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The influence of historic fire on the Midwestern Tension Zone[1]

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Abstract. The Tension Zone (TZ) is a prominent Midwestern ecotone where the flora of two major forest types (Northern Mixed Forests and Southern Broadleaf Forests) commingle, striking diagonally across the states of Wisconsin and Minnesota. Here, we evaluated the TZ's original placement as demarcated by previous scholars relative to the synecological and autecological characteristics of witness trees from US Public Land Survey records. Witness trees were categorized by temperature and fire relations, point data analyzed in GIS, and spatial outputs compared with the original TZ. Our temperature-based line, representing temperature relations of witness trees, generally corresponded with the original TZ. However, in the lee of firebreaks, isolated pockets of cool/cold mesophytic genera occurred south of the TZ, indicating that other environmental factors were involved in TZ expression. A pyrogenic-based line, created by classifying witness trees by fire relations, had two major northward departures from the original TZ where cold-adapted yet pyrophilic northern pines occurred on sandy glacial deposits. Fire was found to play a contributing role, being pervasive south of the TZ, whereas edaphically restricted to dry, sandy landscapes to the north. Climate change and fire suppression will exert future "tension" on the line, forcing uncertain movement across the landscape from these two divergent forces, with projected higher future temperatures pushing the TZ northward and fire suppression and accompanying mesophication (comprised of primarily cool/cold–based trees) pulling the TZ southward. An endpoint to the temperate-based Midwestern TZ was identified in northwest Minnesota, converting over to a Boreal-Prairie TZ northward.

Key words: Climate effects, disturbance ecology, edaphic effects, fire effects, Minnesota, public land surveys, vegetation change, Wisconsin

The Midwestern Tension Zone (TZ) and the underlining concepts it embodies have had a profound effect on ecological thought over the ages. Although the discovery of the TZ as an ecological entity dates to the late 1800s (Andersen 2005), it was eminent ecologist John Curtis whose work elevated the term to prominence (Curtis 1959). In the Midwest, the TZ is an important regional demarcation separating the Northern Mixed Forest from the oak (*Quercus*)-dominated Southern Broadleaf Forest. As currently defined, the line itself is floristically based, occurring where range limits of northern and southern plant species are concentrated. In essence, this ecotone represents a "tension" between northern and southern plants that are vying for dominance. Due to species range incongruences and overlap, the TZ is inherently broad, spanning tens of kilometers in width (Fig. 1; Curtis 1959).

Since the geographic limits of species are thought to be largely controlled by and reflective of climate, much research to date has focused on relating the TZ to climatic factors (Andersen 2005, Hupy 2012). Indeed, it has been established that the TZ has been sensitive to past changes in climate, shifting 320 km and 6° of latitude in Michigan since its formation roughly 10,000 years ago (Hupy 2012). However, this fixation on climate, consistent with early ecological thought and concepts (*sensu* Clements 1916, 1936), has left other influential factors largely unexplored. For instance, it is well known that disturbance factors, specifically fire, have a substantial effect on vegetation expression, oftentimes trumping climate and thus preventing climatic climax conditions from being realized (Nowacki and Abrams 2015). It is estimated that much of the world's vegetation is in a fire subclimax condition and that forest cover would effectively double (from 27% to 56%) in the absence of burning (Bond *et al*. 2005). More locally, it is acknowledged that human-ignited fires maintained the Prairie Peninsula during a cooler and moister climate since the end of the Thermal Maximum Period some 3,500 yrs ago (Anderson

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[1] We would like to thank Robert Vaughan (Remote Sensing/GIS Analyst at RedCastle Resources Inc. and USDA Forest Service Contractor, Geospatial Technology Applications Center, Salt Lake City, UT) for his extraordinary efforts in the identification and analysis of edaphic and climatic datasets for map generation.

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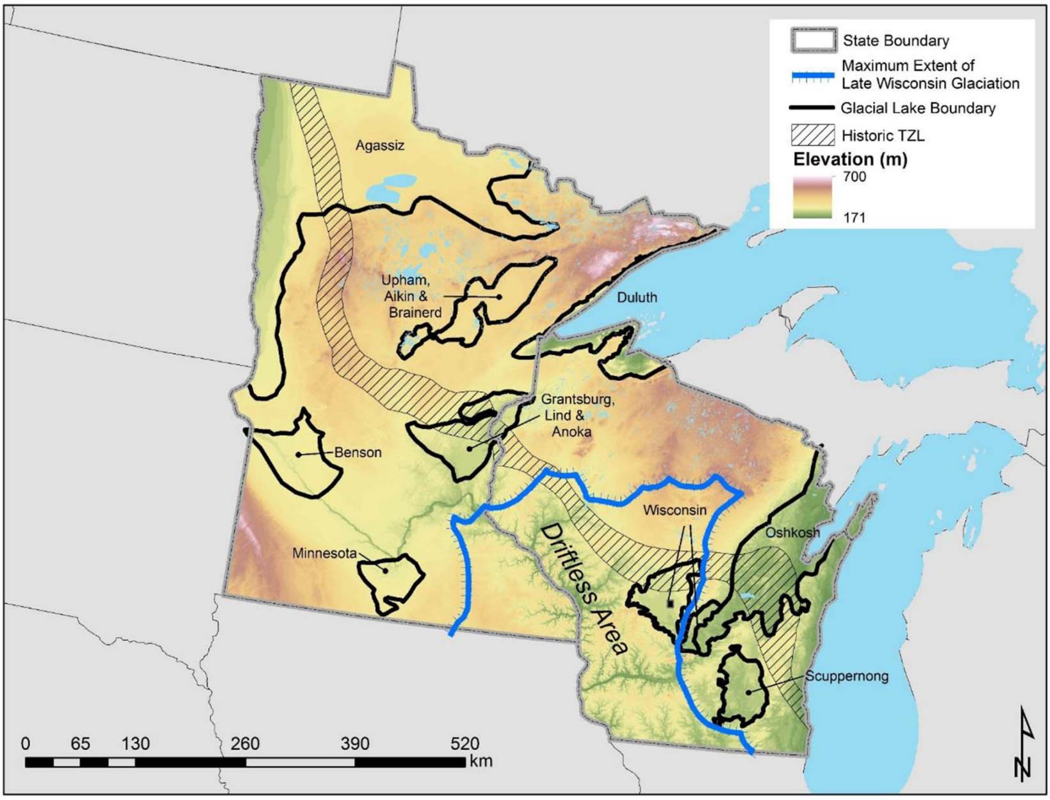

FIG. 1. The Tension Zone (TZ) relative to elevation, Maximum Late Wisconsin glaciation, and glacial lake deposits. The original TZ (hatched) was compiled from the work of Buell and Wilbur (1948; Fig. 1) for Minnesota, and Curtis (1959; Fig. 5) for Wisconsin. Glacial features in Minnesota based on Johnson *et al.* (2016; Figs. 3 and 13) and in Wisconsin on Mickelson and Attig (2017), Clayton (2001; Fig. 19), and Syverson and Colgan (2011). Glacial deposits are typically fine-textured/clay-based except for Glacial Lake Wisconsin, which is sandy.

2006). Without anthropogenic burning, most of the Prairie Peninsula, the eastward expansion of tallgrass prairie described by Transeau (1935), would have probably converted to forested conditions during the current Neoglacial climatic regime (Abrams and Nowacki 2015), as this transition readily occurs where fire is suppressed and natural succession ensues (Nowacki and Abrams 2008).

US Public Land Survey (PLS) records have fostered significant advances in historical and restoration ecology through enhanced understanding of pre-European forest compositions, structures, and disturbance regimes (Bourdo 1956; Lorimer 1977; Canham and Loucks 1984; Whitney 1986, 1987; Schulte and Mladenoff 2001). The advent of Geographic Information Systems (GIS) and digital versions of witness-tree data (trees listed in early land surveys or deeds that identify a corner or line) have resulted in a great acceleration of learning (Manies and Mladenoff 2000, Bolliger and Mladenoff 2005, Wang and Larsen 2006, Hanberry *et al*. 2012a). This epiphany of discovery continues with the coupling of witness-tree data across multiple states in a GIS environment, which now allows for sophisticated geospatial analyses at a regional level (Thompson *et al*. 2013, Goring *et al*. 2015).

Range limits where northern and southern plant species converge have been exclusively used for TZ delineation (Andersen 2005). Now, with the spatial availability of and ability to process massive witness-tree datasets, alternative methods to TZ delineation can be pursued by employing the synecological characteristics of tree species (Nowacki and Abrams 2015). Specifically, this can be accomplished by grouping trees into temperature classes (cool/cold-based "northern" genera vs. warm/hot-based "southern" genera) and geospa-

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tially displaying where these two classes are roughly equivalent in abundance on the landscape. Moreover, to investigate spatial relationships between fire and the TZ, witness trees can also be categorized by fire relations, thus using them as indicators of past fire settings (Thomas-Van Gundy and Nowacki 2013). These spatial analyses will allow for a more thorough examination of the TZ and influencing factors, including the importance of historic fire on its location.

Materials and Methods. Analysis Area. The analysis area covers Minnesota (MN) and Wisconsin (WI) and includes two forest-dominated provinces, the Laurentian Mixed Forest and Midwest Broadleaf Forest (Cleland *et al*. 2007, McNab *et al*. 2007). The climate of the Laurentian Mixed Forest province is continental with maritime influence along the Great Lakes. Most precipitation occurs during the warm summers and winters are moderately long, often with continual snow cover. Past glaciation has created a terrain of low relief with some hilly areas. Forest types are mixes of cold boreal and cool temperate species. In comparison, summers in the Midwest Broadleaf Forest province are considered warm to hot, while the climate regime remains continental. This province experiences frequent growing season droughts. The area was mostly glaciated resulting in flat to undulating terrain, the exception being the highly dissected, non-glaciated Driftless Area. Forests are composed mainly of warm-adapted deciduous species, many of which are able to tolerate periodic droughts.

The forests of the upper Great Lakes underwent relatively rapid and widespread destructive logging from the mid-1800s to the early 1900s, dubbed the "Great Cutover" (Whitney 1987, Schulte *et al*. 2007). Wildfires often followed logging and some areas were converted to agriculture (and some later abandoned) while others were simply left to reforest naturally (Whitney 1987, Andersen *et al*. 1996, Stearns 1997). The current forests in this region are considered homogenized; simplified in structural complexity, lower in species diversity, and lower in functional diversity compared to their presettlement counterparts (Rooney *et al*. 2004, Schulte *et al*. 2007, Hanberry *et al*. 2012b).

Climate and Edaphic Data. To explore the role of climate in the depiction of the TZ, climate data were acquired from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) website for the time period of 1981–2010 (PRISM Climate Group 2014). Specifically, we used the 30-year normal dataset, a set of temperature and precipitation data of average annual conditions over the most recent three full decades. We acquired the 800 m resolution data for mean annual temperature and precipitation for the two-state study area. These long-term data were modeled from weather station data using a digital elevation model as the predictor grid (Daly *et al*. 2008). Mean annual temperature is calculated by averaging daily maximum and minimum temperatures. Mean annual precipitation is the yearly average of rain plus melted snow.

Potential evapotranspiration (PET) was calculated for the conterminous United States using the Hamon equation (Lu *et al*. 2005). First, monthly temperature data for 1981–2010 were acquired from the PRISM data set (PRISM Climate Group 2014). Then, monthly sunlight hours for each raster grid cell (4 km) were calculated using methods found in Allen *et al*. (1998). We used a C factor (or k proportionality, a unitless coefficient) calculated using methods from McCabe *et al*. (2015) and gridded evapotranspiration tables from Farnsworth and Thompson (1982) to estimate PET in mm.

Actual evapotranspiration (AET) was calculated using a Zhang-Budyko curve (Zhang *et al*. 2001) using the same monthly temperature data from the PRISM data set, with an empirical constant (w) set to 2.63. This constant varies with local vegetation and climate from 2.15 to 3.75 (Zhang *et al*. 2004); however, we used 2.63 based on Rasmussen *et al*. (2015) since there is no optimal way to assign a value to individual ecosystems.

Soils data were developed from gridded USDA-NRCS Soil Survey Geographic (gSSURGO) datasets for Minnesota and Wisconsin (https://gdg.sc.egov.usda.gov/; Soil Survey Staff 2016a). The two state files were joined together through the mosaic to new raster function in ArcGIS with a cell size of 10 m. Each cell is assigned a unique map unit key for identification and link to the associated database (Soil Survey Staff 2016b). We queried the SSURGO dataset for cation exchange capacity, soil temperature regime, soil drainage class, and available water storage for each map unit within the two states. Cation exchange capacity (CEC for the top 25 cm), and soil temperature regimes were calculated for the dominant map unit by percentage of area (Soil Survey Staff 2016b). Soil drainage

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class was calculated based on the dominant condition found within the soil map unit. Available water storage capacity (AWS for the top 25 cm) was calculated as a weighted average of map unit components (Soil Survey Staff 2016c).

Witness-Tree Data. We used the aggregated witness-tree database created for Minnesota and Wisconsin by Goring *et al*. (2015) to explore the spatial relationships of tree genera, when categorized by temperature and fire classes, to the TZ. To create the database, PLS data from various sources (Wisconsin—Maines and Mladenoff 2000, Schulte *et al*. 2002; Minnesota—Almendinger 1996) were merged to create a seamless dataset with attention given to reducing common errors and biases known to occur in PLS data (Goring *et al*. 2015).

According to Goring *et al*. (2015), to standardize the dataset and address surveyor bias, no line or meander trees were included; only the two trees closest to the corner were included and were included only if (1) there were at least two trees, (2) the two trees were from different quadrants, (3) the azimuth to each tree was valid, and (4) each tree had a valid diameter breast height (DBH). To reduce transcription errors, points and trees were removed from the dataset where: (1) multiple large DBH trees were recorded within short distances to the corner, (2) trees were recorded with DBH of 254 cm (100 in) or greater, (3) azimuths were unclear, and (4) trees were recorded as corners but azimuths were recorded for those trees as well (Goring *et al*. 2015). Because of confusion between common and scientific names and the large number of surveyors involved in a multistate dataset, trees were only identified to genus level (Goring *et al*. 2015). In most cases, synecological characteristics appear consistent within a genus (Pausas and Keeley 2009, Nowacki and Abrams 2015), so this generalization was not seen as detrimental to our analysis.

Goring *et al*. (2015) aggregated and standardized the tree counts by genera and total number of trees to an 8 × 8 km grid. From this grid, a centroid point was created with each point retaining the grid cell attributes. Water cells were not included in the final dataset but other points and subsequent cells without trees were included.

To assess the TZ location across the two-state study area as a function of tree genera adaptations to a temperature regime, we categorized the witness-tree genera into temperature classes (Table 1) using average annual temperatures across a given genera's range as reported by Nowacki and Abrams (2015). The percentage of stems classified as cold or cool was calculated by summing the number of trees designated as cold or cool and dividing by the total number of stems at each centroid point. No temperature class was assigned to unidentified trees (no genus given).

We assessed the relationship between the TZ and past fire occurrence using witness trees as pyro-indicators. We designated each genus in the dataset as either pyrophilic or pyrophobic (Table 1; Thomas-Van Gundy and Nowacki 2013, Thomas-Van Gundy *et al*. 2015). Pyrophilic trees are those that require fire in part of their life cycle, whereby fire serves as a rejuvenating force by facilitating their regeneration while preventing their elimination through natural succession. Our assignments were based on the responses of species within a genus to a long-term fire regime, not just one fire, as many species can endure a fire event, in part, by resprouting. No species or genus is adapted to fire but is adapted to a fire regime (Keeley *et al*. 2011). Our designations categorize a genus' response to a disturbance regime including frequency, intensity, and what part of the ecosystem is affected (*e.g.,* surface fire or crown fire). Across the analysis area, historic fire regimes range widely based on vegetation and site conditions from periodic, high-intensity crown fires in jack pine (*Pinus banksiana*) on sandy outwash plains to rarely burned northern hardwood systems on loamy mesic landscapes (Cleland *et al*. 2004). Three genera were difficult to classify, possessing both pyrophobic and pyrophilic tendencies: birch (*Betula*), spruce (*Picea*), and tamarack (*Larix*). Since pyrophilic paper birch (*Betula papyrifera*) was distributed across a greater portion of the study area compared to the somewhat pyrophobic yellow birch (*Betula alleghaniensis*; restricted mainly to northern hardwood systems of Wisconsin), we designated birch as pyrophilic. Since spruce is often set back by fire (*e.g.,* aspen [*Populus*] often benefits from fire relative to spruce in subboreal forests), it was designated pyrophobic. Since tamarack is often relegated to wetlands, it was designated pyrophobic.

For each point record, we tallied the number of pyrophilic and pyrophobic genera. Using the total tree count in the original dataset, we then calculated the pyrophilic percentage for each centroid point. Using ArcMap, we converted the point data to a grid (cell size 8 × 8 km to match

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Table 1. Tree genera in the witness tree dataset and their classification by pyrogenicity (Nowacki and Abrams 2015, Thomas-Van Gundy and Nowacki 2013) and temperature class (Nowacki and Abrams 2015).

Common name	Scientific name	Pyrogenicity	Temperature class
Alder	*Alnus*	pyrophobic	NA
Ash	*Fraxinus*	pyrophobic	cool
Basswood	*Tilia*	pyrophobic	cool
Beech	*Fagus*	pyrophobic	cool
Birch	*Betula*	pyrophilic	cold
Blackgum	*Nyssa*	pyrophilic	hot
Buckeye	*Aesculus*	pyrophobic	warm
Cedar/juniper	*Thuja/Juniperius*	pyrophobic	cold
Cherry	*Prunus*	pyrophobic	warm
Dogwood	*Cornus*	pyrophilic	warm
Elm	*Ulmus*	pyrophobic	warm
Fir	*Abies*	pyrophobic	cold
Hackberry	*Celtis*	pyrophobic	warm
Hemlock	*Tsuga*	pyrophobic	cool
Hickory	*Carya*	pyrophilic	warm
Ironwood	*Ostrya or Carpinus*	pyrophobic	warm
Maple	*Acer*	pyrophobic	cool
Oak	*Quercus*	pyrophilic	warm
Pine	*Pinus*	pyrophilic	cold
Poplar	*Populus*	pyrophilic	cold
Spruce	*Picea*	pyrophobic	cold
Sycamore	*Plantanus*	pyrophobic	cold
Tamarack	*Larix*	pyrophobic	cold
Tulip poplar	*Liriodendron*	pyrophobic	warm
Walnut	*Juglans*	pyrophobic	warm
Willow	*Salix*	pyrophobic	cool
Other hardwood		pyrophobic	NA
Unknown tree		pyrophobic	NA

original dataset) and used mean pyrophilic percentage as grid value. The same conversion from point to grid was made for mean percentage of cool/cold genera using the same grid size.

The resulting grids were used to create contours of the mean cool/cold genera and pyrophilic percentage values (Spatial Analyst in ArcMap). From these contours two new depictions of the TZ were created: a temperature-based TZ following the 50% cool/cold genera contour and a pyrogenic-based TZ along the 50% pyrophilic percentage contour. We compared both the temperature-based TZ and the pyrogenic-based TZ to the original TZ as compiled from various published sources.

Results. The undulating TZ, as projected by Buell and Wilbur (1948; MN) and Curtis (1959; WI), takes a northwesterly course from southeast WI to central MN before veering northward (Fig. 1). This line is seemingly indifferent to topographic and glacial features, striking from low elevations along Lake Michigan through the highlands of central MN, across nonglaciated ("driftless") and glaciated terrain, and, within the latter, crossing clay-enriched, glacial lake basins, loam-based moraines, and sandy outwash plains. This indifference seemingly holds for important soil properties as well, including drainage, available water storage (AWS), and cation exchange capacity (CEC; Fig. 2), although there seems to be some relation to AWS and CEC along the western sectors of MN. There is a stronger correspondence to soil temperature regime, an edaphic depiction of climate, at least along the middle segment of the TZ.

Visually comparing the TZ directly with primary climate factors was surprisingly equivocal, as it practically spanned all temperature and precipitation classes (Fig. 3a, b). However, spatial relations emerged when evaluating the TZ against evapotranspiration—a more robust and seemingly ecological metric that couples temperature and precipitation factors. In particular, much of the TZ paralleled and fell within the 400–425 mm class of summer potential evapotranspiration (Fig. 3c). This, along with soil temperature regime, lend credence to earlier notions that the TZ was reflective of climate (Andersen 2005, Hupy 2012).

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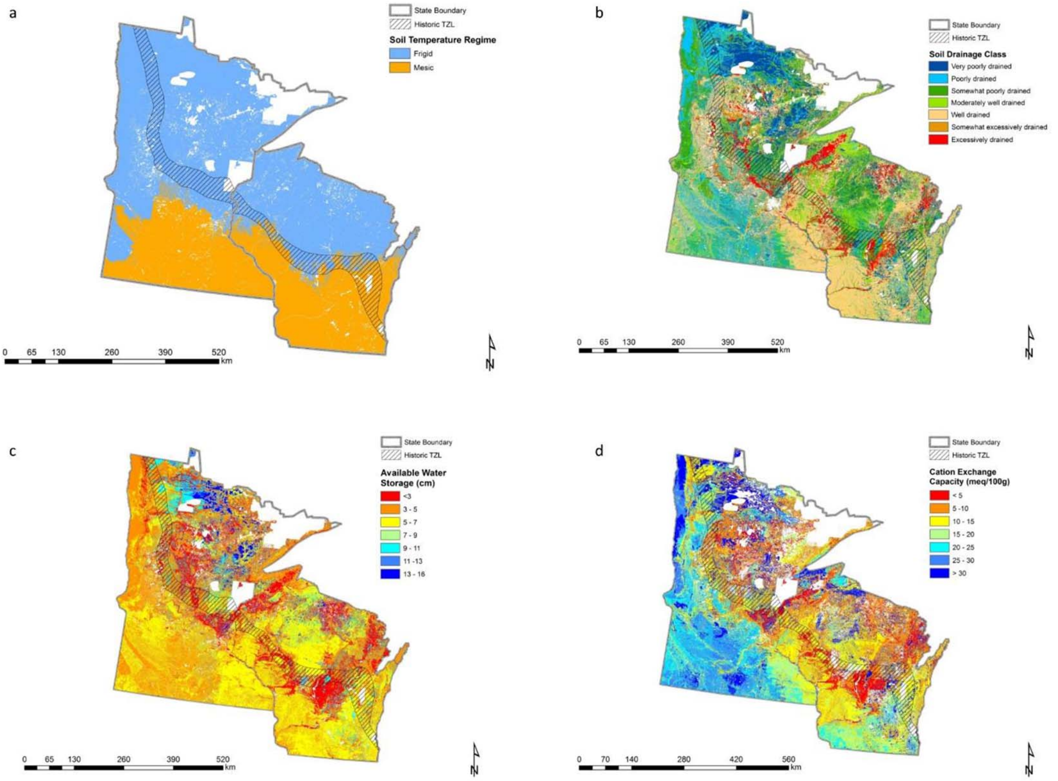

FIG. 2. The Tension Zone (TZ) relative to soil temperature regimes, drainage class, available water storage, and cation exchange capacity. Legend color schemes represent environmental gradients from blues (cooler, wetter, and higher in CEC) to reds (warmer, drier, and lower in CEC).

The witness-tree–based temperature line created from our classification of the genera into cool/cold and warm/hot groupings undulates along a diagonal from southeastern WI to central MN before turning abruptly northward (Fig. 4). Its general trajectory mirrors that of the original TZ (hatched area, Fig. 5). Compared to the original TZ that reflects a spectrum of plant lifeforms, our temperature line strictly based on arboreal vegetation runs a more southerly track (Table 2).

Interestingly, concentrations of cool/cold tree genera form distinct outliers farther south, notably (but not exclusively): (1) the Big Woods of south-central MN (Grimm 1984), (2) an area east of the Kickapoo River within the Driftless Area of southwest WI (Kline and Cottam 1979, Shea *et al*. 2014), and (3) a drumlin field east of the Rock River in southeastern WI (see Fig. 4 for numbered locations). These three examples indicate that isolated populations of cool/cold trees did exist, sometimes in abundance, in locations somewhat removed from the TZ. But what are those circumstances or driving factors that allowed these southern outliers of cool/cold genera to exist, as temperatures increase rather uniformly to the south (Fig. 3a) and all three areas experience high summer PET (Fig. 3c)?

One central factor explaining the geolocation and configuration of these three outlying areas is historical fire occurrence. Surface fires were frequent in this part of the Midwest (Midwest Broadleaf Forest Province; Cleland *et al*. 2007), driven by prevailing westerly winds that pushed fires eastward across the landscape (Gleason 1913, Curtis 1959). Here, firebreaks in the form of rugged topography, waterbodies (lakes, ponds, and wetlands), and large north-south flowing rivers greatly controlled fire expansion and thus had a profound effect on historic fire regimes (Dorney 1981, Grimm 1984, Leitner *et al*. 1991, Thomas-Van Gundy *et al*. 2020). It is important to note that all three outliers are located on the leeward (east) side of known firebreaks. Moreover, these outliers are mainly comprised of fire-sensitive genera of

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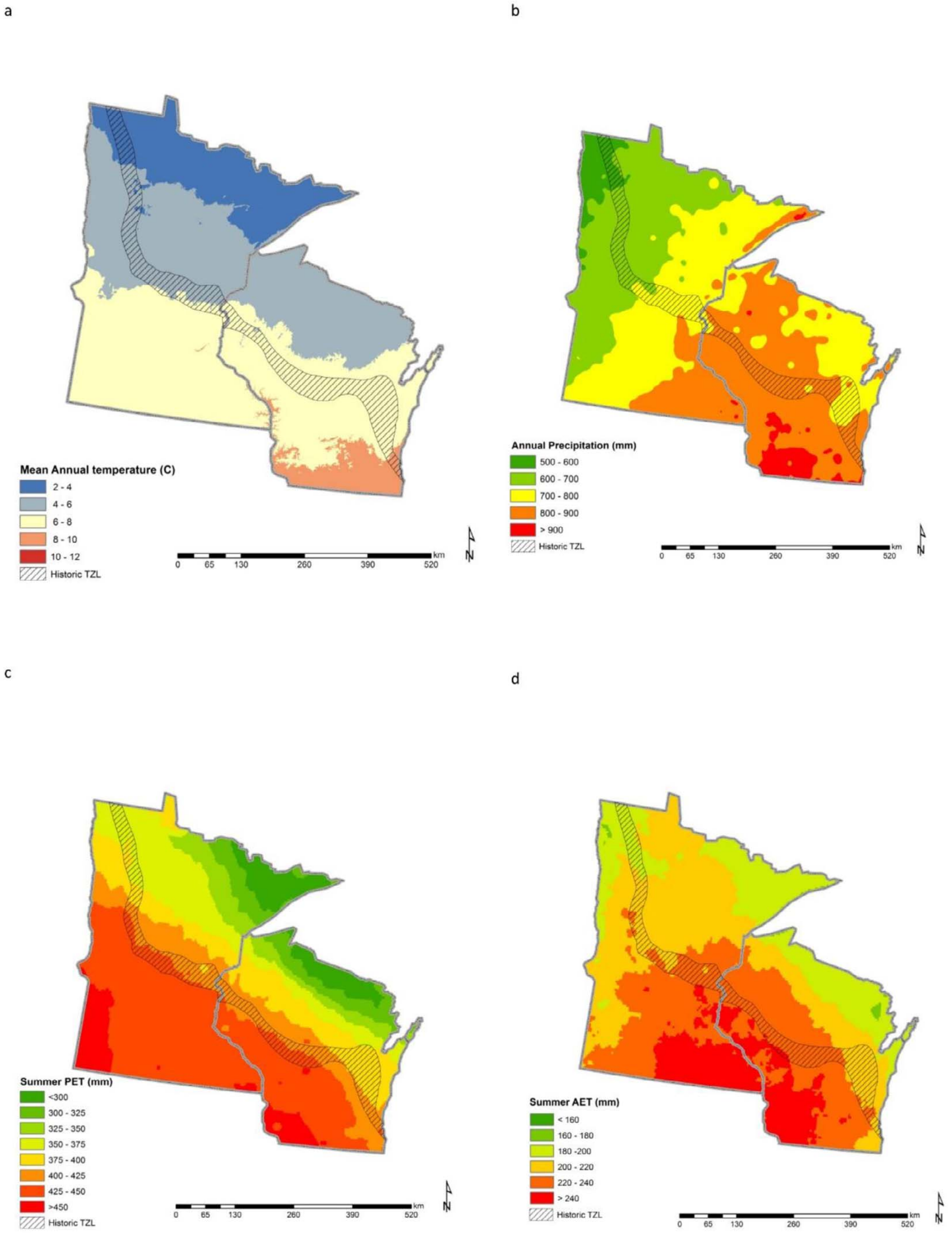

FIG. 3. (a) Mean annual temperature, (b) mean annual precipitation, (c) summer potential evapotranspiration (PET), and (d) summer actual evapotranspiration (AET) over a 30-yr period for the two-state study area.

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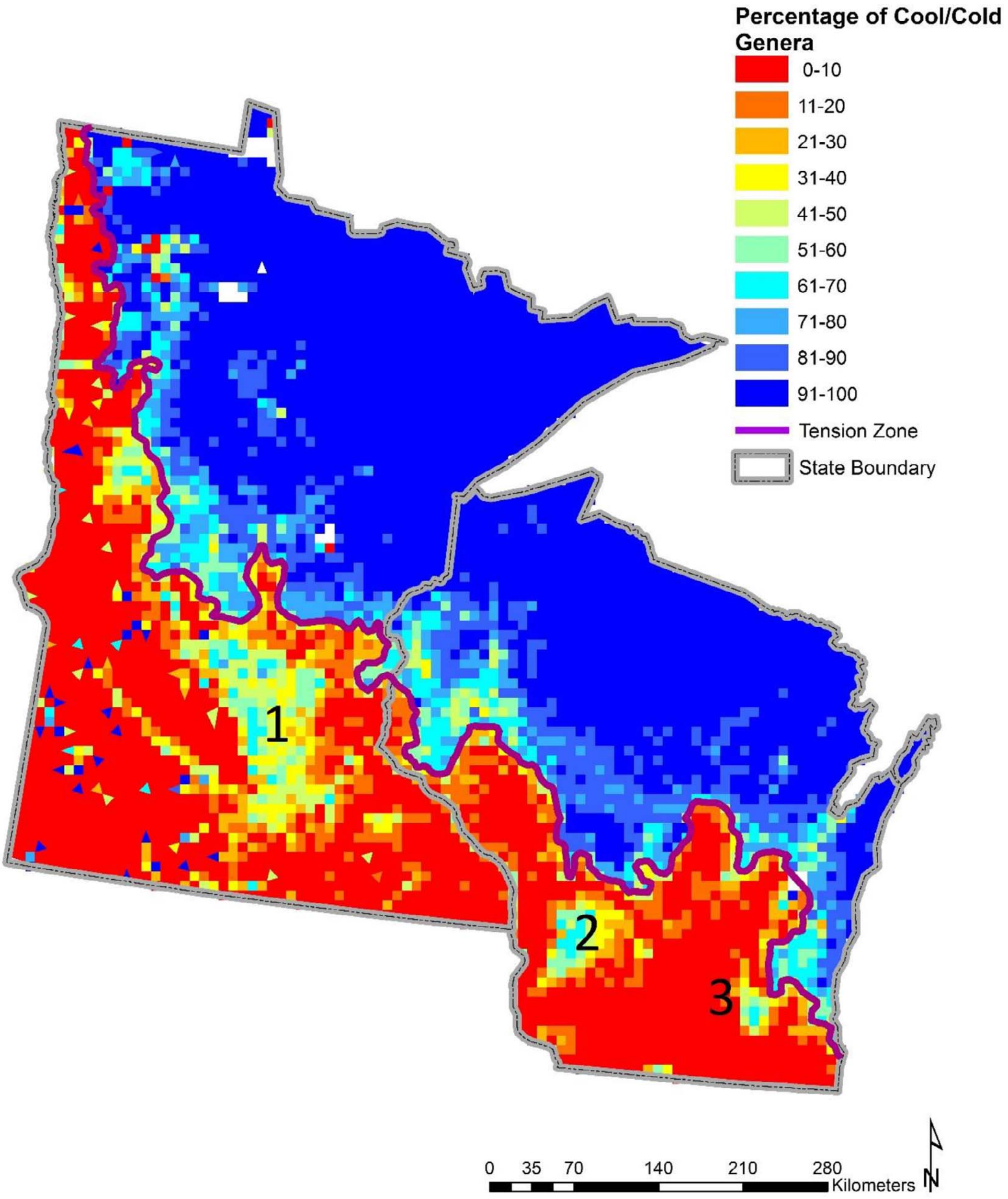

FIG. 4. Spatial display of percentage classes of cool/cold temperature genera. The temperature-based Tension Zone is reflected in the line where 50% of the genera are in the cool/cold category. Three forested cool/cold outliers include: 1 = Big Woods (MN), 2 = Kickapoo River (WI), and 3 = Rock River (WI).

maple (*Acer*), basswood (*Tilia*), elm (*Ulmus*), ash (*Fraxinus*), and ironwood (*Ostrya*; Nowacki and Abrams 2015). In landscapes where fire was the principal disturbance factor, it makes ecological sense that these fire-sensitive mesophytes would be largely confined to areas protected from recurrent fire (Gleason 1913; Grimm 1984; Anderson 2006).

This revelation spurred us to create a second line reflecting arboreal fire relations, thus lending information to further assess the ecological underpinnings of the original TZ (*i.e.,* climate *vs*. fire). Fortunately, the pyrogenic relations of trees have been previously deployed to approximate the TZ in the northeastern U.S. (see Fig. 10 of

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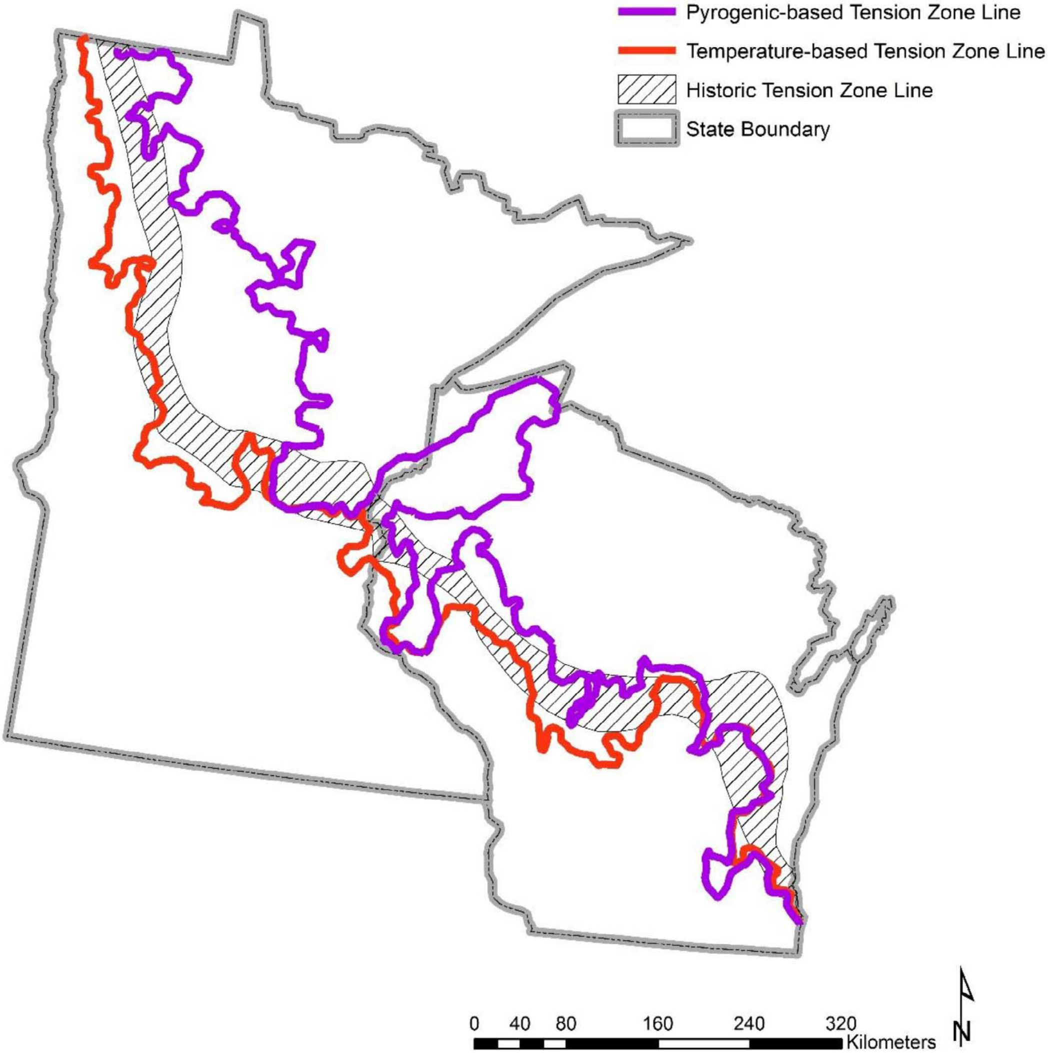

FIG. 5. The original Tension Zone (hatched) of the Upper Midwest in comparison to the temperature- and pyrogenic-generated TZs (this study).

Thomas-Van Gundy *et al*. 2015). By applying the same method (using a 50% contour of witness-tree–based pyrophilic percentage), a "pyrogenic line" was created that generally strikes northwestward from southeast WI to northwest MN (Fig. 6). Two pronounced northward extensions relative to the original TZ exist (see pyrogenic line of Fig. 5), which encompass (1) an elongated, southwest-to-northeast–trending interlobate moraine in northwestern WI (Bayfield Sand Plains; Cleland *et al*. 2007, Radeloff *et al*. 1999) and (2) an expansive sand outwash plain in west-central MN. It appears

Table 2. Locational comparison of fire- and temperature-based depictions of the Tension Zone (TZ) with the original TZ area.

	Length of TZ (km)			
TZ depiction	Within original (% of total)	North of original (% of total)	South of original (% of total)	Total
Fire-based	856.3 (28.8%)	1,624.5 (54.7%)	488 (16.4%)	2,968.8
Temperature-based	776.4 (38.4%)	0	1,243.4 (61.6%)	2,019.8

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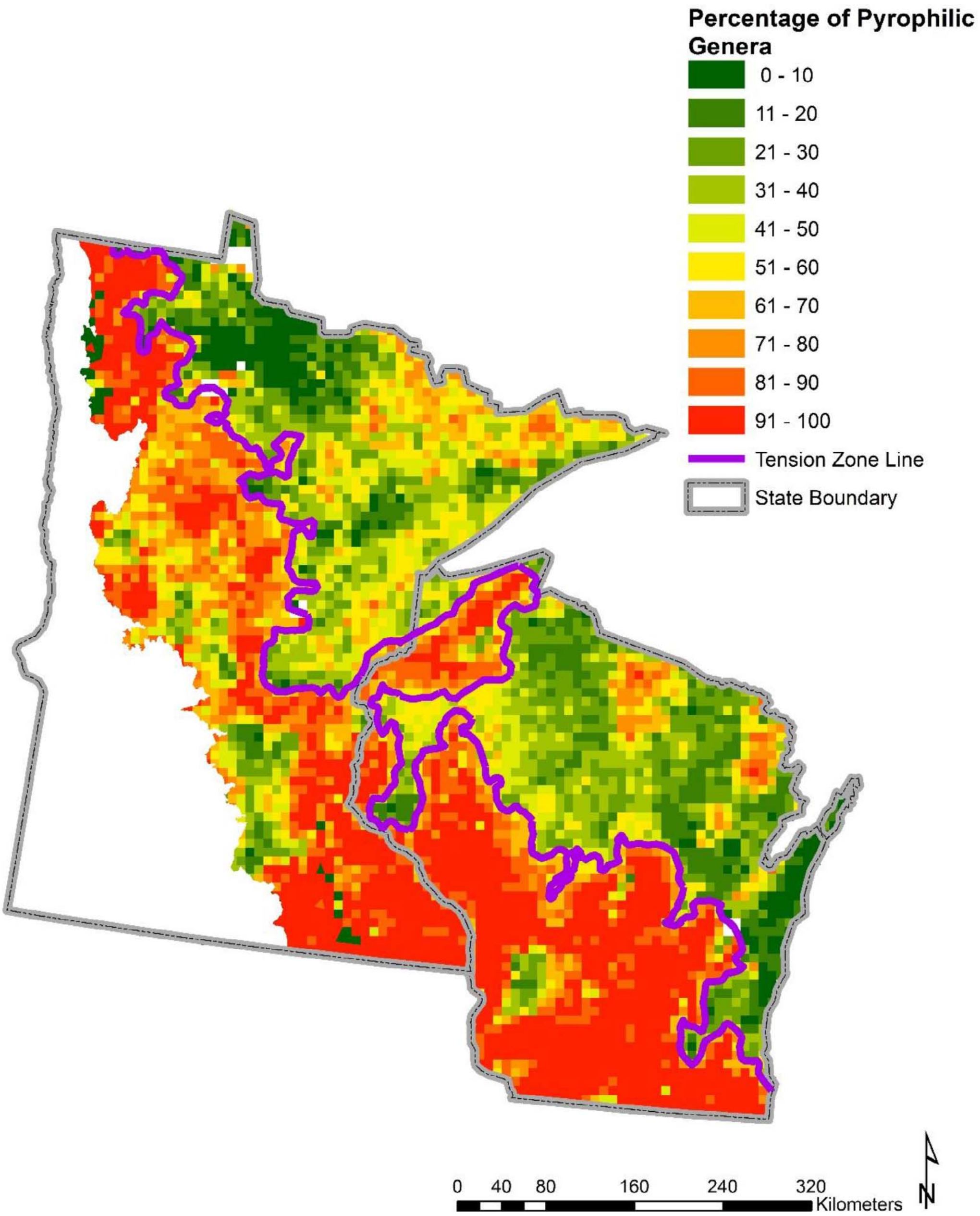

Fig. 6. Spatial display of the percentage of trees considered pyrophilic. The pyrogenic-based Tension Zone is reflected in the line where 50% of the genera are considered pyrophilic.

that the lengthy northward offset of our fire-based TZ (Table 2) is largely due to the presence of northern pines (*Pinus strobus, Pinus resinosa*, and *Pinus banksiana*) that formerly thrived on these dry, infertile, glacially derived sands (Fig. 7a). These northern pines, together with aspen (Fig. 7b), are classified as cold-based, pyrophilic trees (Nowacki and Abrams 2015).

Comparing temperature- and fire-based lines to the original TZ, it is readily apparent that the former provides the best fit (Fig. 5, Table 2), reinforcing climate as the TZ's primary basis.

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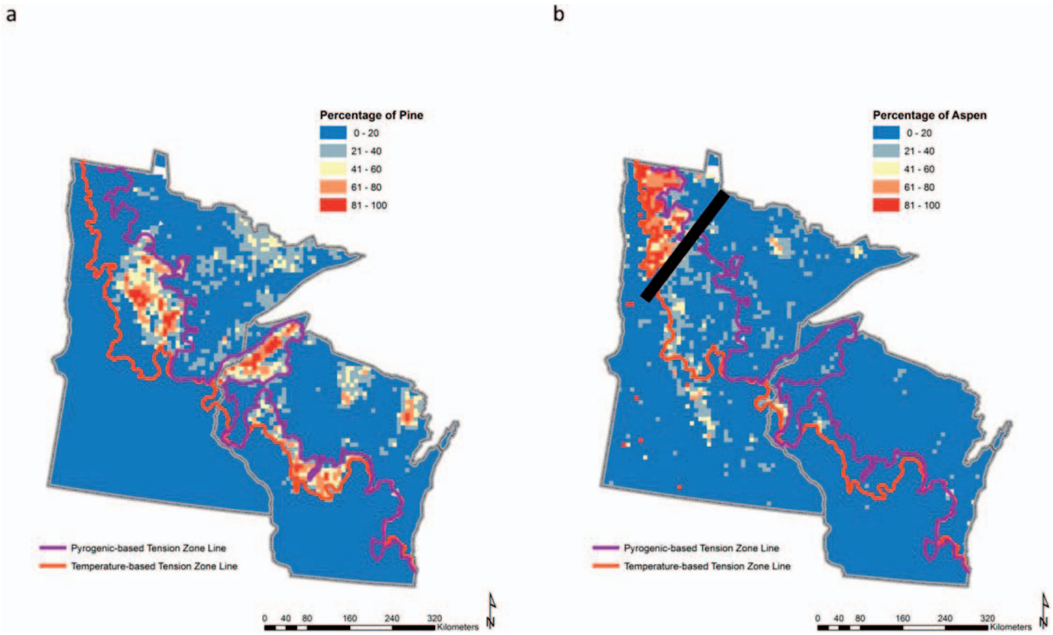

FIG. 7. The witness-tree percentage of (a) pine and (b) aspen compared to the two Tension Zone (TZ) depictions. Note that high concentrations of these two genera lie in between the two TZs. By our estimation, the black line (b) represents the endpoint of the Midwestern TZ, which is supposed to divide floras of two major temperate forest types.

Historic fire did play a role on both sides of the TZ, however differed by being a pervasive disturbance agent to the south whereas spatially restricted to drier, coarse-textured landscapes to the north. It is interesting to note that if the pyrogenic line was redrawn to exclude areas of high pine and aspen abundance, including the outwash/offshore sands of Glacial Lake Wisconsin and sandy pediment valleys in west-central WI (Wisconsin Central Sands; Cleland et al. 2007, Clayton and Attig 1989), the resultant line would closely resemble the temperature-based line across much of its length. The abrupt transition from pine to aspen dominance in northwestern Minnesota probably represents a temperate-boreal interface (see black line on Fig 7b). It is at this juncture where the Midwestern TZ, which theoretically divides the distinguishing flora of two major temperate forest types (northern hardwoods from central hardwoods), truly ends. From this point northward, the line represents a Boreal-Prairie TZ where Boreal Mixed Forests interface the Great Plains. The beginning of the Boreal-Prairie TZ roughly corresponds to the southern margin of the 2–4 °C mean annual temperature class in northwestern Minnesota (Fig. 3a).

Discussion. We employed a novel approach to evaluate the Midwestern Tension Zone by converting witness trees into temperature and fire phytometers based on their synecological and autecological characteristics (Thomas-Van Gundy and Nowacki 2013; Nowacki and Abrams 2015). When comparing our witness-tree-based temperature and pyrogenic lines to the original TZ, the best alignment was with the former. This reconfirms climate as the primary driver of the Midwestern TZ, aligning closely with summer potential evapotranspiration (Fig. 3c). Historic fire spatially differed on each side of the TZ, being pervasive south of the TZ where it supported oak dominance, whereas it was edaphically relegated to dry, sandy landscapes of pine dominance to the north. Historic fire may have played a secondary role in TZ placement, shunting it northward (relative to its true climate location) as islands of cool/cold species existed south of the TZ where firebreaks occurred. Indeed, enclaves of mesic, fire-sensitive trees on the lee (east) side of fire breaks are well

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documented throughout the presettlement Midwest (see Thomas-Van Gundy et al. 2020).

Cool Pyrophobic Forests in a Warm Pyrophilic Region. Within the Midwest Broadleaf Forest Province, forested islands of cool-based, fire-sensitive, mesophytic species occurred in areas adjacent to natural fire barriers such as in the midst of rugged, broken topography or in the lees of north-south running streams, wetlands, and lakes (Gleason 1913; Leitner *et al.* 1991, Anderson 2006, Thomas-Van Gundy and Nowacki 2016, Thomas-Van Gundy *et al.* 2020). The Big Woods of south-central MN is one prime example of one such island south of the TZ (Area #1 of Fig. 4). It is speculated that this ecosystem formed approximately 300 to 600 years ago in the lee of topographic and water-based firebreaks during a period of cooler and moister climate (end of Mediaeval Climate Anomaly; beginning of the Little Ice Age) and possible Native American depopulation (McAndrews 1968, Grimm 1983, Umbanhowar 2004). Here, even under somewhat drier conditions compared to the other identified mesophytic islands to the east (Fig. 3b), an elm-maple-basswood forest existed in pre-European times (Daubenmire 1936, Grimm 1984). There is no correlation between the configuration of the Big Woods (and its oftentimes sharp western edge) and climate (Daubenmire 1936, Grimm 1984). Here, firebreaks were the major controlling factor of presettlement vegetation patterns, with edaphic factors influencing vegetation within that pattern (Grimm 1984). Grimm (1984; page 308) details that “In many places the physical environmental factors (climate, soils, and topography) were virtually identical on opposite sides of the firebreak, yet very different kinds of persistent vegetation occurred”. Furthermore, according to Daubenmire (1936), in the absence of fire, the climatic limit of this forest would lie approximately 100 miles (161 km) to the west.

An extensive maple-basswood-elm forest existed northeast of the confluence of the Kickapoo and Wisconsin rivers (Area #2 of Fig. 4). Although the reason of this mesophytic “island” within an oak-dominated landscape was initially not clear (Trewartha 1940), its origin has been subsequently ascribed to firebreaks, in the form of the Wisconsin River (southern boundary), Kickapoo and Kickapoo West Fork rivers (western boundary), and a prominent ridge system along its northern boundary (Marks 1942, Shea *et al.* 2014). Evaluating fire, soils, and climate as possible causal agents, Kline and Cottam (1979) linked the origin of this mesophytic island to both water and topographic firebreaks. There were no observable differences in soils accounting for spatial changes in forest types (Kline and Cottam 1979). However, when meticulously searching for climate basis for this mesophytic island, Kline and Cottam (1979) speculated that a unique mesoclimate of cool summer temperatures and high annual precipitation existed. The more precise and recent PRISM-based climate data did show increased precipitation in this area (Fig. 3b), yet summer PET and AET was high consistent with surrounding areas (Fig. 3c, d). We agree with Marks (1942), who mentioned that essentially the same climate exists across Vernon County (which spans the mesophytic island border) and that the stark change in presettlement composition can only be explained by active Native American burning along the Mississippi River, which dissipated eastward, especially when encountering the Kickapoo River and its West Fork.

The confluence of the Bark and Rock rivers marked the southwest corner of a mesophytic island in southeastern Wisconsin (see Figs. 1 and 2 of Dorney 1981). From here, the north-south–oriented Rock and Crawfish rivers and affiliated marshlands effectively divided oak savannas (west) from climax maple-basswood forests (east) in Jefferson County (Zicker 1955); a pattern that continued northward along the Rock River to the Horicon Marsh in Dodge County (Neuenschwander 1957, Dorney 1981). Similarly, the Bark and Scuppernong rivers marked this stark change of vegetation along its southern boundary. In the northeasterly lee of this river network lies a concentrated cluster of drumlins within the former lakebed of Glacial Lake Scuppernong (Milfred and Hole 1970; see Fig. 19 of Clayton 2001). Apparently, the north-south orientation of this drumlin field and increased topographic roughness afforded further protections from presettlement fires driven by prevailing westerly winds. Since no significant correlation existed between presettlement vegetation and soil properties (drainage class, soil texture, available soil moisture, etc.), vegetation patterns were found to be the sole reflection of fire occurrence (Dorney 1981). Numerous historical references support this interpretation as a water-based firebreak (Zicker 1955, Vogl 1969). Our research implicates fire as the main determi-

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nant as this area is a disjunct mesophytic island based on temperature relations (Area #3 of Fig. 4), yet it occurs within a pyrophobic peninsula (Fig. 6).

Taken altogether, the existence of cool/cold mesophytic islands south of the original TZ indicates that forces other than climate were at work. The correspondence of these pyrophobic islands in fire-protected locations within a pyrophilic oak-dominated landscape strongly implicates fire. Without recurring historic fire, surely the TZ would have been located substantially southward, as climatic conditions were not the limiting factor of cool/cold–based forests to the south.

Fire Cessation and its Effects on the Midwestern Tension Zone. If past fire influenced the TZ placement on the landscape, then the loss of fire as a primary disturbance agent would seemingly allow the TZ to drift towards its true climate-based limits (Daubenmire 1936). Interestingly, fire suppression has been the case across most of the eastern United States for nearly 100 years (Nowacki and Abrams 2008). If burning continues to be suppressed on the landscape, it is likely that the TZ would shift southward contingent with the expansion of cool-based, shade-tolerant mesophytes (Nowacki and Abrams 2015).

However, other drivers of forest composition changes in the region may make any such shift difficult to determine (*e.g.,* deer herbivory; Frerker *et al*. 2014). Comparisons of current forest in the study area to presettlement forest have shown that homogenization (in the Laurentian Mixed Forest Province) and mesophication (in the Midwest Broadleaf Forest) are both occurring (Hanberry *et al*. 2012b). While different mechanisms and different species are indicative of these two processes, the results are the same—forests increasingly dominated by mesic and shade-tolerant tree species (Hanberry *et al*. 2012b). Both lost forests (forests with no modern equivalent) and novel forests (forests with no past equivalent) have been described for the study area, with lost forests showing a spatial relationship to the historic TZ (Goring *et al*. 2015). These processes of homogenization and mesophication in response to changes in land use and disturbance regimes result in the weakening of ecotones in the region (Hanberry *et al*. 2012b; Goring *et al*. 2015). Compositional shifts due to projected climate change, which might thwart ongoing mesophication through heating and drought, may create further complications, leading to uncertainty in how the TZ might move in the future (Vose and Elliott 2016). Indeed, northwestern shifts in plant distribution and abundance over a 50-yr period in Wisconsin have been linked with climate change (Ash *et al*. 2017)—an illustration of its polarizing effect on mesophication. Ultimately, the true effects of climate change on vegetation are still largely unknown or are just coming into view. For instance, comparisons of co-occurring sugar maple (*Acer saccharum*) and white oak (*Quercus alba*) in the eastern U.S. determined that sugar maple were more affected by late growing-season drought than white oak (Au *et al*. 2020). According to the Tree Atlas (Peters *et al*. 2020), oak is well positioned for future climate change, with its suitable habitat projected to expand in most cases with ongoing increases in temperature and drought occurrence. However, whether this projected expansion can be realized is questionable, given oak's dependence on fire (Nowacki and Abrams 2008). Indeed, species distribution models show that mesophytic trees (maples and beech) are more sensitive to climate conditions, whereas oaks (northern red oak [*Quercus rubra*] and white oak) are more dependent on disturbance, in this case past land use (see Fig. 7 of Chen and Leites 2020).

Conclusion. The roles of climate (temperature) and fire on TZ placement were assessed using witness trees as phytometers. The TZ best aligned with the witness-tree–based temperature line, thus reconfirming its long-held climate basis. However, the TZ does not conveniently follow primary climatic factors such as temperature or precipitation (Fig. 3) but does align with ecologically relevant factors that combine them (*i.e.,* summer potential evapotranspiration). Moreover, where recurrent historic fire occurred across or alongside this zone, a transition from oak (south) to pine and aspen (north) dominance was readily apparent, indicative of a climatic signal. On the other hand, isolated pockets of cool/cold trees were clearly present south of the original TZ, demonstrating that northern species could survive and dominate within an oak-dominated matrix and that climate was not necessarily limiting. Since these cool/cold–based trees were principally comprised of fire-sensitive species occurring in fire-protected areas within an otherwise pyrogenic landscape, fire must have played a role in TZ location. Our research adds a termination point to the temperate-

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based Midwestern TZ in west-central MN where ecosystems grade into a boreal environment.

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