus* and *Ostrya*/*Carpinus* (Figure 4), indicating that the MTZ moved to a position near Sunrise Lake during the latter portion of Zone A.

Zone B (6.5 to 4.1 ka) is defined by the rapid expansion of *Tsuga* and *Fagus*, capturing the mid-Holocene establishment

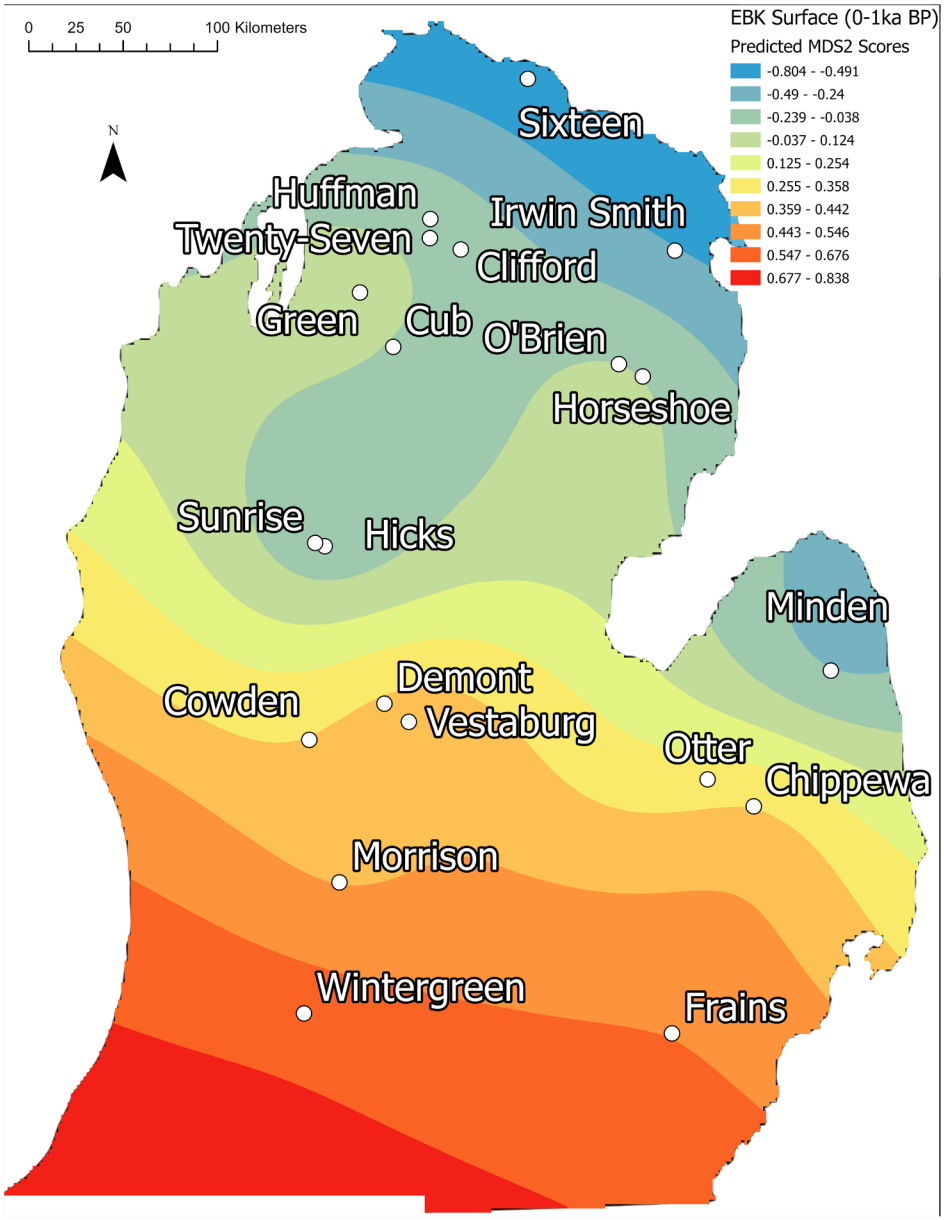



**FIGURE 3** | Kriged interpolation surface of NMDS Axis 2 for 0–1 ka. In this plotting, the sixth band from top (in yellow) has the steepest spatial gradient, as indicated by its narrow width. The position of this band also corresponds well to prior mappings of the MTZ (Figure 1), suggesting that it is a reasonable indicator of MTZ position. Text labels indicate site names (see Table S2 for full site metadata).

of temperate mesic taxa at Sunrise Lake. *Pinus*, *Alnus*, and *Betula* abundances remain low and NMDS scores remain above 0.2, suggesting that the MTZ remained at or north of Sunrise Lake (Figure 4, Table S4). The Zone B onset corresponds to small changes in NMDS Axis 2 and a large increase in NMDS Axis 4 (Figure 4), suggesting that the MTZ position relative to Sunrise Lake was fairly stable. The increasing prevalence of lake-effect snow between 9.5 and 5.5 ka (Henne and Hu 2010) suggests that these mesic-taxa increases were potentially governed by increases in water availability. At 5.0 ka, *Tsuga* populations abruptly decline, while *Fagus* declines in abundance at 4.8 and 4.0 ka. After these *Fagus* declines, *Acer*, *Betula*, and *Quercus* abundances increase, but overall NMDS Axis 2 scores remain high (Figure 4), suggesting that the MTZ remained near Sunrise Lake.

Zone C extends from 4.1 to 1.9 ka and appears to represent a cool mixed forest. *Tsuga* abundances recover slowly, paralleled by increases in *Betula*. *Pinus strobus* is abundant while *P. banksiana*/*resinosa* is mostly absent. NMDS Axis 2 scores decline, consistent with a southward shift of the MTZ.

In Zone D (1.9 to 0.5 ka), *Tsuga* and *Fagus* become the most consistently abundant taxa. *Pinus banksiana*/*resinosa* abundances increase, while *P. strobus* and *Quercus* decline. *Pinus* abundance decreases, accompanied by a greater proportion of *P. banksiana*/*resinosa* within *Pinus*. After 1.0 ka, *Fagus* abundances rapidly decrease, coincident with a rapid expansion of *P. strobus*. Zones A and D thus both represent cool-mixed forests north of the MTZ (similar Axis 2 scores) but differ with respect to Axis 4, indicating a shift from more xeric to mesic mixed forests over the Holocene.

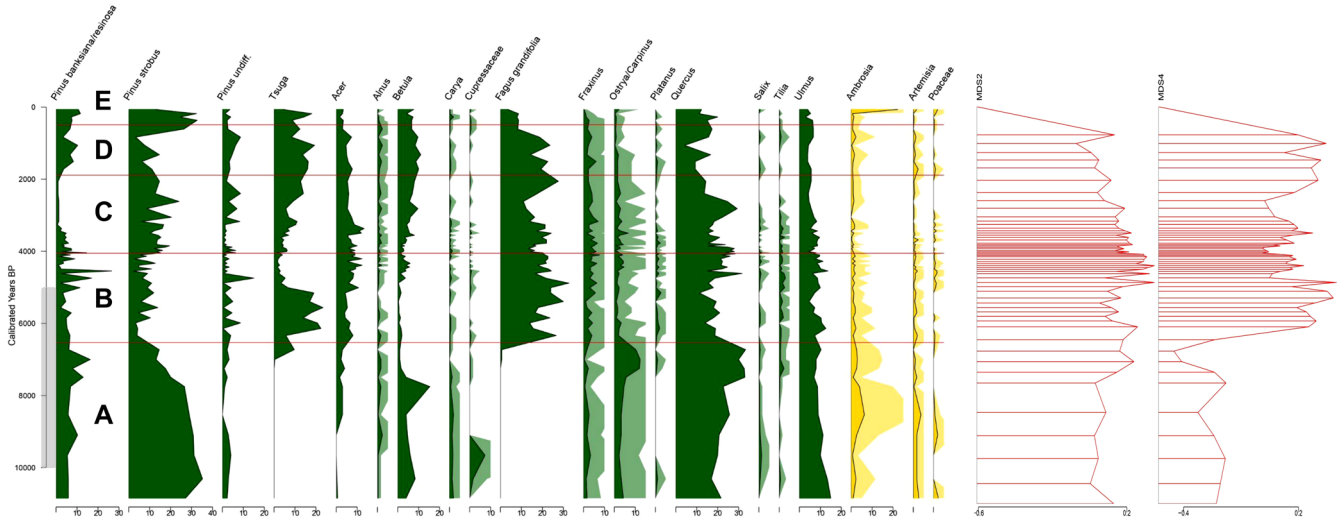



**FIGURE 4** | Pollen diagram for Sunrise Lake, displaying % abundance versus age (calendar year BP). Arboreal pollen types are indicated in green and non-arboreal types in yellow. CONISS stratigraphically constrained clustering and zonation is shown at right (Grimm 1987), with red horizontal lines indicating placement of zone boundaries. Note that much of the early to middle Holocene (10 to 5 ka) is less well constrained by radiocarbon dates (Figure S3); this time window is marked here by a light grey shading along the *y*-axis.

Lastly, Zone E is marked by high abundances of *Pinus strobus* and the *Ambrosia* rapid rise, corresponding to Axis 3 (Figure 2, Figure S6). This rise is interpreted to result from the widespread logging in Lower Michigan in the late 19th and early 20th centuries (Whitney 1987).

### 3.3 | How Far Did the Michigan Tension Zone Move During the Holocene?

The MTZ establishes in southern Michigan between 11 and 10 ka and then shifts northward, reaching its northernmost position between 7 and 6 ka (Figure 5A). After 6 ka, the MTZ shifts southward, reaching its current position by 3–2 ka, and is largely stable thereafter. Between 11–10 and 7–6 ka, the MTZ shifted ca. 150 km north; then, between 7–6 and 3–2 ka, it shifted approximately 90 to 120 km south. Our reconstructed shifts for the MTZ are qualitatively similar in direction to those by Hupy (2012) but of lower magnitude.

### 3.4 | Is Distance to Ecotone a Predictor of Rates of Vegetation Change?

Mapped rate-of-change (RoC) scores (Figure 6A) support the hypothesis that ecotonal communities are more compositionally variable than distant sites. The three sites with the highest average RoC scores were all within or adjacent to the range of ecotonal movements (Figure 6A). Among sites further from the ecotone, rates of vegetation change are lowest at northern sites (Figure 6A) and are apparent as a cluster of sites below the regression line (Figure 6B), while the *Quercus-Carya* dominated forests in the southern half of Lower Michigan experienced intermediate levels of community variability. These maps thus support the ecotonal sensitivity hypothesis, while also indicating that community stability was highest in the northern mixed forests.

This support for the ecotonal sensitivity hypothesis is confirmed by the regression of the site-level mean RoCs for the Holocene against mean distance to the MTZ (Figure 6B). The linear fit to mean RoC shows a significant linear relationship ($R^2 = 0.49$, $p < 0.001$), with sites closer to the MTZ having a higher rate of change. The effect of ecotonal proximity on vegetation rate of change is non-stationary, however, and has strengthened over time, particularly after 6 ka (Figure 7). The regression of RoC against ecotonal position is significantly positive for some individual time periods after 5 ka, and with no significant relationship for individual time periods between 11 and 5 ka (Figure 7, Table S3).

The spatial patterns for maximum RoC values are more complex and show no significant relationship to ecotonal distance when fitted by a linear model with a quadratic term (Figure 6C). The largest maximum RoC scores appear to be at intermediate distances (100–150 km) and are mostly concentrated north of the MTZ. These patterns do not closely correspond to the patterns of mean RoC.

## 4 | Discussion

### 4.1 | Holocene Shifts in the Tension Zone: Magnitude and Comparison to Prior Work

The reconstructed Holocene movements of the MTZ presented here qualitatively agree with prior reconstructions (Hupy 2012) but are smaller (Figure 5). These reconstructions and those of Hupy (2012) both show a northward shift from 10–6 ka, but the MTZ here shifts only ~150 km as opposed to ~320 km in Hupy (2012). The reduced magnitude of the northward shift here is mostly due to a denser site network. Sunrise Lake, close to the present MTZ location and Cub Lake, north of the 6 ka MTZ position (Figure 5A), offer particularly useful constraints. The mid-Holocene Cub record exhibits consistently

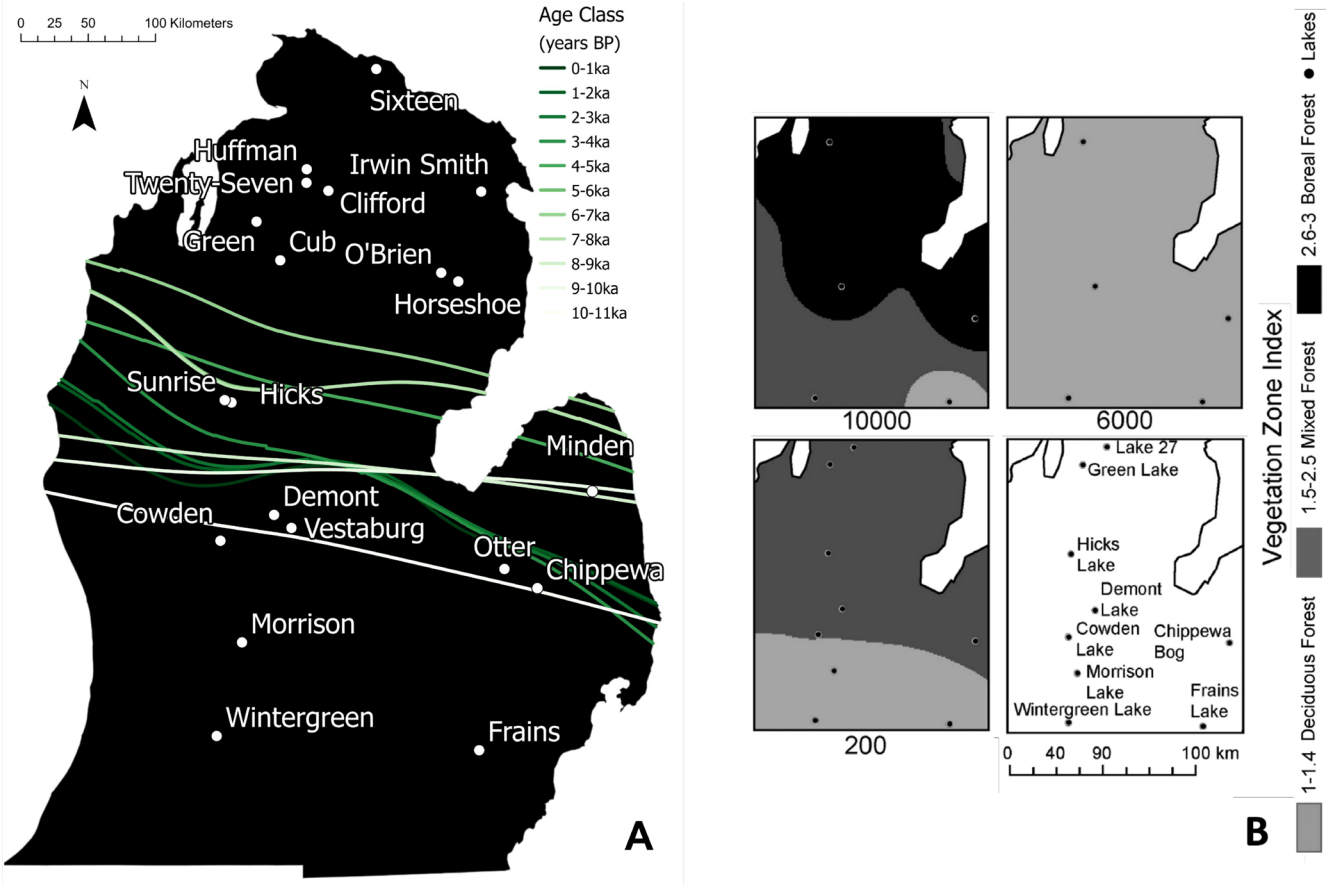



**FIGURE 5** | (A) Positions of the MTZ by 1000-year time windows during the Holocene, based on NMDS Axis 2 and band 6. (B) Previous reconstructions of MTZ position for three Holocene time periods, from Hupy (2012). The Hupy maps present interpolated vegetation zone indices (VZI), in which the MTZ is the border between the Deciduous and Mixed Forest zones. Numbers below each VZI map indicate age in calendar years BP.

high abundances of *Pinus* (Rasmussen 1982), while, at Sunrise, *Pinus* is at low abundances at 6 ka as *Fagus* and *Tsuga* increase in abundance (Figure 4). The differing vegetation histories at Cub and Sunrise Lakes thus help constrain the northernmost MTZ position during the middle Holocene.

The position of the MTZ at 2 ka in western Michigan is roughly similar for this paper and Hupy (2012), but diverges in the eastern region, where the addition here of Minden Bog and Otter Lake helps constrain the late-Holocene position of the MTZ and place it further south than in Hupy (2012). The 90 to 120 km southward shift of the MTZ during the mid- to late-Holocene corresponds to an increase in *Quercus* and *Carya* abundances in the southern broadleaf forests, supported by pollen records from Frains Lake (Kerfoot 1974), Morrison Lake (Hupy and Yansa 2009), and Wintergreen Lake (Manny et al. 1978).

Both the MTZ reconstructions presented here and those of Hupy (2012) are based on pollen abundances and so are more sensitive to changes in the abundance of common taxa, versus changes in the prevalence of marginal populations at species range limits. These MTZ reconstructions, conducted at 1 ka intervals, may miss finer-scale ecotonal movements and community responses to short-term climatic fluctuations. During the late Holocene, site-level reconstructions in northern Michigan show that rapid *Quercus* expansions coincided with the Medieval Climate Anomaly (MCA; ~1200–800 years BP), with increases most pronounced near the MTZ (Hupy and Yansa 2009). As the MCA transitioned to the cooler and generally drier climates of the Little Ice Age (LIA; ~700–150 years BP), *Pinus* abundances increased in the north and near the MTZ, replacing mesic taxa including *Fagus* (Hupy and Yansa 2009). Thus, the MTZ position likely shifted over the late Holocene in response to climatic changes during the MCA and LIA, but these shifts are not captured here.

### 4.2 | Climatic Drivers

The northward advance of the MTZ between 10 and 6 ka and its retreat after 6 ka are congruent with paleoclimatic evidence that much of North America reached a temperature maximum during the mid-Holocene (Marsicek et al. 2018; Axford et al. 2021; Kaufman and Broadman 2023). Earth system model simulations and pollen-based paleoclimatic reconstructions indicate that the northern Great Lakes region reached peak summertime warmth between 8 and 6 ka (Salonen et al. 2025). This mid-Holocene maximum increased July temperatures by ~3.5°C relative to the early Holocene and by ~1.5°C compared to the mid-20th century (Salonen et al. 2025).

In parallel, the latitudinal gradient in temperature steepened over the past 6 ka (Shuman 2022; Shuman et al. 2023). Rapid

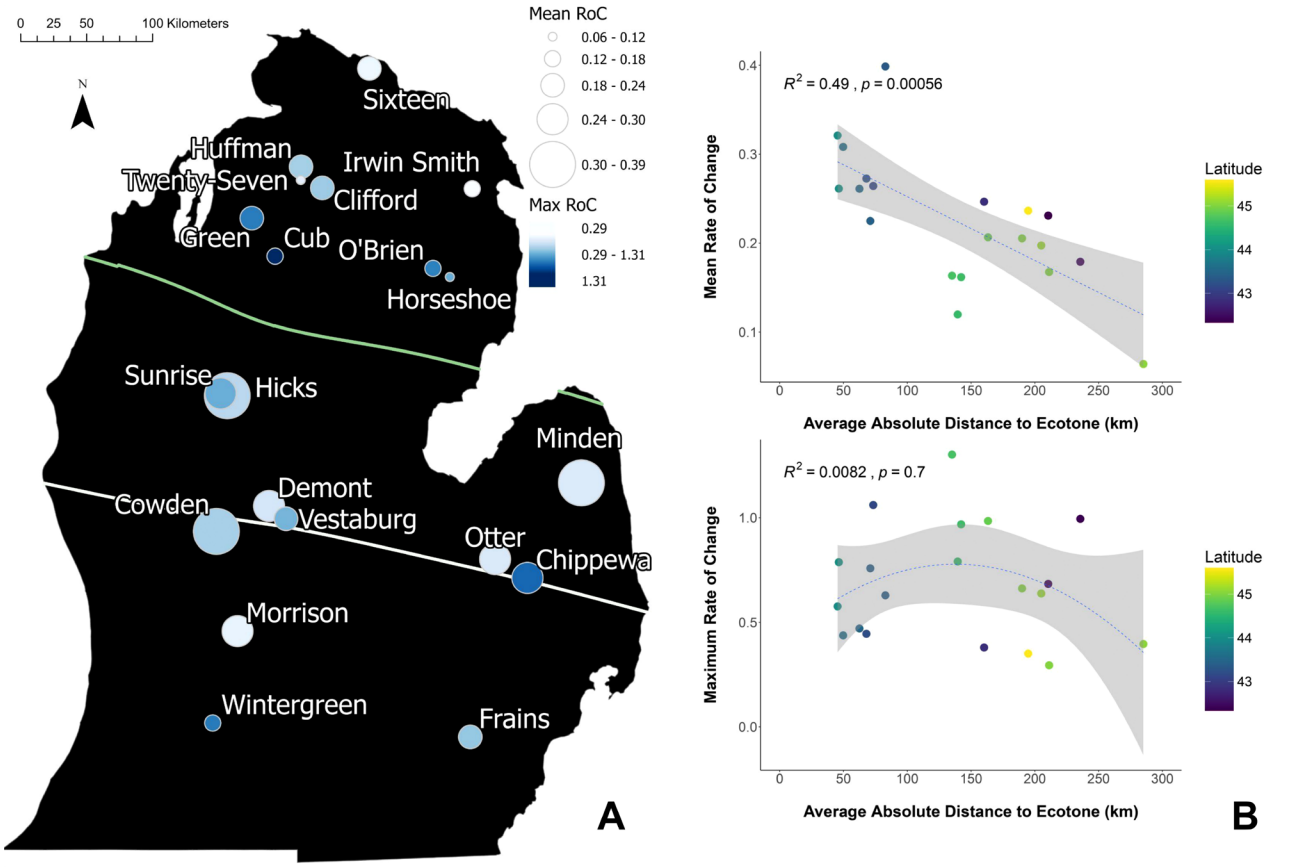



**FIGURE 6** | (A) Mean and maximum vegetation rates of change (RoC) by site based on the *R-Ratepol* R package (Mottl et al. 2021), calculated across all samples between 11.0 and 0.3 ka. RoC means are indicated by symbol size and maxima indicated by colour. The northern- and southern-most positions of the MTZ are shown as green and white lines respectively, taken from Figure 5A. (B) Scatterplots of mean RoC versus time-averaged distance to the MTZ and fitted with an ordinary linear regression. Time-averaged distance for each site is calculated across all Holocene ecotone positions shown in Figure 5A. Points are coloured by latitude, with southern sites as dark blue and northern sites as light blue. (C) As panel (B), for maximum RoC versus time-averaged distance to the MTZ. Data are fitted with a quadratic regression line.

early Holocene warming was followed by sustained cooling of northern areas during the late Holocene as the north–south temperature difference within Michigan steepened by >1°C (Shuman 2022). Precessional forcing likely caused this Holocene strengthening of the temperature gradient: summertime positive insolation anomalies during the early Holocene were larger in high latitudes than mid latitudes (Shuman and Marsicek 2016; Shuman et al. 2023). This steepening of the gradient would have favoured a southward expansion of northern taxa like *Betula* and *Pinus*. Similar responses to the latitudinal temperature gradient appear to have affected the Tension Zone in New England (Shuman et al. 2023).

Paleohydrologic reconstructions suggest that midcontinental North America was drier than present during the early Holocene, reflecting Arctic warming and decreased net precipitation in the mid-latitudes (Williams et al. 2010; Shuman and Marsicek 2016; Routson et al. 2019; Salonen et al. 2025). Other ecotones tracked this early- to mid-Holocene aridity, notably as forest loss along the prairie-forest ecotone (Umbanhowar Jr. et al. 2006; Williams et al. 2009). After 6 ka, the MTZ's southward retreat coincides with mid-continental increases in effective moisture and cooling (Booth and Jackson 2003; Shuman and Marsicek 2016). The long-term increase in effective moisture parallels the steepening of the latitudinal temperature gradient, potentially because this temperature gradient influences storm tracks and moisture delivery (Shuman and Marsicek 2016; Routson et al. 2019). This wetting trend may explain why xeric taxa such as *Pinus* were important at sites like Sunrise Lake before the MTZ shifted northward in the early Holocene, but mesic taxa like *Tsuga* became important when the MTZ moved south later in the Holocene (Figure 4). The lake-effect snowbelt in Michigan developed between 9.5 and 5.5 ka and persisted thereafter, creating an east-to-west gradient in moisture availability across Lower Michigan (Henne and Hu 2010). More work is needed to establish a denser network of paleoclimatic proxy records in Michigan, to better understand the interlinkages between Holocene climate and ecosystem change.

### 4.3 | Testing the Ecotonal Sensitivity Hypothesis: Effect of Ecotone Proximity on Vegetation Rates of Compositional Change

These results support the ecotonal sensitivity hypothesis that ecosystems close to ecotones are more sensitive to climate variability (Neilson 1993; Allen and Breshears 1998), as

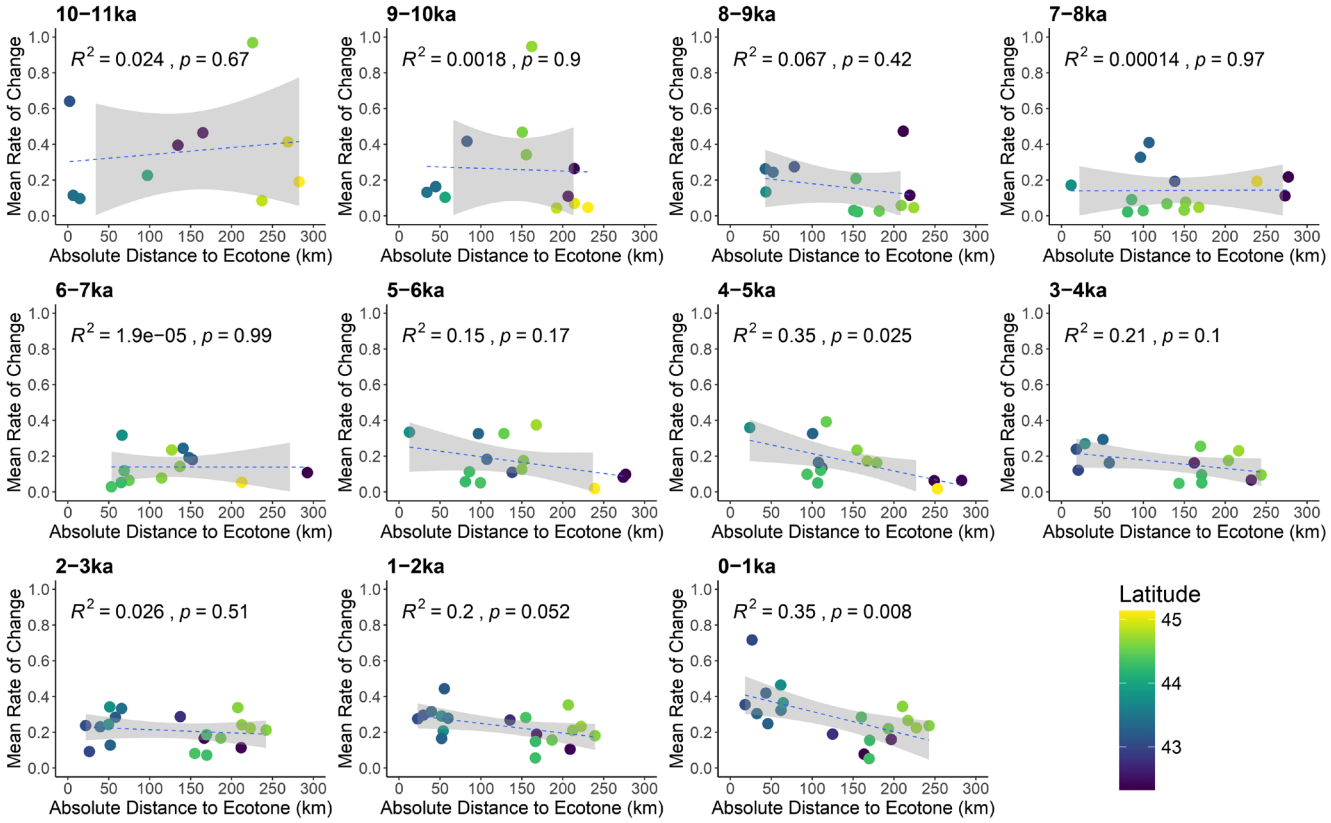



**FIGURE 7** | Scatterplots of mean rate of change scores vs. spatial absolute distance to the ecotone for each site in a given 1000-year period. Points represent individual sites and are colour-coded by latitude. Each plot is fitted with an ordinary linear regression with the shaded grey region indicating the 95% confidence interval. These plots indicate that the relationship between compositional change and ecotone proximity has strengthened over time.

indicated by our findings that mean RoC across sites in Lower Michigan is higher for sites near the ecotone, with community variability highest within 50 km of the MTZ (Figure 6). The strengthening sensitivity of ecotonal populations after 6 ka (as inferred from a strengthening relationship between ecotonal proximity and vegetation rates of change, Figure 7) is an unexpected finding, and the cause of this strengthening relationship is unclear. One hypothesis, suggested by the Sunrise record, is that ecotonal proximity became more important after 7 ka, when mesic and shade-tolerant taxa such as *Fagus* and *Tsuga* became major constituents of the regional vegetation, which enhanced differences among forest types in sensitivity to shifts in water availability and temperature (Schlenker et al. 2024). Another hypothesis is that dispersal limits on species distributions may have been more important during the early Holocene and waned afterwards. During the early Holocene, the establishment and movement of the MTZ was presumably governed at least in part by dispersal limitations, particularly where the Great Lakes created barriers to post-glacial range expansion of temperate taxa (Bennett 1985; Davis et al. 1986). By the mid-Holocene, however, all major taxa were regionally present and MTZ shifts were governed by local shifts in abundance rather than the arrival of new taxa (Webb et al. 1983; Hupy 2012). Analyses of variations in *Fagus* abundances during the middle to late Holocene in the Great Lakes region suggest strong effects of Holocene hydroclimate forcing (Booth, Jackson, et al. 2012) and climate-mediated shifts in fire regime (Schlenker et al. 2024). Thus, as dispersal limitations waned, the importance of climatic variability on ecotonal populations may have intensified over the Holocene.

Pollen records at the Tension Zone show how these past ecotonal dynamics played out at local scales, in which the major patterns observed are continuous changes in taxon abundances and community composition, as taxa from adjacent communities intermix. At Sunrise Lake, the largest changes are associated with the rapid expansion of *Tsuga* and *Fagus* populations after 7.0 and 6.7 ka respectively, followed by the abrupt decline in *Tsuga* abundance at 5.0 ka. *Quercus* and *Pinus* abundances tend to be antiphased with those of *Fagus* and *Tsuga* (Figure 4). In the NMDS analyses, these taxa are differentiated by NMDS Axis 4, which is interpreted to differentiate taxa according to moisture sensitivity (Figure 2). Sunrise thus shows how the MTZ ecotone itself may be regulated by temperature, fire history, and edaphic factors (Curtis 1959; McCann 1979; Gregory and Van Thomas-Gundy 2021; Shea et al. 2022) but that community variability in this ecotonal region is amplified by the joint effects of shifting temperature and moisture availability.

This finding that ecotonal populations at the MTZ show higher compositional variability (and, by inference, higher ecoclimate sensitivity) implies that the broader ecotone between temperate broadleaved forests and northern mixed

hardwood-conifer forests that stretches across the northern U.S. from Minnesota to Maine is similarly climate sensitive. The past sensitivity of this ecotone reinforces the utility of experimental and monitoring efforts in the Tension Zone to study forest responses to present and past climate change (Reich et al. 2018). Similarly, the Tension Zone may be a good place to conduct adaptation experiments intended to build a portfolio of management alternatives for Resist-Accept-Direct strategies (Crausbay et al. 2022).

Too narrow a focus on a single ecotone, of course, risks masking other phenomena. For example, the high maximum turnover at northern sites in Michigan (Figure 6) is linked to large changes in *Pinus* and *Tsuga* abundances during the late Holocene (Figure S6) (Henne 2006; Booth, Brewer, et al. 2012). Compositional variation at sites in southern Michigan and northern Indiana is linked to shifting variations in the relative abundance of *Quercus* woodlands and mesic forests dominated by *Fagus grandifolia* (Wang et al. 2015; Schlenker et al. 2024). *Tsuga canadensis*, *F. grandifolia*, and *Betula lenta* expanded their ranges northward and westward through Michigan and into Wisconsin throughout the Holocene (Bennett 1985; Woods and Davis 1989; Jackson and Booth 2002). These species-level range dynamics interact with the MTZ dynamics studied here.

More broadly, other investigations have shown that, during the climate changes of the late Quaternary, eastern North American ecosystems experienced widespread changes in composition and structure, including, but not limited to, ecotonal regions (Gajewski 1987; Shuman et al. 2002, 2009, 2023; Williams et al. 2004). Similarly, dendroclimatic-based forecasts indicate that tree growth responses to 21st-century climate change will be widespread and spatially varying (Charney et al. 2016). Hence, the Tension Zone may be a locus of high sensitivity to climate change, but it is not the only one.

More sites would help sharpen reconstructions of past ecotonal dynamics. Notable gaps include western Michigan (Figure 1), where lake effect precipitation is highest (Henne et al. 2007) and where more sites may add further nuance to our understanding of the multiple environmental factors governing the past and future dynamics of the MTZ. Differences among sites in temporal extent may also affect the observed patterns of rates of change, particularly for maximum rates of change. While not all sites with full-Holocene extents experienced high RoC maxima, the sites with the highest RoC maxima all had full-Holocene extents (Figures 1 and 6).

### 4.4 | Ecoclimate Sensitivity of Tension Zone Position

If one assumes that the Tension Zone was in dynamic equilibrium with climate at the suborbital time scales studied here (Webb 1986; Williams et al. 2021), and that temperature primarily regulates Tension Zone position, then these analyses enable a first-order estimate of the ecoclimate sensitivity (Williams et al. 2022) of the Tension Zone. The northward shift of 150 km during the early Holocene warming of 2.5 to 3.5°$C_{July}$ (Salonen et al. 2025) indicates an approximate ecoclimate sensitivity of this ecotone of 40 to 60 km °$C_{July}^{-1}$, while the southward shift of 90 to 120 km during the late Holocene cooling of 1°C to 1.5°C suggests a sensitivity of 60 to 100 km °$C_{July}^{-1}$. If an alternative mapping of the MTZ, based on a fixed NMDS value of 0.244 is used (Figure S7), then the range of movement of the MTZ over the Holocene is reduced to 50 to 100 km, suggesting an ecoclimate sensitivity of 20 to 100 km °$C_{July}^{-1}$. For comparison, observed Michigan winter temperatures have increased over the past century (i.e., between 1901–1960 and 2002–2021) by ca. 1.2°C and summer temperatures by ca. 0.8°C (Marvel et al. 2023). 21st-century global temperature increases under IPCC scenarios range from 1.5°C to 4.5°C by 2100 CE (IPCC 2023), and temperature increases in Michigan are expected to be 1.5 times larger than the global mean (Marvel et al. 2023). Although vegetation lags will slow the rate of ecological response (Williams et al. 2021), these estimates of ecoclimate sensitivity and projected temperature changes imply near-future shifts in the Tension Zone by hundreds of kilometres.

However, these sensitivity estimates are preliminary, for several reasons. They attribute all shifts of the MTZ to July temperatures and assume spatially uniform climate changes, which are simplifications. Additionally, data and models differ over the magnitude of Holocene temperature changes (Salonen et al. 2025). Nonetheless, these estimates provide a useful precursor to future work to better estimate the ecoclimate sensitivity of the MTZ and other ecotones; this work needs to incorporate the best available paleoclimatic reconstructions and multivariate modelling with uncertainty of the climate factors governing the ecotonal dynamics of the MTZ.

## 5 | Conclusions

This work more tightly constrains the ecoclimate sensitivity of the Tension Zone in the eastern U.S. and supports the ecotonal sensitivity hypothesis that ecotonal ecosystems are more sensitive to climate change than distal regions. These findings suggest that the Tension Zone will be a locus of high ecological sensitivity to current climate changes.

At Sunrise Lake, large compositional variations at the Tension Zone manifest as declines in northern conifers and increases in southern hardwoods, interpreted to be temperature-governed, and as large variations in *Tsuga* and *Fagus* abundances that may be governed by shifting lake-effect snow and moisture availability. The high variability of Sunrise Lake and other sites near the MTZ supports the ecotonal sensitivity hypothesis, while also indicating that multiple environmental factors govern these past ecological changes.

Range of movement of the Tension Zone in Michigan during the Holocene spanned roughly 150 km, between a southernmost minimum at 11–10 ka and a northernmost maximum at 7–6 ka. With the additional data now available, past MTZ shifts were less extreme than previously reconstructed. Our analyses suggest a rough estimate of ecoclimate sensitivity for the Tension Zone of 40 to 120 km per °C of regional July temperature change.

To our knowledge, these are the first quantitative estimates of the sensitivity of this continental-scale ecotone. Given these ecoclimate sensitivity estimates and global warming scenarios of 1.5°C to 4.5°C by 2100 CE, the Tension Zone can be expected to respond by shifting hundreds of kilometres northwards. This research into past ecotonal dynamics supports expectations that contemporary ecotonal systems should be similarly sensitive to rising temperatures, making them both well suited for ecological monitoring and experiments and a focal area for experimental climate adaptation interventions.


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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The pollen and radiocarbon data from Sunrise Lake presented here have been deposited in the Neotoma Paleoecology Database (www.neotomadb.org, https://doi.org/10.21233/N09T-HB71), along with associated charcoal data (https://doi.org/10.21233/1CXH-KV93) and loss-on-ignition data (https://doi.org/10.21233/309s-2h92). The original data files for all other pollen datasets analysed here are available in the Neotoma Paleoecology Database (www.neotomadb.org) with Table S2 listing the citations and DOIs for all individual datasets. All R-based analytical workflows, the input datasets, and intermediate output data tables used to generate figures have been published to Dryad: https://doi.org/10.5061/dryad.pnvx0k71z.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Stress plot of NMDS solutions from the *vegan* package (Oksanen et al. 2022). **Figure S2:** Contours produced from empirical Bayesian kriging of NMDS Axis 2 scores, for the eleven 1000-year windows for the Holocene. **Figure S3:** The *Bchron* age-depth model (Parnell et al. 2008) from Sunrise Lake. **Figure S4:** Loss-on-ignition (LOI) percentages versus age at Sunrise Lake. **Figure S5:** Charcoal variations at Sunrise Lake, plotted as charcoal counts against age. **Figure S6:** Time series of NMDS scores for Axes 1–4, for each of the 20 sites in the Lower Michigan fossil pollen dataset. **Figure S7:** Alternative mapping of MTZ positions over time based on defining the MTZ as the NMDS2 value 0.244. **Table S1:** Age controls for the Sunrise Lake age-depth model. **Table S2:** Site metadata for each Lower Michigan fossil pollen record used in this analysis. **Table S3:** Statistical results ($R^2$ and $p$-value) for all linear models fitted in the main text. **Table S4:** NMDS values of the isoband 6 midline contour for each 1000-year interval, for the MTZ mapping shown in Figure 5.