Environmental drivers and species traits of mesophication and xerophication in forests of western New York State

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ABSTRACT

Forests of the eastern US have exhibited widespread taxonomic shifts involving decreasing abundances of many species of *Quercus*, *Pinus* and *Carya* and increasing abundances of many species of *Acer*, *Fagus*, *Prunus* as well as other genera. These taxonomic changes have been called mesophication and explained variously as decreased tolerance of fire, drought, and heat; decreased palatability for deer browsing; and increased tolerance of shade. The major driver of those shifts in taxonomy and ecological traits has been attributed to decreased surface burning due to Native American depopulation, cessation of settler-colonial land clearance, larger deer populations, and decreased drought, among other drivers. We endeavored to test which traits exhibited the most mesophication and which environmental factors best predicted that mesophication. We collected size-stratified taxonomic data for 2488 trees from 160 plots, converted that into measures of mesophyticness for each trait in each plot, and then inferred mesophication in each plot as the difference between the mesophyticness of small trees and large trees. Mesophyticness of each trait ranged from zero for a xerophytic trait to one for a mesophytic trait. We also collected site-specific data for 22 potential environmental predictors of trait changes (including abiotic, biotic, anthropogenic, and spatial predictors). All traits exhibited strong mesophication; these are, in descending order of percent of sites with strong mesophication: fire tolerance, white-tailed deer browse preference, Native American diet tree, cold tolerance, shade tolerance, drought tolerance, and general browse preference. For all traits, mesophication of small relative to large trees was greatest in plots where large trees were xerophytic, and least where large trees were mesophytic. We further found that mesophication was similar for plots regardless of the abundance or presence of *Quercus*, indicating that mesophication is not the same as oak decline. A diverse set of predictors best explained mesophication of taxonomic and ecological traits, but three were consistently chosen: cooler summer temperature, higher small tree density, and shorter distance to pre-1700 Native American towns. In addition to mesophication, there was also some evidence of xerophication, most strongly for an increase in heat tolerance as might be expected due to recent climate change. Our results show that forest mesophication is a complex syndrome involving changes in independent species traits that are driven by many environmental factors, creating a challenge for land managers.

1. Introduction

Many factors have influenced eastern US forests over the past three centuries including: Native American depopulation; fire suppression; widespread settler-colonist forest clearance and agricultural development followed by land abandonment; increased numbers and changing types of browsing animals; and climate change (Foster, 1992; Whitney, 1996). Forest mesophication has been identified as a syndrome encompassing many of those changes and attendant impacts on tree species composition (Nowacki and Abrams, 2008; McEwan et al., 2011).

Impacts of recent climate change and drought have also been detected on tree growth and forest composition in the eastern US (Clark et al., 2016; Druckenbrod et al., 2019), and are creating forest xerophication. An understanding of how, why, and where forests are mesophying (i.e. becoming more mesophytic) and xerophying (i.e. becoming less mesophytic) is essential to manage changing forest conditions (Woodbridge et al., 2022).

Mesophication was introduced as a term by Nowacki and Abrams (2008) to describe how relatively open forests in the eastern US that were dominated by fire-tolerant and shade-intolerant tree species pre-

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1900, have become closed forests dominated by fire-intolerant and shade-tolerant tree species. They suggested this process was initiated by reduced fire activity due first to Native American depopulation resulting in less Native American surface burning, and later to a wave of forest clearance by settler-colonists followed by fire suppression. Reduced fire activity would result in forests becoming more shady, cool, and moist, thus amplifying mesophication processes. Mesophication has subsequently been identified and described in hundreds of studies in the eastern US and elsewhere (see reviews by Hanberry et al., 2020; Alexander et al., 2021) with suggestions being made that mesophication was also initiated by other post-1800 changes. These include decreased drought (McEwan et al., 2011; Pederson et al., 2014); decreased Native American agroforestry (Abrams and Nowacki, 2008); increased anthropogenic nitrogen deposition and its influence on mycorrhizal associations (Alexander et al., 2021); and increased browsing pressure by larger white-tailed deer (*Odocoileus virginianus*; hereafter deer) populations (McEwan et al., 2011; Thomas-Van Gundy et al., 2014). Relatedly, although mesophication was initially identified as a response to historic reductions in fire (Nowacki and Abrams, 2008) and drought (Pederson et al., 2014), more recent research has found that mesophication is also occurring in response to recent changes in environmental drivers (Knott et al., 2019; Woodbridge et al., 2022). Although mesophication in the eastern US is often described as a large decline in abundance of oak (*Quercus* spp.; Nowacki and Abrams, 2008; Hanberry et al., 2020; Alexander et al., 2021), given that some non-oak tree species exhibit xerophytic traits, it would be useful to know if mesophication also occurs in forests that contain no oak.

Xerophication can be considered the opposite syndrome of mesophication in two key regards. First, if the post-1800 reductions in drought can be considered a cause of soil moistening and forest mesophication (Pederson et al., 2014), then the increases in drought over the past few decades can be considered a cause of soil drying and forest xerophication as observed in northern Spain by Rubio-Cuadrado et al. (2018). Second, if forests are becoming more mesophytic due to the causes outlined above (e.g. reductions in fire and temperature, increases in browsing and shade), then forests must have been more xerophytic in the past than they are now; in other words, for there to be a mesophytic state, there must also be a xerophytic state. Although Nowacki and Abrams (2008) did contrast xerophytic and mesophytic species of trees, most subsequent research, with a few notable exceptions (Hwang et al., 2020; Kutta and Hubbart, 2018), have discussed only the mesophytic state.

Forest mesophication has been observed, and its processes studied, using a variety of data and techniques. Mesophication was first described by comparing forest composition of large areas recorded in frontier-era land surveys with those recorded in modern forest surveys (Nowacki and Abrams, 2008). Mesophication has also been observed in repeat surveys of small areas (Palus et al., 2018) sometimes in combination with remote sensing (Hwang et al., 2020). Environmental models and tree-ring records have been used to explore the drivers of mesophication at the scale of the eastern US (Nowacki and Abrams, 2015; Knott et al., 2019) and smaller areas (Rubio-Cuadrado et al., 2018; Vanhellemont et al., 2019). Others have noted that differences in species relative abundances between forest understory and forest canopy provide evidence of mesophication, with smaller trees established under a recent mesophying environment while canopy trees established under a past xerophying environment (Hart and Kupfer, 2011; Palus et al., 2018; Alexander et al., 2021; Woodbridge et al., 2022).

A recent review concluded that the primary driver of mesophication has been the reduction in fire, with localized mesophication due to loss of chestnut trees and increased deer populations, but no mesophication due to increased precipitation (Hanberry et al., 2020). Others have found localized to sub-continental evidence for mesophication related to all above-mentioned traits and drivers (e.g. soil moisture; Hwang et al., 2020). No study, however, has directly assessed if mesophication varied in relation to past Native American land use. This is a notable research void since research in New York State has indicated that Native Americans discouraged mesophytic vegetation by cultivating xerophytic food trees and creating oak savannas close to Native American towns (NATs; Tulowiecki and Larsen, 2015; Tulowiecki et al., 2020a). As a result, the impacts of Native American land dispossession on mesophication would be expected to be greatest close to former NATs. In other words, older xerophytic overstory vegetation in present-day forests near former NATs may be a Native American land-use legacy (Abrams et al., 2021), and mesophication near former NATs may be the result of forest traits being selected by current environmental conditions.

In this research we explore whether mesophication or xerophication (MoX) is occurring in forests of western New York State, a region with Native American impacted forest composition and structure at the time of settler-colonialism (Tulowiecki and Larsen, 2015; Fulton and Yansa, 2019; Tulowiecki et al., 2020a). We examine differences in tree species traits in four tree size-classes. We consider seven traits of MoX: browsing by deer; general browsing by animals; drought; fire; Native American diet; shade; and temperature. We address five questions regarding MoX of those traits in western New York forests. (1) Does MoX exhibit more change for the traits of fire tolerance and Native American diet than for other traits? (2) Do traits exhibit more MoX in forests with more oak? (3) Has the study area undergone equal amounts of mesophication and xerophication? (4) Which environmental and land-use drivers best predict the occurrence of MoX and how do they vary by trait of MoX? (5) Do groups of traits have similar patterns in MoX and relations with environmental and land-use predictors? In answering these questions, this study addresses limitations in previous research by exploring the role of past Native American land use in driving current mesophication; by using a trait-based rather than species-based approach; by assessing whether mesophication occurs in non-oak dominated forests; and by investigating whether some sites have xerophied while others have mesophied. Our findings should also help inform land-use management related to oak decline and forest mesophication.

2. Study area

We studied a 6480 km^2 portion of western New York (Fig. 1) containing parts of two physiographic provinces: the warmer and drier Erie-Ontario Lowland to the north, and the cooler and moister Allegheny Plateau to the south (Fenneman, 1938). The mean annual temperature within the study area varies from 6.8° to 9.5 °C, while mean growing-season (May-September) precipitation varies from 38 to 52 cm (PRISM Climate Group, 2021). Prior to settler-colonialism, forests here experienced rare and localized disturbances including catastrophic blowdown events about every 1000 years (Seischab and Orwig, 1991). Native American landscape burning also occurred, typically within 15 km of NATs and trails (Tulowiecki et al., 2020b). The pre-1850 CE mean fire interval, predicted using fuel chemistry and regional climate but not anthropogenic factors, was 15–30 years (Guyette et al., 2012). The study area was chosen to contain major NATs and to maximize environmental variability. The Onöndowa'ga:' (Seneca) people of the Haudenosaunee (Iroquois) Confederacy were the most recent Native American inhabitants, occupying the study area from ca. 1400 (Engelbrecht, 2003). Their traditional land-use practices included forest clearance and surface burning to open land for agriculture and hunting. Those practices, along with planting, promoted trees such as oak that provided mast (large nuts) that they collected for their own diet and to provide food to wild animals they hunted. Mast species with increased abundances near NATs included black walnut (*Juglans nigra*), chestnut (*Castanea dentata*), hickory (*Carya* spp.) and oak (*Quercus* spp.) (Tulowiecki and Larsen, 2015). Oak savannas are predicted to have been present in 2 to 17 percent of the study area during the 1400s to 1700s, in response to burning by Native Americans along with drier soil and climate conditions (Tulowiecki et al., 2020a). Settler-colonialism in the area ca. 1790 involved rapid Onöndowa'ga:' land dispossession and depopulation and the replacement of Native American land use.
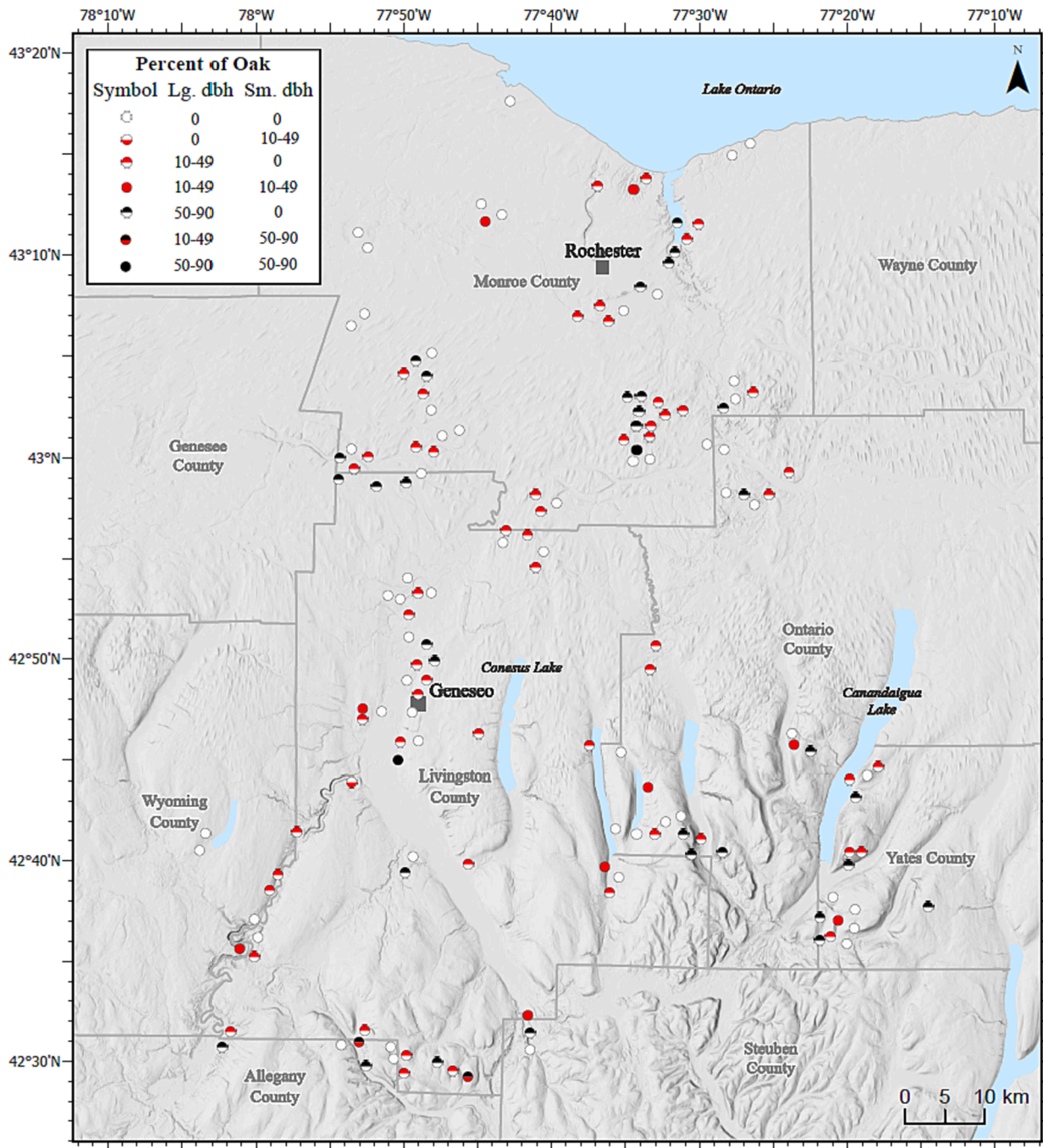
Fig. 1. The 160 study plots and the percentage of trees that are oak (*Quercus*) with a large Diameter at Breast Height (≥15.0 cm DBH) and/or a small DBH (1.0–14.9 cm DBH).

3. Data and methods

To evaluate the occurrence of mesophication and xerophication in relation to environmental and land-use predictors, our analyses had seven main steps described below. The core of the analyses was a point-centered quarter method to sample four trees in each of four size classes (16 trees in total) at 160 environmentally unique plots. Note the use of three terms. "Mesophyticness" refers to the state of large or small trees in a plot and spans a gradient from xerophytic to mesophytic. Mesophyticness is used rather than mesicness, as the former refers to tree traits while the latter refers to environmental conditions. The terms "Mesophication" or "xerophication" (MoX) refer to the change in mesophyticness of small trees versus large trees.

Tasks requiring geographic information systems (GIS) software were performed using Esri ArcGIS software (Esri, 2019), and dendrochronological analyses and environmental models were developed using R statistical computing (R Core Team, 2018).

3.1. Implementing a forest sampling scheme

A sampling design was implemented to capture detailed, site-specific data on forests and soils unavailable from existing FIA data. To distinguish environmental from past anthropogenic controls on site mesophyticness and MoX, we wanted maximal variability in combinations of environmental conditions including distance to NATs in upland forests. We sought forested sites that comprised all combinations of distance to

nearest NAT (four classes), climate (four classes), soil drainage (four classes), terrain aspect (two classes), and forest age (two classes). The climate data we employed were 30-year means of May-September precipitation; because of strong intercorrelations between the 30-year means of precipitation and temperature due to elevational effects in the study area, this stratum captured the general climatic gradient from warm-dry to cool-moist. This yielded 256 unique environmental combinations. To develop sampling strata, GIS-format data were acquired from these sources: NATs from Tulowiecki et al. (2020a); soil drainage from USDA-NRCS (2015); climate from PRISM Climate Group (2021); terrain data from USGS (2013); and forest age from historic topographic maps (USGS, 2020). Native American and climate strata were each divided into four equally-sized classes. For forest age, a site was designated as "older" if the location was symbolized as forest in 1940s-1950s USGS topo maps. Forests on the wettest soils were not sampled since these areas correspond with inaccessible and/or seasonally-flooded wetlands. Forest land cover data from the National Land Cover Database (Homer et al., 2020) narrowed-down candidate sampling locations to forests.

Using GIS software, we mapped unique combinations of the aforementioned environmental conditions within forests, then determined where they overlapped with accessible, mostly public lands (USGS Gap Analysis Project, 2018). We plotted candidate forest sites within each unique combination, targeting the largest forested patch for each combination first, and then locating plots towards the geographical center of the patch. We requested owner or manager permission to implement plots. Not every combination of conditions could be sampled. Some combinations covered a small percentage of land or did not exist here, and some did not exist on accessible lands.

Data were collected at 160 plots using a point-centered quarter method (Cottam et al., 1953) from May to July 2018. Four undergraduate research assistants were trained to collect data on forest and soil conditions and were almost always accompanied by an author of this study. After locating the predetermined plot center using a GPS unit, the plot was divided into four quadrants (north, east, south, west). Data were collected in each quadrant for the closest woody stem in each of four diameter-at-breast-height (DBH) classes (1.0–4.9 cm, 5.0–14.9 cm, 15.0–39.9 cm, ≥40.0 cm), producing data for 16 trees per plot: species, DBH, distance from plot center (30 m maximum), and compass-bearing. A range of size-classes was desired as progressively smaller trees are typically younger and thus exposed to a progressively more mesophying environment. The specific size-classes were chosen based on reconnaissance fieldwork that found they enabled each size-class to be represented within a 30 m radius that would ensure a relatively homogenous environment. To estimate forest age and understand site history, a tree-ring core was obtained using an increment borer from a canopy tree in the ≥ 40 cm DBH class with a typical size and form for that plot. Stem densities of small DBH (1.0–14.9 cm) and large DBH (≥15.0 cm) trees were calculated using the closest tree in each of the four cardinal directions per class using the Morisita (1957) plotless density estimator.

Soil samples 0–10 cm below the mineral soil surface were collected 3 m away from the plot center in each cardinal direction, mixed, and stored in a refrigerator for later shipping to Ward Laboratories (http s://www.wardlab.com) for analysis of 18 variables; four were retained (Table 1: pH, cation exchange capacity, nitrogen, phosphorous) that had well-recognized importance for plants and that had low intercorrelations. Soil depth was estimated at each site using a penetrometer by recording at 8 points each 3 m from the plot center in cardinal and ordinal directions, the median of which was calculated.

3.2. Quantifying plot mesophyticness and plot mesophication or xerophication (MoX)

Calculation of MoX had four main steps described below. Note the following numerical criteria and terminology: zero is the state of xerophyticness and one is the state of mesphyticness; and mesophication or xerophication (MoX) indicates the state of a trait for small trees versus large trees. Small trees in a plot could be mesophytic but if less mesophytic than the large trees in the plot then the small trees have become relatively more xerophied. This trait-based approach follows from and builds on previous studies (Nowacki and Abrams, 2015; Abrams et al., 2016; Abrams and Nowacki, 2019; Woodbridge et al., 2022) though we note the challenges and simplifications in determining traits states (Wigley et al., 2020). For example, we consider *Prunus serotina* (black cherry) to be mesophytic for pyrogenicity (Supplementary Table 1) because its thin bark makes it highly susceptible to top-kill by fires of moderate severity, even though those top-killed individuals can produce stem-sprouts from their roots (Uchytil, 1991).

First, the state of mesophyticness of species traits ranged from zero

Table 1
Predictors considered in boosted regression tree (BRT) models, abbreviations, descriptive statistics, and sources. NYSDEC = New York State Department of Environmental Conservation, NRCS = Natural Resources Conservation Service, PRISM = PRISM Climate Group; USGS = United States Geological Survey. Predictors are in alphabetical order by the abbreviation.

Predictor	Abbreviation	Unit	Min	Median	Mean	Max	Source and/or Notes
Deer harvest by DEC management unit	Deer harvest	# km^{-2} yr^{-1}	0.1	3.8	4.1	8.2	NYSDEC
First 5 years of rings if pith, mean	First 5 rings	mm	0.2	2.7	3.0	13.8	Our tree-rings
Growth release, years since last 50% release	Growth release	yr	10	43	49	172	Our tree-rings
Stand density trees ≥ 15 cm dbh	Large trees	# ha^{-1}	64	287	336	1776	Our tree survey
Terrain aspect northness	Northness	Unitless	−1.00	0.04	0.00	1.00	USGS; −1 = S, 0 = W or E, 1 = N
Palmer drought severity index (30 yrs)	PDSI	unitless	0.4	1.0	0.9	1.4	PRISM; higher = moister
Palmer drought severity index trend (30 yrs)	PDSI trend	yr^{-1}	−0.04	0.09	0.08	0.14	PRISM; positive = moistening
Distance to post-1700 Native American town	Post-1700 NAT	km	0.0	8.3	9.4	39.6	Various; closest town
Distance to pre-1700 Native American town	Pre-1700 NAT	km	0.0	14.6	17.3	46.3	Various; closest town
Stand density trees < 15 cm dbh	Small trees	# ha^{-1}	7.3	747	1139	7754	Our tree survey
Soil cation exchange capacity	Soil CEC	meq 100 g^{-1}	4.7	12.5	12.9	24.3	Lab analyses of our samples
Soil depth (field-based)	Soil depth	cm	1.9	26.1	28.8	61.5	Our field measurements
Soil saturated hydraulic conductivity (top 100 cm)	Soil hyd cond	mm hr^{-1}	1.2	7.6	14.4	79.2	NRCS
Soil nitrogen	Soil N	µg g^{-1}	0.1	5.4	7.0	38.6	Lab analyses of our samples
Soil phosphorous	Soil P	µg g^{-1}	3.0	13.0	30.5	254.0	Lab analyses of our samples
Soil pH	Soil pH	pH	4.0	5.8	5.7	8.0	Lab analyses of our samples
Temperature, May-Sept. (30-year mean)	Temp0509	°C	6.9	8.8	8.5	9.5	PRISM
Temperature trend, May-Sept. (30-year period)	Temp trend	°C yr^{-1}	0.01	0.03	0.03	0.05	PRISM; positive = warming
Terrain compound topographic index	Terrain CTI	Unitless	3.6	6.4	6.6	17.7	USGS; lower = flatter
Tree age (field based)	Tree age	yr	22	94	100	256	Our tree-rings
Vegetation patches in 500 m radius	Veg. patches	# 20 ha^{-1}	4.0	16.0	17.0	38.0	Google Earth
Vegetation that is wooded in 100 m radius	Wooded	%	59.0	98.8	93.9	100.0	Google Earth

(xerophytic) to one (mesophytic), with intermediate values for intermediate states (Table 2). The number of states of mesophyticness for a trait range varied in the source literature: two for pyrogenicity (PYRO) and Native American diet (DIET); three for shade tolerance (SHADE) and temperature tolerance (TEMP); four for general browse preference (BROWSE); six for drought tolerance (DROUGHT); and nine for white-tailed deer browse preference (DEER; Supplementary Table 1).

Second, the mesophyticness (trait states) of each species was assigned (Supplementary Table 2) using various sources. DIET was developed from Abrams and Nowacki (2008). PYRO, SHADE and TEMP were developed from Nowacki and Abrams (2015) with additional data from Prasad et al. (2007-ongoing), though we joined their warm and hot tolerance as we had few species in their hot class. DROUGHT was developed from Prasad et al. (2007-ongoing). DEER was calculated as the mean of browse palatability from four sources (Abrahamson, n.d.; Burns and Honkala, 1990; Rawinski, 2014; Van Dersal, 1938) each rescaled to range from 0 to 1 prior to averaging. Although deer can change tree species composition by browsing on vegetation and by feeding on nuts (McEwan et al., 2011) we followed Nowacki and Abrams (2008) and Hanberry et al. (2020), and only considered browse palatability. BROWSE was developed from the PLANTS Database (USDA-NRCS, 2022). While doing fieldwork some trees could only be assigned to a genus; the eight resulting genera had their trait levels assigned the average of all the species in that genus known to be in our study region (not just the species we identified).

Third and fourth, the mesophyticness of a trait in each plot was calculated as the mean separately using small (1–14.9 cm DBH) and then large (≥15 cm DBH) trees in the plot, then the degree of MoX for each trait for a plot was calculated as the mesophyticness of small trees minus the mesophyticness of large trees. The two smallest and two largest size classes were each combined as it made the MoX signal less noisy. Since the xerophytic state equals zero and the mesophytic state equals one, positive MoX values indicate that small trees were more mesophytic than large trees and that the plot had mesophied; negative MoX values indicate that small trees were more xerophytic than large trees and that the plot had xerophied. MoX therefore ranges from 1 (maximal mesophication) to −1 (maximal xerophication). This evaluation of MoX by comparing traits of small versus large trees builds upon Hart and Kupfer (2011) and follows from Woodbridge et al. (2022). If trait differences between the small and large trees are due to succession rather than MoX then Boosted regression tree (BRT) analyses (section 3.4) should select tree-age as a strong predictor.

Table 2

Relative mesophyticness for the seven traits. The xerophytic state has a value of zero (0), the mesophytic state has a value of one (1), and intermediate states have intermediate values.

Trait	Abbreviation	Xerophytic state	Intermediate states	Mesophytic state
Browsed generally	BROWSE	Preferred	Intermediate	Not palatable
Browsed by white-tailed deer	DEER	Preferred	Intermediate	Not palatable
Native American diet	DIET	Eaten	None	Not eaten
Drought tolerance	DROUGHT	Drought tolerant	Intermediate	Not drought tolerant
Pyrogenicity	PYRO	Fire tolerant	None	Not fire tolerant
Shade tolerance	SHADE	Not shade tolerant	Intermediate	Shade tolerant
Temperature tolerance	TEMP	Heat tolerant	Intermediate	Cold tolerant

3.3. Collecting data on environmental conditions, Native American towns and tree-rings

Site-specific climate, soil and Native American town (NAT) data were collected as potential predictors of the seven different traits of MoX (Table 1). These data were different than those used to select sites as described in section 3.1. Since different MoX traits likely have different drivers, various predictors were collected. However, as the processes of mesophication are intertwined and as this first application of our approach to studying mesophication is exploratory, we did not restrict any environmental predictor to any one trait. Environmental predictors were comprised of GIS-format climate, soil, and topographic data (USDA-NRCS, 2015; USGS, 2013; USGS, 2020), and field-based soil and forest-age data from each site. GIS-format soil data supplemented field-based soil data. Trends in mean May-September temperature were evaluated for each 4x4 km PRISM grid cells which contained a plot; linear regressions were applied for 1988–2017 and the regression slope was used to represent the temperature trend (positive trends would indicate warming, negative trends would indicate cooling). Since the rate of warming in temperate forest understories in Europe was found to on average be the same as the regional rate of warming, as mediated in part by forest canopy dynamics (Zellweger et al., 2020), the regional climate data we employ should be representative of the understory condition.

We developed two NAT variables: distance to nearest ca. 1500–1700 (pre-1700) NAT, and nearest ca. 1700–1800 (post-1700) NAT. These variables were created by mapping locations of NATs within and outside the study area. NATs were grouped into these two periods because many NATs could not be resolved to finer dates. Jones (2010) provided precise pre-1700 NAT locations, and additional pre-1700 NAT locations outside the study area were estimated using White (1978). Most post-1700 NATs were located using locational descriptions in Parker (1920), but other sources were consulted for post-1700 NATs (Cappon, 1976; Grumet, 1995; Jennings and Fenton, 1995; Morgan, 1901). Although the post-1700 data represents the more recent situation, Native Americans were experiencing displacement in our study area at that time.

We developed two drought-related predictors: mean Palmer Drought Severity Index (PDSI) and PDSI trend (both 30-year periods). Monthly Palmer Drought Severity Index (PDSI) values were calculated for 1988–2017 using the R package scPDSI (Zhong et al., 2018) using latitude, potential evapotranspiration (PE) monthly temperature (PRISM Climate Group, 2021), and available water capacity (AWC) (USDA-NRCS, 2015). Potential evapotranspiration was calculated using the R package SPEI (Begueria and Vincente-Serrano, 2017) and the Thornthwaite method. Mean PDSI values were calculated for May-September for 1988–2017; PDSI values range theoretically from −10 (dry) to + 10 (wet). Linear regressions were applied to mean May-September PDSI values for 1988–2017 and the regression slope represented the PDSI trend; positive slope indicated increasing moistness.

Increment cores from the plots were mounted, sanded, and dated according to standard dendrochronological procedures (Phipps, 1985) to create three predictors: Tree age, First 5 rings, and Growth release. Ring-widths were measured under a stereomicroscope with a crosshair reticle and a Velmex measuring system with a Unislide linear stage with a resolution of 0.001 mm. The MeasureJ2X program was used to process the measurements. Crossdating of cores from the same species was first performed visually and then confirmed using functions of the R package dplR (Bunn et al., 2020) with 40-year segments lagged in 20-year increments. The Tree-age predictor for the 160 plots was determined in three ways. In 95 plots where the increment core had a pith the number of rings indicated the total age of the tree. In 33 plots where the increment cores had curved inner rings but no true pith the total age was estimated using graphical methods (Rozas, 2003). In another 32 plots where the cores did not reach pith due to damage or rot, total tree age was estimated using mathematical methods (Altman et al., 2014). The First 5 rings predictor was determined for complete cores reaching pith;

the mean of the first five growth rings was calculated to infer if the tree began growing in an open (wide rings) or closed (narrow rings) forest. The Growth release predictor in increment cores was evaluated using a 50% release (Lorimer and Frelich, 1989) and the first year of the last release was used to evaluate whether the most recent growth release might have influenced MoX.

We developed three variables to represent deer browse potential. White-tailed deer density was inferred, like Lesser et al. (2019), from annual deer harvest reports (NYSDEC online). Reports of total deer take were obtained for 2007–2018 from the 39 towns in which our plots were located. Harvest per town was converted to mean deer yr^{-1} km^{-2} and then associated with each plot. To evaluate deer habitat potential, percent of forested area around each plot was estimated within a 100 m radius using 100 regularly-spaced points (Reimoser and Gossow, 1996). To further evaluate deer habitat potential, heterogeneity of the distinct vegetated patches was counted within a 500 m radius around each plot (Hurley et al., 2012). Distinct vegetation (e.g. tall forest, coniferous forest, field) was identified for patches > 25 m radius. Percent wooded and number of patches were estimated in January 2021 using Google Earth imagery. Higher forest cover and vegetation heterogeneity were expected to facilitate larger deer populations.

After assessing for collinearity, 22 variables were selected for developing Boosted Regression Trees models of MoX. Table 1 lists predictors, data sources, and other characteristics, including nine variables not described above. Due to collinearity between temperature, precipitation, and elevation, only temperature was employed.

3.4. Developing Boosted regression tree (BRT) models

BRT is a machine-learning technique widely used in ecological modeling (Elith et al., 2008), including evaluation of Native American and environmental influences on past forests (Tulowiecki et al., 2020a). We developed BRTs to assess the degree of influence of a predictor on MoX. For technical details regarding BRT, including its ability to handle predictors with missing predictor values, see Elith et al. (2008). BRT models were developed using the "dismo" (Hijmans et al., 2013) package in R (R Core Team, 2018). We used a tree complexity of two to model up to second-order interactions between predictors. We then tested different values of learning rate to find the value that achieved the lowest predictive deviance on a holdout test dataset using cross-validation via the "gbm.step()" function (Elith et al., 2008; Hijmans et al., 2013), while also yielding a number of regression trees between 1000 and 5000. Parameters yielding the lowest mean predictive deviance using holdout data were chosen for the final model. For all models, the number of predictors was reduced by omitting those that did not appreciably improve predictive performance. To determine the maximum number of predictors to omit, we used cross-validation techniques of the "gbm.simplify" function (Elith et al., 2008; Hijmans et al., 2013).

3.5. Examining BRTs

Two measures of model performance were calculated to assess overall quality of BRT models of MoX. First, total variance explained by the model was obtained. Second, Pearson's correlation coefficients were calculated to assess the linear relationship between (a) training data versus predicted trait values, and (b) holdout data during cross-validation and predicted trait values.

We calculated relative variable importance using the "summary()" function (Elith et al., 2008; Hijmans et al., 2013). Relative variable importance was calculated as the number of times a predictor was used for splitting in the regression trees, weighted by how much improvement (squared) in model fit that each of a predictor's splits produced (Elith et al., 2008); measures were scaled as percentages so the sum of all predictors equals 100%. Partial dependence plots were generated to show relationships between MoX and each predictor, using the "plot.

gbm()" function (Elith et al., 2008; Hijmans et al., 2013). These plots showed changes in the prediction made by a model when one predictor's values were changed while all other predictors were kept at their mean. We plotted values on the same scale as our original MoX outcome values. Positive MoX values in partial dependence plots indicated levels of a predictor at which mesophication occurred, and negative values indicated levels of a predictor at which xerophication occurred.

3.6. Evaluating MoX by traits

Patterns of MoX for each trait were evaluated in five manners. (1) BRT model strength was compared using percent deviance explained; and the median of percent deviance explained, training correlation and cross-validation correlation. (2) MoX graphs were created by plotting plot mesophyticness of large DBH trees (≥15 cm) on the X-axis and MoX of small DBH trees (<15 cm) on the Y-axis. Positive MoX values indicate plot mesophication and negative values indicate site xerophication. For example, a MoX of one indicates the plot's large DBH trees all had the minimum mesophyticness of zero (i.e. xerophytic) and its small DBH trees all had the maximum mesophyticness of one. Conversely, a MoX of negative one indicates the plot's large DBH trees all had the maximum mesophyticness of one and its small DBH trees all had the minimum mesophyticness of zero (i.e. xerophytic). A MoX of zero indicates no difference in mesophyticness of small versus large DBH trees. (3) Relations between the amount of MoX for each of the seven traits in the 160 sites was assessed using Spearman rank correlations for these ordinal data. (4) Slopes and R^2 of the regression lines in MoX graphs were determined for five sets of data: all plots; plots in which oak comprised ≥ 50% of large trees; plots in which oak comprised 10–49% of large trees; plots in which no large trees were oak; and plots in which no large trees were oak or pine (no sites had 1–9% oak). Regression slopes were compared to see if MoX occurred similarly for each trait regardless of oak presence or abundance. (5) The percent of plots mesophying and percent xerophying was evaluated for each trait using critical X- and Y-axis parameters from the MoX graph regressions that used all plots. Critical X- and Y-axis values were calculated to ensure that only significant and meaningful variations were inferred as MoX.

Plots with weak or strong MoX were inferred using critical X- and Y-values calculated using standard errors of intercepts and slopes. Weak mesophication was inferred for plots significantly above the Y-axis value of zero; weak xerophication was inferred for plots significantly below the Y-axis value of zero. Strong mesophication was inferred for plots significantly above a Y-axis value of zero that also meaningfully had X-axis values significantly lower and more xerophytic than the point where the regression line crossed the Y-axis value of zero. Strong xerophication was inferred for plots significantly below a Y-axis value of zero that also meaningfully had X-axis values significantly higher and more mesophytic than the point where the regression line crossed the Y-axis value of zero.

3.7. Evaluating MoX by predictors

Predictors of each trait of MoX were evaluated in five manners. (1) Identifying which BRT predictors best explained each trait's MoX using relative variable importance measures. (2) Identifying which predictors were most often chosen in BRT models, what their mean variable importance was, and if their partial dependence plots had a consistent shape for all traits. (3) Assigning four general trends to the partial dependence plots: "/" trait mesophies at higher predictor values, "\" trait mesophies at lower predictor values, "Λ" trait mesophies at intermediate predictor values, and "V" trait mesophies at extreme predictor values. (4) Evaluating whether appreciable MoX occurred in response to a predictor. Appreciable mesophication was inferred where the fitted function in the partial dependence plot was ≥ 0.01 for ≥ 20% of the plots; appreciable xerophication was inferred where the fitted function was ≤ -0.01 for ≥ 20% of the plots; neither MoX was inferred if neither

threshold was reached. Appreciable MoX was evaluated separately for three ranges of data: the 30% of plots with the lowest predictor values, the intermediate 40% of plots, and the 30% of plots with the highest predictor values. For each trait, the total number of instances of either appreciable MoX was summed and the proportion of those traits due to mesophication and xerophication was calculated separately. (5) Similarities among BRT models for different traits were compared by the predictors selected and the general shape of the partial dependence plots.

4. Results

4.1. Species

A total of 2488 trees were recorded from 68 taxa in the 160 plots: 60 species were identified but some individuals could only be identified to one of 8 genera (Supplementary Table 1). The three species with the most large trees (DBH ≥ 15 cm) were *Acer saccharum* (sugar maple, 15.3%), *Quercus rubra* (red oak, 12.8%) and *Acer rubrum* (red maple, 12.3%); the three tree species with the most small trees (DBH < 15 cm) were sugar maple (18.9%), *Fraxinus americana* (white ash, 11.5%) and *Fagus grandifolia* (American beech, 10.8%) (Supplementary Table 2). The three most abundant taxa among very large trees (DBH ≥ 40 cm) were red oak (19.7%), sugar maple (10.3%), and *Quercus alba* (white oak, 10.1%). Seven different oak species were recorded, with at least one large (DBH ≥ 15 cm) oak in 63.1% of the 160 plots and at least one small (DBH < 15 cm) oak in 8.8% of the plots (Fig. 1).

When comparing changes in relative abundances from the large to the small DBH size classes only for maximally mesophytic (trait state of 1) or maximally xerophytic (trait state of 0) species, different species emerged as the top increaser (more in the small DBH class) or decreaser (less in the small DBH class) depending upon which trait was examined (Supplementary Tables 1 and 2). Of the small trees that had the maximally mesophytic DEER, DIET, PYRO and SHADE traits, *Ostrya virginiana* (American hophornbeam) had the largest increase of 7.6%; of the small trees that had the maximally mesophytic BROWSE trait beech had the largest increase of 6.1%; of the small trees that had the maximally mesophytic DROUGHT trait white ash had the largest increase of 5.1%; and of the small trees that had the maximally mesophytic TEMP trait *Crataegus* spp. (hawthorn) had the largest increase of 2.9%. Of the small trees that had the maximally xerophytic DEER, DIET and PYRO traits, red oak had the largest decrease of 11.9%; of the small trees that had the maximally xerophytic TEMP trait red maple had the largest decrease of 5.2%; of the small trees with the maximally xerophytic DROUGHT trait *Carya* spp. (hickory) had the largest decrease of 3.5%; of the small trees with the maximally xerophytic SHADE trait *Liriodendron tulipifera* (tulip tree) had the largest decrease of 1.7%; and of the small trees with the maximally xerophytic BROWSE trait *Populus tremuloides* (quaking aspen) had the largest decrease of 0.6%.

4.2. MoX by traits

The range of mesophyticness of large DBH trees in individual plots varied by trait from the maximum possible range of 0 to 1 for DIET, PYRO, SHADE; to the lowest range of 0.08 to 0.75 for DROUGHT (Fig. 2). The range of mesophyticness for small DBH trees in individual plots varied by trait from the maximum possible range of 1 to −1 for DIET and PYRO to the lowest range of 0.38 to −0.50 for BROWSE. When considered for all four DBH size-classes, mesophyticness trended from most mesophytic in the smallest DBH class to least mesophytic in the largest DBH class (Table 3). This trend was consistent across all four DBH size-classes for DEER, DIET, and PYRO. For the other four traits, three DBH size-classes exhibited this trend and one DBH size-class did not.

The degree of MoX in the 160 plots was significantly correlated for 11 of the 21 pairs of traits (Table 4). The number of other traits with

which they were correlated ranged from a high of four for BROWSE, DIET and SHADE to a low of two for DEER and PYRO. The three highest correlations were positive between DIET and PYRO ($r_s = 0.681$); negative between TEMP and BROWSE ($r_s = -0.557$); and positive between DROUGHT and TEMP ($r_s = 0.533$).

For all traits, mesophication of small DBH trees was greatest in plots where large DBH trees were xerophytic and least where large trees were mesophytic (Fig. 2); graphs of those data all had significantly negative regression slopes (Table 5). The regression with the highest R^2_{adj} and steepest slope was PYRO; second highest and steepest was DIET; and lowest and least steep was SHADE. For plots where oak comprised 50–90% of the large DBH trees, all significant regression slopes were negative with the highest R^2_{adj} and steepest slope for DROUGHT and non-significant regressions for DEER and SHADE. For plots where oak comprised 10–49% of large DBH trees, all significant regression slopes were negative with the highest R^2_{adj} for PYRO, the steepest slope for TEMP, and a non-significant regression for SHADE. For plots where oak comprised 0% of large DBH trees, all significant regression slopes were negative with the highest R^2_{adj} and steepest slope for PYRO, and non-significant regressions for DROUGHT and SHADE. For plots where either oak and pine comprised 0% of large DBH trees, all regression slopes were slightly more negative and all R^2_{adj} were higher than for the regressions for plots where just oak comprised 0% of large DBH trees. The steepest slope for BROWSE, DIET and DROUGHT was for plots where oak comprised 50–90% of large DBH trees; and for DEER and PYRO was for plots where oak and pine comprised 0% of large DBH trees.

BRT models could be developed for six of the seven traits, with the deviance explained decreasing from a high of 62.6% to a low of 37.9% in the sequence: DIET, TEMP, BROWSE, DEER, PYRO, and DROUGHT (Table 6). The same order of traits occurs for the median of the values for percent deviance explained, training correlation and cross-validation correlation. No BRT model could be developed for the MoX of SHADE as it returned a nt < 1000 and was thus considered unreliable (Hijmans et al., 2013).

Weak mesophication occurred in a high of 72.2% of the plots for PYRO to a low of 31.7% of the plots for DROUGHT with a mean of 48.3% of the plots for the seven traits (Table 7, Fig. 2). Strong mesophication occurred in a high of 65.8% of the plots for PYRO to a low of 2.5% of the plots for BROWSE, with a mean of 29.4% of the plots for the seven traits. Weak xerophication occurred in a high of 37.3% of the plots for TEMP to a low of 9.5% of the plots for PYRO, with a mean of 23.6% of the plots for the seven traits. Strong xerophication occurred in a high of 13.3% of the plots for TEMP to a low of 0.0% of the plots for DEER, PYRO and SHADE, with a mean of 3.6% of the plots for the seven traits. The percent of strongly or weakly mesophied plots was highest for PYRO, DIET and DEER; the percent of strongly or weakly xerophied plots was highest for TEMP, BROWSE and DIET. The percent of strongly or weakly mesophied plots was higher than the strongly or weakly xerophied plots for all but two traits: DROUGHT had 0.6% fewer weakly mesophied than weakly xerophied plots, and BROWSE had 3.2% fewer strongly mesophied than strongly xerophied plots. However, since DROUGHT and BROWSE had ≤ 10% of their plots strongly xerophied, these results are considered minor.

4.3. MoX by predictors

All 22 predictors of MoX were included in a BRT model for at least one of the 6 traits for which BRT models could be created, and 12 of the predictors were selected for all 6 of the traits (Table 8). The five predictors with the highest mean variable importance measures across all six models were, in descending order: Soil hyd cond, Temp0509, Small trees, Pre-1700 NAT, and Post-1700 NAT (see Table 1 for units and full names of predictors). The strongest predictor varied by trait: Soil pH for BROWSE; Temp0509 for DEER and DROUGHT; Post-1700 NAT and Tree age for DIET; Tree age for PYRO; and Pre-1700 NAT for TEMP.
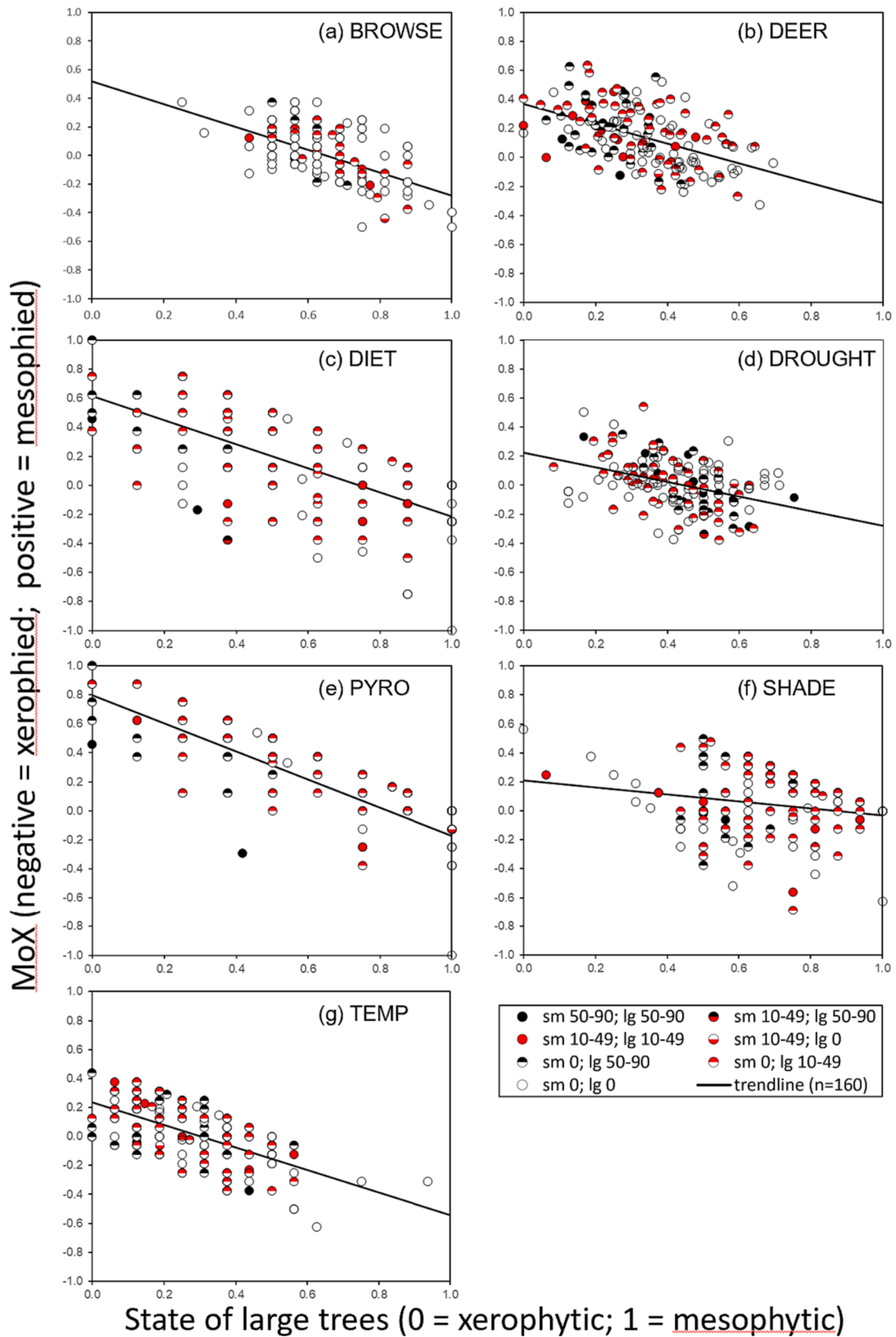
Fig. 2. Relations between the state of mesophyticness of large DBH trees and the degree of mesophication or xerophication (MoX) of small DBH trees relative to large trees for seven traits (full names in Table 2). Symbols are not visible for all 160 plots due to overlapping states, thus some trendlines (e.g. SHADE) appear to be improperly fit.

Table 3

Mean mesophyticness of seven traits for the trees in the four tree DBH size classes. Zero is maximally xerophytic and one is maximally mesophytic. Full names of traits are in Table 2.

Trait	DBH size class (cm)			
	1.0–4.9 (n = 623)	5.0–14.9 (n = 633)	15.0–39.9 (n = 637)	≥40.0 (n = 595)
BROWSE	0.653	0.641	0.645	0.621
DEER	0.487	0.466	0.367	0.294
DIET	0.716	0.690	0.627	0.442
DROUGHT	0.451	0.412	0.387	0.463
PYRO	0.889	0.861	0.720	0.460
SHADE	0.683	0.744	0.718	0.603
TEMP	0.289	0.304	0.285	0.274

Table 4

Spearman's rank correlations between the values of MoX for pairs of the seven traits in the 160 plots. Bolded values are correlations significant at p = 0.05 (two-tailed).

	BROWSE	DEER	DIET	DROUGHT	PYRO	SHADE
DEER	**0.389**					
DIET	**−0.430**	−0.114				
DROUGHT	**−0.301**	−0.150	0.058			
PYRO	−0.078	0.006	**0.681**	−0.003		
SHADE	−0.127	**−0.234**	**0.348**	**−0.389**	**0.512**	
TEMP	**−0.557**	−0.018	**0.393**	**0.533**	0.104	0.067

Appreciable MoX occurred for all 6 traits and ranged from 26 instances for DIET to 9 for BROWSE (Table 8). Three combinations of trait and predictors had instances with fitted functions > 0.25 indicating strong mesophication (Fig. 3): PYRO when Tree age was old (>70 yrs), PYRO when Small trees were abundant (>1500 ha⁻¹), and DIET when distance to Post-1700 NATs was short (<5 km). Only three traits had instances of xerophication: six instances for DROUGHT, two instances for TEMP, and one instance for BROWSE.

Appreciable MoX was caused by 16 of the 22 predictors, with a total of 92 instances of appreciable mesophication and 10 instances of appreciable xerophication (Table 8). Three predictors caused ≥ 10 instances of appreciable MoX: Temp0509, Temp trend, and Small trees. A

total of seven predictors caused at least one instance of appreciable xerophication. Temp trend was the only predictor that caused appreciable xerophication of more than one trait: DROUGHT and TEMP.

The shape of the partial dependence plots for predictors of MoX were similar for multiple traits (Table 8, Fig. 3) suggesting potential importance for land management. Four predictors had the same plot shape for at least five of the six traits: Small trees and Temp trend had higher mesophication at higher predictor values (/); Northness and PDSI 0509 had higher mesophication at lower predictor values (\). Five predictors had the same plot shape for four traits: Temp0509, Pre-1700 NAT and Soil depth had higher mesophication at lower predictor values (\); Tree age and Terrain CTI had higher mesophication at higher predictor values (/).

Pairs of traits exhibited differences in the proportion of predictors shared in the BRT models (e.g. BROWSE and DEER share the predictor Soil hyd cond but not Soil P) and how many of their partial dependence plots had the same shape (e.g. while BROWSE and DEER share Soil hyd cond it does not exhibit the same shape, but Temp0509 is both shared and has the same shape). The number of shared predictors ranged from 14 for DROUGHT and TEMP to 18 for DEER and DIET. The proportion of those shared traits that had the same shape ranged from 0.33 for BROWSE and DIET to 0.67 for DIET and TEMP; three additional pairs had > 0.64 of their predictors with the same shape: BROWSE and DEER, DIET and PYRO, DROUGHT and TEMP.

Table 6

Performance parameters for BRT models of MoX for six traits (n = 160). No results are provided for the trait of shade tolerance as BRT could not develop a model for it. Full names of traits are in Table 2.

Parameter	BROWSE	DEER	DIET	DROUGHT	PYRO	TEMP
Deviance explained (%)	50.0	46.2	62.6	37.9	40.6	57.1
Training correlation	0.797	0.804	0.873	0.749	0.826	0.864
Cross validation correlation	0.366	0.350	0.382	0.220	0.271	0.384

Table 5

Linear regression parameters between the mesophyticness of the large trees and MoX of the small trees. Regressions were performed for all plots, and for plots grouped by percent of large oak trees and with no large oak or pine. P-values are two-tailed. Parameters are not provided for non-significant (n.s.) slopes. Full names of traits are in Table 2.

Trait	Parameter	All sites (n = 160)	Lg. oak: 50–90% (n = 35)	Lg. oak: 10–49% (n = 65)	Lg. oak: 0% (n = 60)	Lg. oak & pine: 0% (n = 56)
BROWSE	Slope	−0.799	−1.066	−0.866	−0.731	−0.767
	R^2_{adj}	0.311	0.216	0.300	0.301	0.333
	p-value	0.000	0.003	0.000	0.000	0.000
DEER	Slope	−0.683		−0.591	−0.729	−0.755
	R^2_{adj}	0.250	n.s.	0.190	0.292	0.313
	p-value	0.000		0.000	0.000	0.000
DIET	Slope	−0.840	−0.839	−0.806	−0.583	−0.651
	R^2_{adj}	0.438	0.216	0.338	0.203	0.255
	p-value	0.000	0.003	0.000	0.000	0.000
DROUGHT	Slope	−0.504	−1.377	−0.776		
	R^2_{adj}	0.147	0.464	0.286	n.s.	n.s.
	p-value	0.000	0.000	0.000		
PYRO	Slope	−0.874	−0.885	−0.811	−0.971	−0.979
	R^2_{adj}	0.685	0.314	0.527	0.610	0.615
	p-value	0.000	0.000	0.000	0.000	0.000
SHADE	Slope	−0.242				
	R^2_{adj}	0.031	n.s.	n.s.	n.s.	n.s.
	p-value	0.025				
TEMP	Slope	−0.779	−0.610	−0.871	−0.792	−0.821
	R^2_{adj}	0.386	0.196	0.443	0.410	0.657
	p-value	0.000	0.004	0.000	0.000	0.000

Table 7

Percent of plots in which small trees exhibit mesophication or xerophication for the seven traits. Regression parameters are between mesophyticness of large trees (x-axis) and MoX of small trees (y-axis; see also Table 5). Critical X- and Y-axis values (X_{crit} and Y_{crit}) must be exceeded for mesophication or xerophication of a plot to be significant. Percent of plots exceeding critical values for just the X- or just the Y-axis, and for both X- and Y-axes, are based on X_{crit} and Y_{crit}. Full names of traits are in Table 2. Meeting Y_{crit} is considered weak mesophication or xerophication; meeting both X_{crit} and Y_{crit} is considered strong mesophication or xerophication.

	BROWSE	DEER	DIET	DROUGHT	PYRO	SHADE	TEMP
Regression Parameters							
Intercept	0.5184	0.3702	0.6164	0.2233	0.7996	0.2116	0.2358
SE of intercept	0.0610	0.0339	0.0456	0.0423	0.0312	0.0673	0.0252
Slope	−0.7994	−0.6833	−0.8328	−0.5036	−0.8739	−0.2417	−0.7789
SE of slope	0.0943	0.0936	0.0753	0.0950	0.0472	0.0986	0.0781
Mesophication Parameters							
Y_{crit}	0.1200	0.0664	0.0894	0.0829	0.0612	0.1312	0.0495
X_{crit}	0.4637	0.3585	0.5925	0.2573	0.8223	0.6822	0.1497
Xerophication Parameters							
Y_{crit}	−0.1200	−0.0664	−0.0894	−0.0829	−0.0612	−0.1312	−0.0495
X_{crit}	0.8333	0.7253	0.8878	0.6298	1.0074	1.0687	0.4558
Mesophied (percent of sites)							
$< X_{crit}$	7.6	60.1	55.1	12.0	70.9	51.9	28.5
$> Y_{crit}$ (weakly mesophied)							
	34.2	58.9	59.5	31.7	72.2	34.2	47.5
$> Y_{crit}$ & $< X_{crit}$ (strongly mesophied)							
	2.5	47.5	44.3	7.0	65.8	17.1	21.5
Xerophied (percent of sites)							
$> X_{crit}$	16.5	0.0	10.1	4.4	0.0	0.0	14.6
$< Y_{crit}$							
(weakly xerophied)	28.5	16.5	24.7	32.3	9.5	16.5	37.3
$< Y_{crit}$ & $> X_{crit}$							
(strongly xerophied)	5.7	0.0	5.1	1.3	0.0	0.0	13.3

5. Discussion

Analyses of forests in this portion of western New York effectively answered our five questions. (1) Traits differed by amount of MoX, measured as the sum of the percentages of strongly mesophied and strongly xerophied plots, in descending order: PYRO, DIET, DEER, TEMP, SHADE, DROUGHT and BROWSE. Somewhat similar is the R^2 of the MoX trendlines, in descending order: PYRO, DIET, TEMP, BROWSE, DEER, DROUGHT and SHADE. This supports species-based findings that many traits are mesophying (McEwan et al., 2011) but that fire-tolerant species have typically decreased the most (Hanberry et al., 2020). That said, given the challenges in measuring species traits and especially in reducing multiple related traits (e.g. fire's different impacts on the burning of trunk and crown and inducing root or seed sprouting) we encourage future research to explore methods to choose amongst relevant traits (Funk et al., 2016). We expect, however, that other areas with different land-use histories and other environmental predictors would differ in the relative amounts of trait mesophication and xerophication. Since different traits mesophied in response to unique combinations of drivers, land management approaches to reverse mesophication will be complex (Woodbridge et al., 2022). In part, this may explain why prescribed fires have had limited success establishing oak (summarized in McEwan et al., 2011).

(2) For five traits, the rate of change in MoX did not vary with the abundance of large DBH oak or large DBH oak and pine; only BROWSE and DIET had less change in MoX in plots that had less large DBH oak. This contrasts with studies suggesting that mesophication in the eastern US is largely related to oak decline (Nowacki and Abrams, 2008), though Woodbridge et al. (2022) also found mesophication in non-oak dominated forests.

(3) Strong mesophication occurred in > 8X the number of plots than did strong xerophication and the only trait with > 10% of its plots strongly xerophied was TEMP. This comports with results elsewhere that mesophication predominates throughout the eastern US with xerophication occurring infrequently (Supplementary Figs. 1 and 7 in Woodbridge et al., 2022). Moreover, that the only marked xerophication occurred in response to a climatic driver is reasonable as climate is the only driver expected to return to a xerophytic state (Nowacki and Abrams, 2015).

(4) A diverse set of predictors best-explained MoX in terms of their percent variable importance in BRT models and dependence plot shape consistency (Table 8). However, 3 of the 22 predictors had a top 5 mean percent variable importance (bracketed number in the right-most column of Table 8) and also had partial dependence plots with the same shape for ≥ 4 traits: Temp0509, Small tree density, and Pre-1700 NAT. Two of those predictors are similar to those in BRT models of oak savannas in western New York (Tulowiecki et al., 2020a) signaling mesophication in former oak savannas associated with Native American surface burning.

(5) Three pairs of traits exhibited similarity in both their patterns of MoX across the 160 plots (Table 4) and the proportion of the predictors in the BRT models with the same partial dependence plot shape (Table 8): Native American-related traits DIET and PYRO ($r_s = 0.681$, Table 4); climate-related traits DROUGHT and TEMP ($r_s = 0.533$); and animal-related traits BROWSE and DEER ($r_s = 0.389$).

The remainder of the Discussion focuses on ecological interpretations of MoX predictors as this should help land managers address MoX challenges. To increase generalizability, interpretations are made for strong and consistent predictors of MoX; this is done for the three pairs of traits identified above and for SHADE. Pairs of traits are discussed in descending order of the mean deviance explained by their BRT models (Table 6). Predictors are considered strong and consistent if the partial dependence plots for paired traits exhibit the same general shape and if the mean variable importance for the two traits is ≥ 7% (Table 8). Predictors are described in descending order of their mean percent variable importance.

5.1. Native American-related traits: DIET AND PYRO

Of the three pairs of traits, DIET and PYRO had the highest mean BRT deviance explained (51.6%, Table 6), most mean plots strongly mesophied (55.1%, Table 7), and third-most mean plots strongly xerophied (2.6%). Similar changes in these traits and their predictors were expected as Native American surface burning could have selected for both traits. Native Americans in this area used fire to passively increase nut-bearing (mast) tree species such as oaks, and to facilitate travel, security, and improved browse for game (Abrams and Nowacki, 2008). Native American diet trees were also actively selected and planted with non-

Table 8

Influence of predictors on MoX traits (full names in Tables 1 and 2). The right-most column gives the number of traits for which a predictor was chosen in the BRT model, and the mean (μ) of relative importance calculated with blanks treated as zeros. Predictors are in descending order of mean relative importance. (a) Relative percent variable importance; empty cells were not chosen as a predictor for that trait by BRT. (b) General trends in the partial dependence plot for that predictor and trait pair: "/" trait mesophies at higher predictor values; "\" trait mesophies at lower predictor values; "Λ" trait mesophies at intermediate predictor values; "V" trait mesophies at extreme values. (c) whether appreciable MoX occurred: "m" is appreciable mesophication, "x" is appreciable xerophication, "-" is neither, no symbol means no appreciable MoX. Appreciable MoX is assessed for three data-ranges: the 30% of plots with lowest x-axis predictor values, the intermediate 40% of plots, and the 30% of plots with highest predictor values. "m + x" is total number of instances of either appreciable mesophication or xerophication for a predictor or trait; "m(p)" is the proportion of instances that were appreciable mesophication; "x(p)" is the proportion that were appreciable xerophication.

| Predictor	BROWSE			DEER			DIET			DROUGHT			PYRO			TEMP			Appreciable			# traits; (μ %)
	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	m + x	m(p)	x(p)	
Temp0509	3	\		19	\	mmm	9	Λ	mmm	15	/	xmm	9	\	mmm	3	\		12	0.9	0.1	6 (9.7)
Soil hyd cond	17	Λ	-m-	4	\		8	v	mmm	13	\	m–	5	v		10		mm-	7	1.0		6 (10.6)
Small trees	9	Λ	-m-	4	/		6	/	mmm	9	/	xxm	7	/	mmm	10	/		10	0.8	0.2	6 (8.2)
Pre-1700 NAT	12	/		2	/		6	\	mmm	6	\	m–	3	\		15	\	mmm	7	1.0		6 (7.3)
Post-1700 NAT	14	/	xmm	4	\		12	\	mmm				4	\		10	v	m–	7	0.9	0.1	5 (7.3)
Soil pH	20		mmx	9	\	mmm	3	/					6	\	mmm	3	/		9	0.9	0.1	5 (6.8)
Tree age	1	/		2	\		12	/	mmm	1	\		22	/	mmm	2	/		6	1.0		6 (6.7)
Temp trend	1	\		1	/		10	/	mmm	11	/	xmm	5	/	mmm	9	/	x-m	11	0.8	0.2	6 (6.2)
Soil depth	3	\		11	\	mmm	3	/		4	\		5	\	mmm	6	/		6	1.0		6 (5.3)
First 5 rings	4	/		2	\		5		mm-	3	/		3	/		10	\	mmx	5	0.8	0.2	6 (4.5)
Soil N	1	\		3	\		4	/		11	/	xxm	4	/		4	Λ		3	0.3	0.7	6 (4.5)
PDSI trend	2	\		9	\	mmm	3	/		7	/	-mm	5	/	mmm				8	1.0		5 (4.3)
Terrain CTI	3	/		4	/		5	\	mmm	3	/		4	\		4	/		3	1.0		6 (3.8)
Northness				1	\		3	\		5	\	m–	9	\	mmm	4	\		4	1.0		5 (4.4)
Large trees	1	/		4	/		3	\		4	\		3	/		2	\					6 (2.8)
Soil CEC	7	/	–m	3	/					3	\					4	\		1	1.0		4 (2.8)
PDSI 0509	1	\		5	\		2	\		2	\		3	Λ		2	\					6 (2.5)
Growth release	2	/		3	\		3	/					3	/								4 (1.8)
Wooded				4	\		2	/		3	\											3 (1.5)
Veg. patches				2	/											4	/					2 (1.0)
Soil P				5	\	mmm													3	1.0		1 (0.8)
Deer harvest													3	\								1 (0.5)
Appreciable m + x		9			15			26			17			24			11		102			
Appreciable m(p)		0.9			1.0			1.0			0.6			1.0			0.8		0.9			
Appreciable x(p)		0.1									0.4						0.2		0.1			
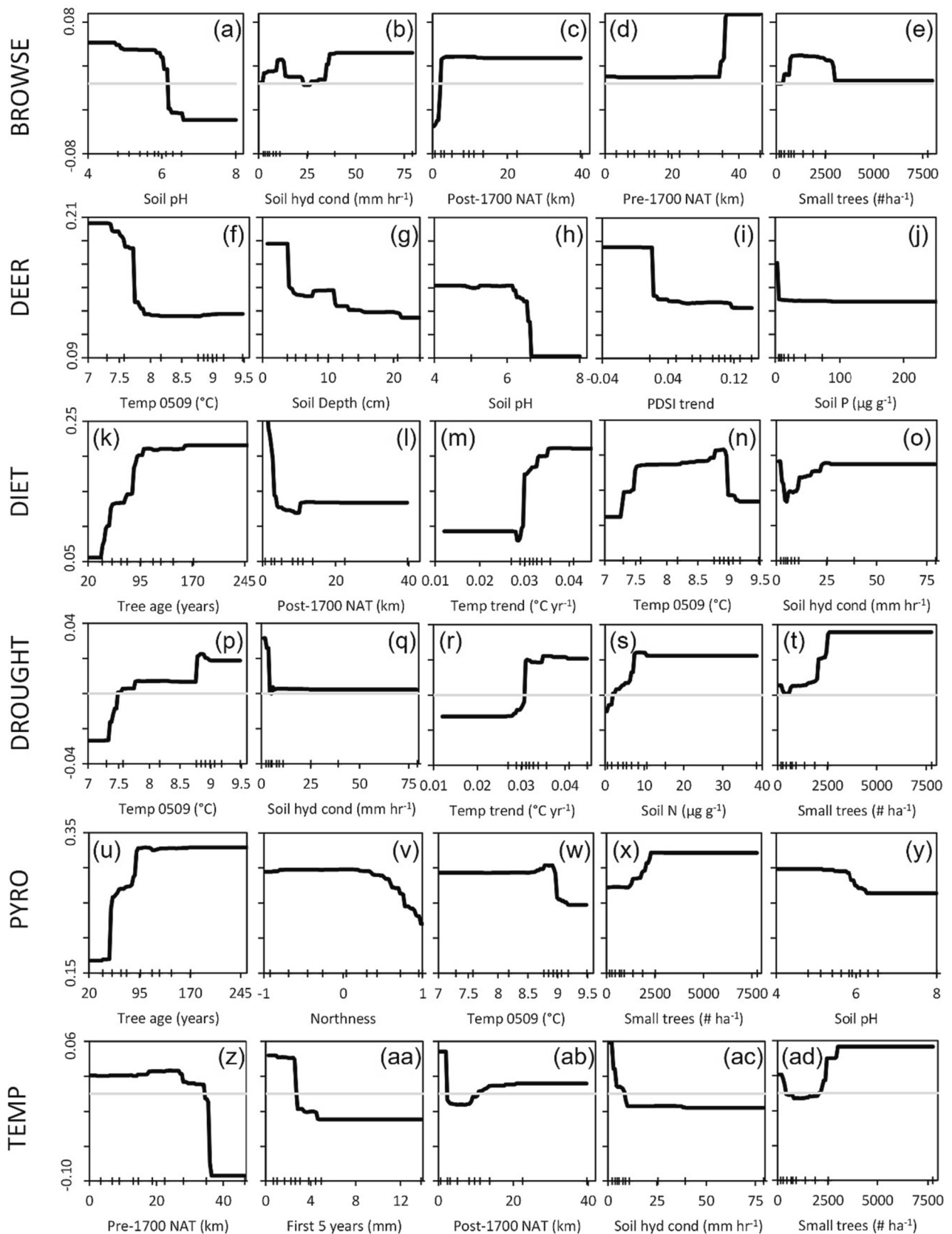
Fig. 3. Partial dependence plots for predictors with the five highest relative importance measures for each trait (highest on left). Curves show how the relationship between the traits and the predictors changes with different levels of the predictors. Positive y-axis values indicate mesophication and negative values indicate xerophication. See Table 1 for predictor names and Table 2 for trait names. The 11 tics that cross the x-axis indicate deciles of the percentage of plots (0, 10… 90, 100%).

diet trees being girdled. Surface burning was also used to clear land during the settler-colonial period (McEwan et al., 2011) ending in the study area by about 1880 (Wang et al., 2010). Cessation of Native American land-use practices and settler burning would decrease selection for xerophytic PYRO and DIET traits and increase selection for species with mesophytic traits (Nowacki and Abrams, 2008).

Mesophication of DIET and PYRO traits was especially strong in sites with older forests, closer to post-1700 NATs, and where summers are rapidly warming. Increase in the mesophytic state of the DIET and PYRO traits with tree age plateaued in 100-year old forests. Intriguingly, separate BRT models of SHADE for small and large DBH classes both similarly plateaued at 100 years (results not shown). This suggests that mesophication of the DIET and PYRO traits relates to the amount of successional time required for shady forest conditions to develop and select for shade-tolerant tree taxa. Indeed, increased mesophication of these traits with increased numbers of small trees also suggests that shade facilitates small tree establishment and growth. This conforms with appreciable instances of shade-intolerant small trees in plots younger than 70 years old (see section 5.4). A forest age of 100 years was similarly found by Wang et al. (2010) to be the age when long-lived shade-tolerant trees regained the dominance they had in western New York forests prior to settler-colonialism. Mesophication of PYRO and SHADE traits was also found to increase with oak forest age in the eastern US by Woodbridge et al. (2022).

Higher rates of mesophication within a 5 km radius (and lower but still appreciable positive rates in a 5–40 km radius, Fig. 3 l) around post-1700 NATs likely relates to past Native American land-use practices increasing the abundance of xerophytic DIET trees near NATs (Tulowiecki and Larsen, 2015; Fulton and Yansa, 2019). The spatial scale and degree of mesophication would likely be different in different biomes and where Native American population sizes and land-use practices were different. Legacy trees from their land use here, or the progeny of those legacy trees, would result in the current older, large DBH trees being more xerophytic for that trait. Relatedly, greater mesophication occurring on south-facing slopes could be due to the occurrence of hotter Native American fires on that terrain selecting for xerophytic PYRO species. Indeed, increased abundance of Native American mast species due to inferred Native American land-use practices has been observed on high insolation sites (Tulowiecki and Larsen, 2015).

The lower relative percent variable importance for both pre- and post-1700 NATs for PYRO than for DIET (Table 8) may be due to the propagules of DIET trees being better able to grow in the new forests while PYRO is less preserved. Another possible reason is that, as noted in Section 3.2, since trees are adapted in various ways to fire (e.g. bark thickness, seed survival, sprouting) our use of 0 or 1 for the PYRO trait, based on Nowacki and Abrams (2015), may have not best captured their response to fire.

Higher mesophication of the DIET and PYRO traits with more rapid rates of summer warming is counter-intuitive, especially as it also occurred for the TEMP trait for which the mesophytic state is cold tolerance as that favors the ability to tolerate the cooler conditions of shady, mesophied forests. One possible explanation is that more rapid warming might lead to more rapid tree growth and cooler and shadier understory temperatures that in turn selects for mesophytic small trees (Bhatta and Vetaas, 2016). A second possible reason is that more rapid rates of warming are occurring in sites impacted by deforestation and urbanization (Zhang et al., 2020) and that those land-use changes select for these traits.

Few to no plots demonstrated strong xerophication of the DIET and PYRO traits, and no predictors of these traits occurred with instances of appreciable xerophication. This reflects the fact that surface burning and Native American dietary tree selection are no longer forces shaping the landscape. Although some controlled burns of oak savannas have occurred in the study area (Keister, 1998), and initiatives aimed at increasing Native American dietary trees have been pursued in nearby areas (Bosco, 2022), these actions have only influenced small areas of

forest. The lack of xerophication supports the suggestion that Native American forest composition impacts were transient in forests of the eastern US (Abrams et al., 2021).

5.2. Animal-related traits: BROWSE AND DEER

Of the three trait pairs, BROWSE and DEER had the second highest mean BRT deviance explained (48.1%, Table 6); the second-most mean plots strongly mesophied (25.0%, Table 7); and the second-most mean plots strongly xerophied (2.9%). The similar changes in the BROWSE and DEER traits across plots, and in their predictors, are reasonable as they both occur due to changes in animal browse activity. Although settler-colonialism likely resulted in opposite trends in population sizes in the 1800s with decreasing game animals and increasing domestic browsing animals, since the late-1800s the population sizes of both have continued to increase (Whitney, 1996; McEwan et al., 2011). This increased browsing animal abundance would have reduced the abundance of the preferred browse species (trait's xerophytic state) and increased the abundance of non-preferred species (trait's mesophytic state).

Mesophication of BROWSE and DEER was especially high at sites where soils had low pH, there were low summer temperatures (or low precipitation, given collinearity between temperature and precipitation in the study area), and shallow soil depths. These patterns conform with the observation that browse impacts are typically highest on sites with low soil fertility and productivity (Gill, 1992; Royo et al., 2017). These two traits had higher summed variable importance for the six soil predictors (Table 8) with 48% for BROWSE and 35% for DEER, than did the other four traits which ranged from 31% for DROUGHT to 18% for DIET. Thus, although plants may experience more browse in sites with high fertility (Tripler et al., 2002), browsing induced reduction of preferred species and increase in non-preferred species, was highest in those sites with low quality soils and low summer temperatures (or low precipitation, given collinearity between temperature and precipitation in the study area) that would be expected to lead to reduced fertility and productivity. Relatedly, oak forests of the eastern US exhibited more mesophication of PYRO, DROUGHT AND SHADE at low pH values (Woodbridge et al., 2022; but they did not evaluate mesophication for DEER and BROWSE).

It was surprising that deer harvest was not selected by the BRT models to explain DEER or BROWSE MoX. This was not due to deer hunting restrictions in built-up areas (cf. Lesser et al., 2019) as a BRT that excluded deer harvest data for our 59 urban-area plots resulted in variable importance of deer harvest increasing to only 1.0% (results not shown). Possibly the towns for which deer harvests were reported (mean = 96 km^2) were too large to represent spatial variation of deer browsing as their typical home range is < 3 km^2 (Quinn et al., 2013).

5.3. Climate-related traits: TEMP AND DROUGHT

Of the three trait pairs, TEMP and DROUGHT had the third highest mean BRT deviance explained (47.5%, Table 6); the fewest mean plots strongly mesophied (14.3%, Table 7); and the most mean plots strongly xerophied (7.3%). Similar changes in the TEMP and DROUGHT traits across plots, and in their predictors, is surprising as their mesophication was expected to occur for different reasons: mesophication of TEMP was expected to occur due to increased forest density causing increased shade and thus cooling of the forest understory (Nowacki and Abrams, 2008), while mesophication of DROUGHT was expected to occur due to reductions in drought (Pederson et al., 2014).

TEMP and DROUGHT exhibited the most mesophication in sites with low soil hydraulic conductivity, short distances to Pre-1700 NATs, higher temperature trends, and more small trees. Sites with those conditions now select for small DBH trees with mesophytic traits of cold tolerance and DROUGHT intolerance. In the past, however, when the large DBH trees established, conditions in those sites would have

selected for the xerophytic traits of heat tolerance and DROUGHT tolerance.

Burning by Native Americans created open oak savannas often extending tens of km around pre-1700 NATs (Tulowiecki et al., 2020a). These would have sunny, warm and dry microclimates that would increase selection for sun-, heat- and drought-tolerant species. Cessation of surface burning would result in these forests becoming more dense, shady, cool and moist, thus selecting for small DBH trees that had mesophytic TEMP and DROUGHT traits especially on the moister soils with low hydraulic conductivity. Mesophication of TEMP and DROUGHT being greatest on dry, south-facing slopes that would have had high moisture stress in the past when forests were more open further supports the logic of this process. The influence of burning around Pre-1700 NATs suggests long-term legacy effects on species composition (Abrams et al., 2021). Mesophication of TEMP in plots with many small DBH trees and xerophication in plots with few small DBH trees is likely due to moister sites being able to support more small DBH trees than drier sites. Relatedly, mesophication of oak forests of the eastern US was generally higher on moister soils (Woodbridge et al., 2022).

Counterintuitively, xerophication occurred in plots with low temperature trends of slow warming, and mesophied in plots with high temperature trends of rapid warming. These would typically be expected to favor increased abundance of xerophytic traits. These unexpected temperature trend results match those found for DIET and PYRO and might have a similar explanation: warmer conditions and rapid warming resulted in more rapid tree growth and the formation of cool and shady conditions (Zellweger et al., 2020); or, land-use changes lead to localized temperature conditions. However, it is possible that the 30-year period over which trends in temperature and drought were calculated might only be an appropriate length of time for forests 40 years of age or younger, while drought trends over longer periods would be more appropriate for older forests. Future research would do well to explore the impact of using climate trends for different periods and lengths of time for different ages of forests.

Strong xerophication occurred in more plots for DROUGHT and TEMP than it did for other traits. This provides support for the theory that xerophytic traits will increase in forests due to ongoing climate change (Clark et al., 2016; Druckenbrod et al., 2019). However, our finding that higher rates of warming lead to mesophication might reduce concern for that theory in the short term while climate change remains minimal in this area.

5.4. SHADE

SHADE could not produce a BRT model of MoX, had the third-fewest plots strongly mesophied (17.1%, Table 7) and the fewest plots strongly xerophied (0.0%). SHADE displayed similar changes in the plots as DIET and especially PYRO ($r = 0.365$ and 0.490, Table 4) likely due to the cessation of burning causing decreased selection for DIET and PYRO and the resulting forest closure selecting for shade-tolerant tree species (Nowacki and Abrams, 2008). Unlike DIET and PYRO which had the strongest MoX trends (Table 5) and strong BRT models predicting their MoX, SHADE had the weakest MoX trend and produced no BRT model of MoX. BRT models could be created of SHADE for only small DBH and large DBH trees. While the model for small DBH was moderate (30.4% deviance explained) and had instances of appreciable MoX, the model for large DBH was weak (7.3% deviance explained) and had no instances of appreciable MoX. The weakness of the large DBH model is potentially due to SHADE, which unlike other traits is secondary and not directly selected for by environmental changes driving MoX (e.g. less fire, more deer). The partial dependence plots from the BRT model of small DBH trees show appreciable instances of shade-intolerant trees in plots younger than 70 years, and appreciable instances of shade tolerance in plots with low soil N that grew in closed forests when young and have a low density of small DBH trees (results not shown). Those conditions did not have a strong enough influence on SHADE to generate a strong BRT

model for MoX. Unlike the other six traits, it appears that MoX of SHADE is not strongly selected for by any of our 22 predictors of mesophication.

6. Conclusion

Our research confirms that there are many causes of forest mesophication and that fire suppression is not the only cause (Woodbridge et al., 2022). Our research also shows that mesophication is not limited to just oak dominated forests. In western New York, forests of all types have experienced mesophication of multiple traits in response to unique sets of environmental drivers. For example, distance from Post-1700 NATs was a strong predictor of mesophication of DIET, but not DROUGHT. Yet, Temperature trend was a strong predictor of both traits. Given this complexity, forest mesophication might be best considered a complex syndrome rather than a singular process.

Our use of site-scale analyses elucidates local-scale predictors of mesophication including distance to NATs and tree age. Site-scale analyses also detected potential climate-related xerophication of TEMP, complementing research focused on detecting the influence of climate change on eastern US forests. Similar site-scale analyses should prove useful for land managers tasked with identifying and modifying mesophication factors affecting tree species traits. Knowledge of which traits are most changed and what predictors best explain those changes would allow land managers to better determine what management approaches might most appropriately shift the forest composition in the desired direction. For example, rather than assuming that fire suppression is the cause of forest mesophication and re-introducing fire, managers might recognize acidic soil as a key predictor and choose to lime the soil. Alternatively, if soils with high hydraulic conductivity were, as we found, not experiencing mesopication or xerophication of TEMP or DROUGHT, then managers might want to protect new areas with those soil conditions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121433.

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