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Spatial and Temporal Pervasiveness of Indigenous Settlement in Oak Landscapes of Southern New England, US, During the Late Holocene

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Abstract: The relative influence of climate and Indigenous cultural burning on past forest composition in southern New England, US, remains debated. Employing varied analyses, this study compared data on Indigenous settlements from over 5000 years before present (YBP) with relative tree abundances estimated from pollen and land survey records. Results suggested that fire-tolerant vegetation, mainly oak (*Quercus* spp.), was more abundant near Indigenous settlements from 4955 to 205 YBP (i.e., 86–91% fire-tolerant trees), and significantly ($p < 0.05$) higher from 3205 to 205 YBP; fire-tolerant vegetation was less abundant away from settlements, where it also experienced greater fluctuations. Correlative models showed that warmer temperatures and distance to Indigenous settlement, which are both indicators of fire, were important predictors in the 17th–18th centuries of fire-tolerant tree abundance; soil variables were less important and their relationships with vegetation were unclear. A marked increase in oak abundance occurred above 8 °C mean annual temperature and within 16 km of major Indigenous settlements. Pyrophilic vegetation was most correlated with distance to Indigenous villages in areas with 7–9 °C mean annual temperature, typical of higher latitudes and elevations that usually supported northern hardwoods. Widespread burning in warmer areas potentially weakened relationships between distance and pyrophilic abundance. Indigenous land use imprinted upon warmer areas conducive to burning created patterns in fire-tolerant vegetation in southern New England, plausibly affecting most low-elevation areas. Results imply that restoration of fire-dependent species and of barrens, savannas, and woodlands of oak in southern New England benefit from cultural burning.

Keywords: Holocene; Indigenous; land survey records; mesophication; Native American; New England; oak; palynology

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1. Introduction

Fire has influenced plants, animals, and ecosystems for >400 million years [1]. Hominin fire use likely started more than 1 million years before present (YBP), with regular use by 300–800 thousand YBP [1,2]. Frequent surface fires reduced shrub and understory tree densities, allowing for the dominance of grasses and forbs in grasslands, and for their coexistence with trees in savannas and woodlands [3]. Grassland and semi-forested landscapes supported foodways of edible plants and wildlife for people, whereas closed forests today are managed to provide mainly timber products [4]. Cultural burning by Indigenous peoples maintained rare grasslands, savannas, and woodlands, which promoted unique associated plants and animals including many of conservation concern [5]. Typically, active management to control fire-sensitive tree establishment is necessary to maintain these ecosystem types and species [6]. In eastern North America, pyrophilic (i.e., fire-tolerant) trees, such as oak (*Quercus* spp.), pine (*Pinus* spp.), and hickory (*Carya* spp.), which historically grow in fire-maintained ecosystems, possess both fire-adaptive traits (such as thick insulating bark and flammable leaf litter) [7] and great cultural value to subsistence economies of Indigenous groups [8].

European colonisation and settlement resulted in dramatic decreases in Indigenous populations, fire exclusion through land-use breaks and policy implementation, replacement of open landscapes by forests or other land uses, increased tree densities, and replacement of fire-tolerant vegetation with fire-sensitive vegetation (termed mesophication) [9]. This has occurred in North America [10,11], South America [12,13], Australia [13–15], southern Africa [13], southern Asia including India [16], and probably Eurasia [17]. Moreover, the loss of megaherbivores has increased tree densities; alternatively, where megaherbivores such as elephants (*Elephantidae*) still occur, they may maintain non-forested ecosystems [18,19].

Despite the historical global extent of fire-maintained ecosystems, widespread documentation of traditional cultural burning for ecosystem management [20], and commonalities of forestation and fire exclusion, the European narrative of climate control over forests remains in place in eastern North America. This perspective includes an economic and cultural emphasis on forests for products, fire exclusion to protect forests, and a forest-based ecology driven by climate rather than disturbances that reduce tree densities [4,21]. Because current ecosystems consist of closed forests, and frequent surface fires have been excluded, the burden remains to provide evidence of the past predominance of alternative, non-forested ecosystems maintained by Indigenous management practises including fire.

Compared to other North American regions such as the southeastern US [22,23], the Great Plains [24,25], the Midwest [26,27], and western US [28,29], the dispute over ecosystems fire-maintained by Indigenous people remains strong in the northeastern US, including in southern New England [30]. These circumstances are likely due to early colonisation with less documentation: Anglo-American settlement began in 1620 in southern New England, with widespread settlement by the first US Census in 1790 [31], resulting in less documentation than inland locations of the northeastern US. Moreover, burnings at a landscape scale did not occur in northern New England and in the northernmost parts of the high-latitude states of the eastern US [32]. On the other hand, fire exclusion and ecosystem transitions in open longleaf pine (*Pinus palustris*) woodlands in the southeastern US occurred during the 1900s, with continuity between historical cultural burning and current prescribed burning [22].

Methods using charcoal and pollen records have examined the relationships between climate, Indigenous settlements, fire, and vegetation in North America. However, studies have produced conflicting interpretations of the same physical data. These records generally indicated that fire frequency in New England was higher in populous coastal areas within oak-pine forests [32–34], but some have suggested that climate drove fire frequency there [35]. Aforementioned studies analysed individual records, but interpretations vary when aggregating records produce regional averages: some have interpreted the changes in combined charcoal frequencies in the northeastern US as a change in anthropogenic burning frequency due to climatic changes [36], whereas others have attributed the variations as mostly climate-driven in southern New England [30]. Comparing population estimates from archaeological data with tree abundance estimates from pollen records across North America, another study found only intermittent correlations between the fire-tolerant vegetation (e.g., oak) and population [37]. Though the authors acknowledged that these relationships existed at smaller extents, a continental-extent analysis would obscure correlations at local and regional scales because taxon ranges are geographically limited, whereas human populations were not.

Ethnohistorical and documentary records in both qualitative and quantitative approaches have provided another venue for examining and debating human–climate–fire–vegetation connections. Descriptions by early Europeans throughout the northeastern US have suggested widespread use of cultural burning [28,38–40], but the reliability of such accounts has been questioned [41–43]. Geographic patterns estimated from historical tree surveys show that fire-tolerant oaks dominated most of the northeastern US [44,45], suggesting that fire filtered out other tree species. Employing correlative modelling to study circa 17th–18th century taxon abundances using these estimates, one study did not find any strong correlations between pyrophilic vegetation and distance to Indigenous settlements in the northeastern US; however, temperature (the most important predictor) and distance to Indigenous settlement were correlated, suggesting that the effects of temperature and settlement may be intertwined [46]. In contrast, finer-resolution geographic modelling in western New York State suggested that fire-tolerant vegetation distribution was explained largely by Indigenous land use [47,48]. Together, the studies of physical, ethnohistorical, and documentary records generally find relationships between Indigenous settlement and fire frequency and/or fire-tolerant vegetation when data are (1) disaggregated and/or analysed at finer resolution, (2) analysed across smaller geographic extents, and (3) historical rather than archaeological records of Indigenous settlement.

Despite disagreement and conflicting results, physical and ethnohistorical evidence places Indigenous cultural burning in southern New England. Fossil charcoal (Figure 1b) has been recovered from lake sediments here [30,32], a region where lightning-caused fires are rare [11]. Charcoal was more common in highly populated areas of southern New England in lower elevations and along coastal regions [32]. At some sites here, charcoal amounts during Indigenous and European occupations were comparable, suggesting burning at similar frequency and/or intensity [32]: differences in charcoal influx were statistically non-significant before and after the European settlement for 4 out of 16 charcoal sites in one study here [35]. Firsthand 17th-century European accounts described widespread Indigenous burning [28,38,39], and many town and county histories described parklike oak landscapes before the Euro-American settlement [40], similar to how colonising Europeans described Indigenous landscapes observed elsewhere such as Australia [14].

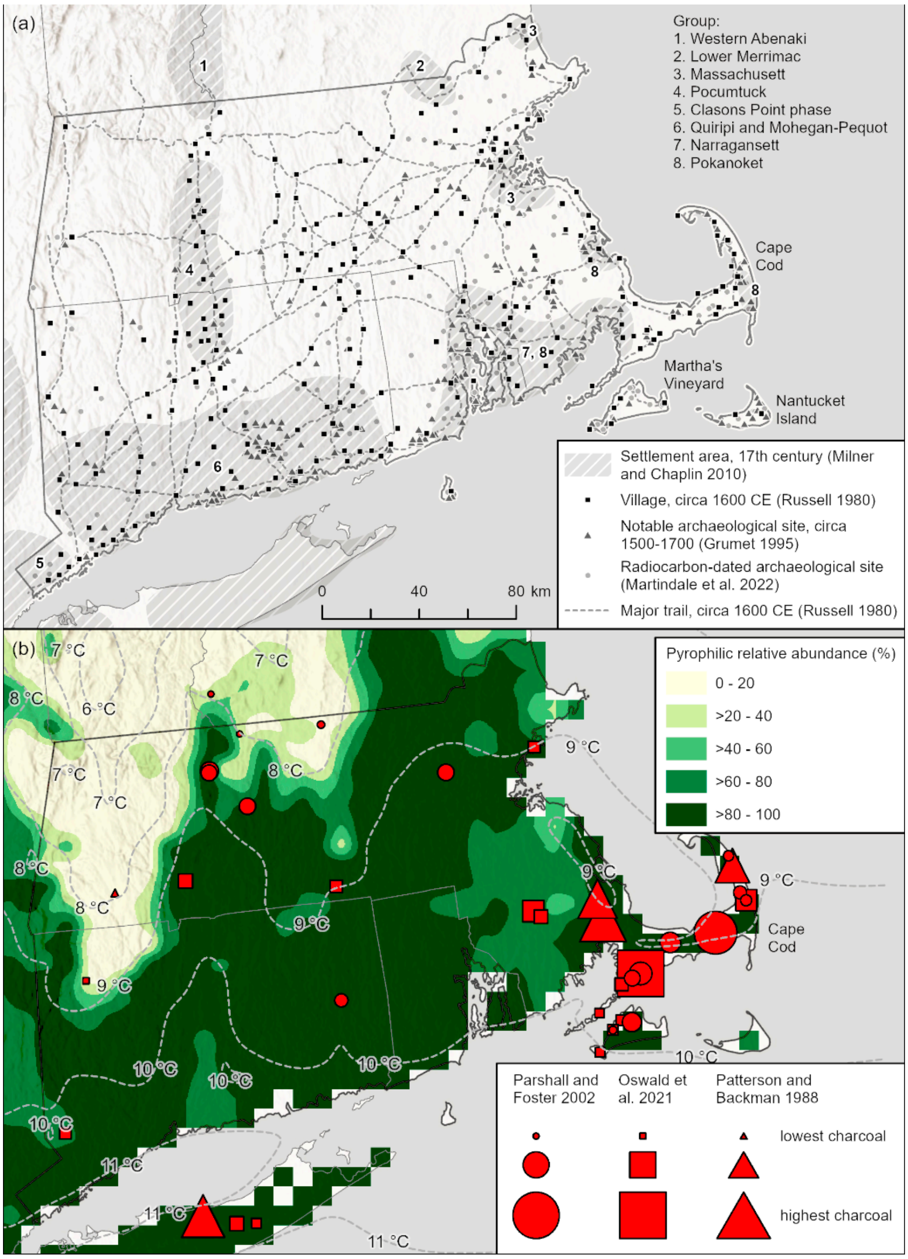

Figure 1. (**a**) Indigenous geography with 17th century settlement areas [49], 17th century villages [50], notable 16th–18th century archaeological sites [51], radiocarbon-dated archaeological sites [52], and 17th century major trails [50]. The same Indigenous site can appear in multiple layers. (**b**) Relative abundance of pyrophilic tree taxa circa 17th–18th centuries CE [45], charcoal from palynology sites, and mean annual temperature [53]. Charcoal records are scaled from 0 (lowest) to 1 (highest) for each dataset to create a common scale, because they are provided in different units: mean pre-European charcoal-to-pollen ratios [33,35] and mean number of charcoal pieces [30]. Time periods vary across charcoal sites, and some records include post-European charcoal [30].

This study advances characterizations of human–environment–vegetation relationships in southern New England by offering a novel analysis of geographic data on Indigenous settlement and fire-tolerant vegetation. We synthesise data on Indigenous geography from historical and archaeological sources, with estimates of tree taxon abundances from pollen and land survey records. We focus on the latter half of the Holocene, starting circa 5000 YBP and especially on the 17th–18th centuries CE. We test three hypotheses: (1) Pyrophilic vegetation was consistently greater throughout the later Holocene where Indigenous settlement occurred. (2) Pyrophilic relative abundance was correlated with distance to Indigenous settlement, alongside climate and soil variables, upon European colonisation. (3) The effects of Indigenous settlements were the most observable in climatically marginal (i.e., cooler) areas, where burning more clearly overrode climatic controls and caused a conversion from mesic- to xeric-dominated vegetation. This study contributes to revealing the spatiotemporal impacts of Indigenous land management (likely via fire) upon vegetation patterns, thus serving to address research priorities in fire ecology and related fields [54].

2. Study Area

The study area encompasses Massachusetts, Connecticut, and Rhode Island (34,000 km^2 in land area). Though sometimes included in southern New England [30], we excluded Long Island (New York State) as many datasets were specific to the three-state region. Its original forest consisted of (1) oak and pitch pine (*Pinus rigida*) atop sandy glacial outwash soils of eastern Massachusetts; (2) oak and other angiosperm species throughout Massachusetts, Connecticut, and Rhode Island; (3) pine and oak forests in central Massachusetts, and (4) mesic angiosperm species such as American beech (*Fagus grandifolia*), maples (*Acer* spp.), and American basswood (*Tilia americana*) with an admixture of gymnosperm species in northwestern Massachusetts [35,44,45]. The latter three vegetation communities generally occur across a temperature gradient from warm to cool. The study area possesses a humid-continental climate, with warm summers and cold winters; Table 1 and Figure S1 summarise climate and soil conditions.

Table 1. Selected characteristics of the study area. Values are based on aggregated 8 km resolution data. Forest composition and climate predictors are for circa 17th–18th centuries. See text for predictor sources.

Type	Predictor	Unit	Min	25th	Median	75th	Max
Forest composition	Chestnut	% of all trees	0.0	0.8	4.4	10.1	41.6
Forest composition	Hickory	% of all trees	0.1	2.3	5.5	9.9	33.5
Forest composition	Oak	% of all trees	0.2	42.9	57.6	68.2	89.5
Forest composition	Pine	% of all trees	0.0	0.8	4.9	13.1	77.1
Forest composition	Pyrophilic	% of all trees	0.7	73.0	85.3	91.2	99.1
Climate	Annual mean temperature	°C	6.7	8.7	9.2	9.7	11.1
Climate	Maximum temperature of warmest month	°C	19.4	24.1	25.1	25.7	26.6
Climate	Minimum temperature of coldest month	°C	−10.4	−7.9	−6.5	−5.1	−1.7
Climate	Annual precipitation	mm	973	1144	1201	1262	1432
Climate	Precipitation seasonality (coefficient of variation)	unitless	5.9	7.8	8.7	9.5	13.4
Soil	Available water supply	cm	8.5	14.1	15.8	16.6	33.3
Soil	Bulk density	g/cm	0.9	1.4	1.5	1.6	1.7

Table 1. *Cont.*

Type	Predictor	Unit	Min	25th	Median	75th	Max
Soil	Percent clay	% by weight	2.1	6.0	7.8	10.9	16.4
Soil	Entisol order	% of total area	0.0	3.2	8.2	16.2	84.3
Soil	Histosol order	% of total area	0.0	0.9	2.3	5.0	84.5
Soil	Inceptisol order	% of total area	0.0	66.3	82.9	90.4	100.0
Soil	Mollisol order	% of total area	0.0	0.0	0.0	0.0	14.7
Soil	Ultisol order	% of total area	0.0	0.0	0.0	0.0	12.3
Soil	Permeability rate	cm/hr	10.7	37.4	60.7	75.6	140.9
Soil	Organic matter content	% by weight	1.2	4.6	6.2	8.4	49.2
Soil	pH	unitless	4.2	5.2	5.4	5.8	6.8
Soil	Depth to bedrock	cm	20.9	47.1	71.5	77.3	201.0
Soil	Soil passing sieve #10 (coarse)	% by weight	58.6	71.3	72.9	75.8	87.4
Soil	Soil passing sieve #200 (fine)	% by weight	10.8	30.9	35.3	38.7	60.8
Terrain	Terrain slope angle	°	0.6	2.3	3.3	4.6	11.7
Indigenous	Distance to nearest notable 16th–18th century archaeological site	km	1.6	5.4	9.9	17.4	47.3
Indigenous	Distance to nearest 17th-century village site	km	1.9	3.9	6.1	9.4	26.0
Indigenous	Distance to nearest radiocarbon-dated archaeological site	km	2.0	4.6	7.4	12.3	32.6

Indigenous peoples have inhabited southern New England beginning 12,000–14,000 YBP, with generally increasing population until European contact [30,52,55], and with little disruption to populations until that time [56]. Marked population increases and cultural changes occurred during the Middle Woodland (circa 0–1000 CE) and Late Woodland (1000–1620 CE) [30,36,55]. Archaeological evidence circa 800–1100 CE suggests an increasing population, increasing site complexity, longer site habitation, and trade with groups across the eastern US [56]. Upon European arrival in the 17th century, the region was culturally diverse with eastern Algonquian-speaking groups collectively called the Ninnimissinuok [56]. They comprised the Pawtucket (Lower Merrimac), Massachusett (Wampanoag), Pokanoket, Narragansett, Pequot/Mohegan, Pocumtuck, and additional sachemships [49,56–58]. Pre-epidemic population was estimated at over 100,000 persons, ranging from 22 to 250 persons per 100 km^2, with highest densities in coastal areas and the Connecticut River Valley [49,56]. Indigenous sites and travel routes existed (Figure 1a), generally corresponding with fire-tolerant vegetation (Figure 1b).

Emerging by 1000 AD and continuing until European colonisation circa 1620 CE, Indigenous groups practiced mixed and diverse subsistence strategies for estuarine, riverine, and upland environments [56]. Groups in coastal areas practiced conditional sedentism to exploit the different timing of marine and estuarine resources. Riverine groups practiced semi-sedentary to sedentary year-round occupation of village sites in the Late Woodland period and grew at least some cultigens including corn (*Zea mays*) as a dietary supplement [43,56,59]. Upland groups were generally hunter-gatherers. Inland groups used rainfed agriculture, suggested by the archaeological evidence of farming tools and the geographical correspondence between archaeological sites and soils ideal for horticulture [60]. Ethnohistorical literature, and some archaeological and paleoethnobotanical evidence, suggested that Indigenous people practiced diverse horticultural strategies to cultivate small herbaceous and large woody plants, including via slash-and-burn horticulture [60].

3. Materials and Methods

We compared archaeological and historical data with estimates of the relative abundance of fire-tolerant trees. We also trained correlative models to examine which Indigenous, climate, and soil predictors explained geographic patterns in relative abundance. GIS-related tasks were performed with ArcGIS Pro 3.1 [61], and statistical analysis was performed with R 4.2.2 [62,63].

3.1. Comparing Archaeological Sites to Tree Relative Abundances, 3005 BCE–1745 CE

We compared archaeological site locations to tree relative abundances over the last 5000 YBP. We downloaded archaeological site data from the Canadian Archaeological Radiocarbon Database (CARD) [52] for Massachusetts, Connecticut, and Rhode Island. We mapped sites resolvable to the town level or finer using locational descriptions in site metadata. About 45% of sites lacked normalised ages, so for these sites we calculated normalised ages when metadata was sufficient to estimate $\delta^{13}C$ [64]. Normalised ages were converted to calendar age (median estimates) using the IntCal20 curve [65] via the "rcarbon" package, Version 1.5.1 [66]. After discarding sites with unnormalized ages, geographically imprecise sites, and/or non-archaeological sites, 1342 sites remained in the three-state region. Some sites just outside the study area were also mapped to support later data processing.

Archaeological sites were compared to a 24 km resolution estimate of relative abundances of five taxa: oak, pine, chestnut (*Castanea dentata*), hickory, and combined pyrophilic (oak + pine + chestnut + hickory). The estimates came from the Spatio-Temporal Empirical Prediction from Pollen in Sediments (STEPPS) model, a process-based Bayesian hierarchical spatial pollen-vegetation model calibrated from fossil pollen and land survey data [67–71]. Pollen data were derived largely from the Neotoma Paleoecology Database [72]. In southern New England, 51 lake sediment records provided pollen data for STEPPS, which are listed in the Supplementary Materials of [65]. The estimates were provided at 250 YBP intervals for 8000 years, from 7955 to 205 YBP (6005 BCE–1745 CE). We used mean STEPPS predictions of relative abundances at each grid cell.

For each timestep, we compared taxon relative abundances to the presence/absence of archaeological sites in each grid cell (n = 70) in the preceding 250 yr: for example, for the 455 YBP time step (1495 CE) we used sites inhabited from 705 to 455 YBP (1245–1495 CE). This choice assured a sufficient sample size, and 250 yr is also a plausible estimate of how long Indigenous land use legacies persisted [73]. A total of 100 comparisons were made: five taxa for 20 timesteps from 4955 to 205 YBP (3005 BCE–1745 CE). We did not compare beyond 3005 BCE due to low numbers of sites. Nonparametric Wilcoxon Rank Sum Tests with $\alpha = 0.05$ assessed whether taxon abundances were significantly higher in cells with or without archaeological sites. We also performed a separate analysis of cells (n = 52; 100 more comparisons) that excluded higher elevation ecoregions [74,75] in the northwestern portion of the study area, to test whether Indigenous settlement coincided with higher taxon abundances even within warmer areas.

3.2. Comparing Indigenous Geography to Tree Relative Abundances, Circa 17th–18th Centuries

We compared locations of Indigenous settlement to taxon relative abundances circa 17th–18th centuries. We used relative abundance layers at 8 km resolution, interpolated from witness-tree tallies of town proprietor surveys [45]. We used three representations of Indigenous geography to assess if any representation was correlated with fire-adapted vegetation: radiocarbon-dated archaeological sites [52], notable 16th–18th century archaeological sites [51], and 17th century village sites [50]. Regarding his map, Russell wrote that "no site. . .is intentionally included for which the author has not, from long study of documents, local histories, and personal correspondence, found evidence that it was in use at or about the time" of European arrival [50]. The latter two representations were digitised from scanned maps that were georeferenced into ArcGIS Pro 3.1 software [61]. All sources had an estimated mean positional error of 5–10 km. We tested these different representations of Indigenous settlement given the inherent complexities of representing it. Wilcoxon Rank Sum Tests assessed whether the taxon abundances were significantly higher in grid cells with or without a settlement feature. Tests were performed for southern New England (n = 566 cells) and separately for lowlands (n = 439 cells).

3.3. Assessing Relationships Between Oak Abundance, Indigenous Settlement, and Climate, 505 BCE–1495 CE

We singled out oak, the most abundant fire-adapted taxon in the study area, to examine climatic and Indigenous predictors of its relative abundance geographically over the late Holocene. We developed five correlative models of abundance based on climate predictors and a proxy of Indigenous settlement: every 500 yr from 505 BCE to 1495 CE. These timesteps ensured proper temporal alignment between relative abundance (with data every 250 yr) and climate estimates (with data every 100 yr). The aforementioned 24 km resolution layers of relative abundance were used as dependent variables.

For climate predictors, we acquired CHELSA-TraCE21k reconstructions [53] of mean annual temperature and mean annual precipitation at 1 km resolution for each of five 500-yr timesteps, which we resampled and aggregated to match the 24 km resolution grid cells (n = 70). We also developed a proxy for Indigenous settlement patterns: for each timestep, we interpolated a 24 km resolution surface with archaeological site presences in the preceding 250 yr ("1"s; see Figure 2 later) and an equal number of random absences ("0"s) using an empirical Bayesian kriging tool in ArcGIS Pro [61], to create a surface that represented the general settlement distribution in a given timestep. This surface ranged from 0 (low settlement) to 1 (high settlement). We left tool settings at their default allowing it to automatically parameterize the kriging model. We interpolated the surface due to the incomplete nature of archaeological data, precluding the creation of a "distance to nearest archaeological site" variable. Too few archaeological sites existed prior to 505 BCE to create kriged surfaces. This surface was considered as a predictor in model development (see below) alongside temperature and precipitation.

We trained correlative boosted regression tree (BRT) models [76–78] using the "gbm.auto" Version 2024.10.1 R package [79] to understand the geographic distribution of oak relative abundance. We chose this method to increase the comparability with similar studies that utilised BRTs [46–48,80]. For BRT model details, see Supplementary Material. We examined model outputs such as model performance measures (e.g., percent deviance, cross-validation correlation), predictor importance measures, and marginal response curves. Given the nonlinear response curves that are modelled by the BRT method, we calculated the absolute value of Pearson's r correlation coefficients between the predicted relative abundance and predictor values as a rough measure of response curve simplicity, with values closer to 1 indicating a more linear relationship model.

3.4. Assessing Relationships Between Relative Abundances, Indigenous Settlement, and Environment, 17th–18th Centuries

To understand predictors of geographic patterns in taxon abundances circa 17th–18th centuries, we developed correlative models using climate, soil, terrain, and Indigenous land use predictors. We obtained a dataset from a previous study [46] that compiled data on relative abundances [45], climate [81], soil [82,83], terrain [84], and distance to Indigenous settlement, at 8 km resolution. We replaced the climate data with bioclimatic predictors estimated for 1700–1800 CE from the CHELSA-Trace21k dataset [53]; we resampled and aggregated these data to 8 km resolution. Some predictors were eliminated due to collinearity. We developed four models for each of the five taxa, totalling 20 models. Each model included 4 climate predictors, 14 soil predictors, and 1 terrain predictor (Figure S1). One set included only climate and soil predictors. The other three models per taxon included one of the three proxies of Indigenous land use: distance to nearest radiocarbon-dated archaeological site of any age [52], distance to nearest notable 16th–18th century archaeological site [51], or distance to nearest 17th-century village site [50]. We trained BRT models [76–78] of relative abundance using the "gbm.auto" R package [79]. We chose the BRT method to increase comparability with other models in this study and in previous studies. We interrogated the aforementioned model outputs and measures of response curve complexity.

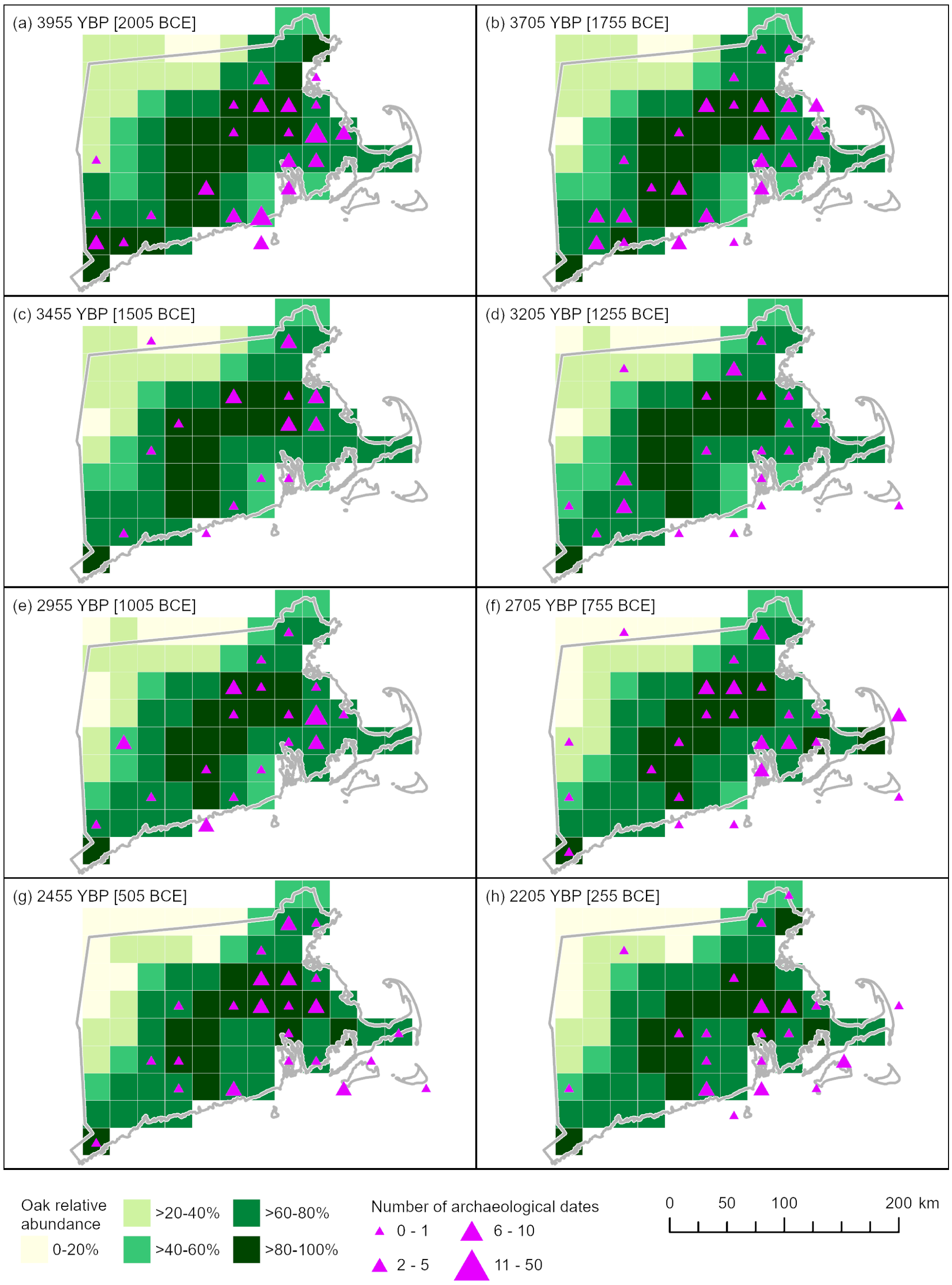

Figure 2. *Cont.*

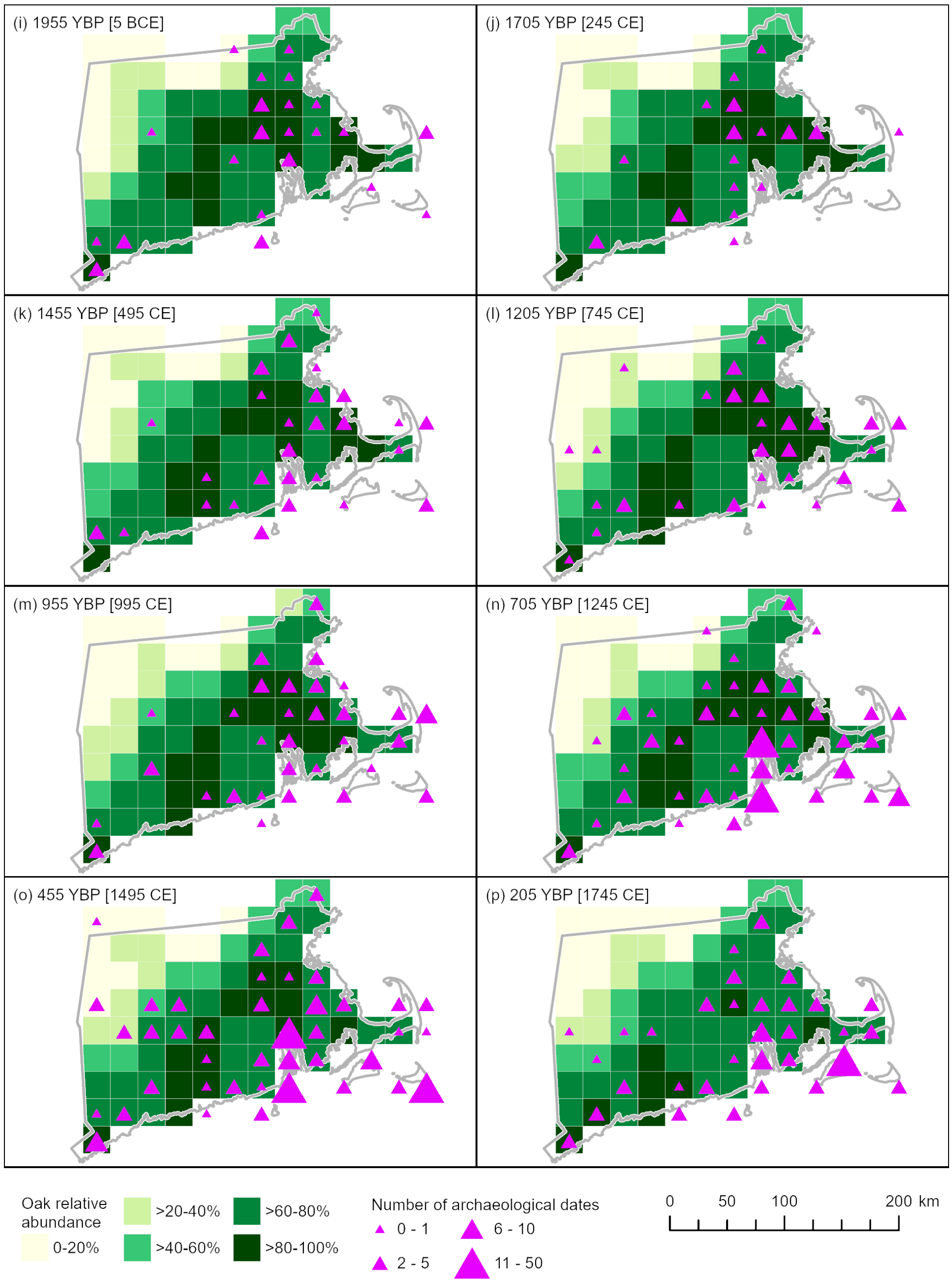

Figure 2. Oak relative abundance [71] from 2005 BCE to 1745 CE (3955–205 years before present [YBP]), and number of archaeological dates [52] from the preceding 250 yr. Abundance estimates did not exist for some coastal areas.

3.5. Testing the Influence of Indigenous Settlement Along a Temperature Gradient

To assess if Indigenous land use was more observable in shaping the compositional patterns in climatically marginal areas for pyrophilic vegetation, we developed models focusing on the effects of temperature and distance to settlement but within certain temperature ranges. We divided the study area into four regions based on mean annual temperatures using 1 °C intervals (Figure 1b). We then trained linear regression models for each taxon within each region, relating the relative abundance to mean annual temperature and distance to nearest 17th century village site [50]. We interpreted R^2, regression coefficients (standardised and unstandardized), and *p*-values. We focused on temperature and distance to villages given their higher importance and interpretability in the aforementioned BRT models (see Results). We used linear regression for formal hypothesis testing and because BRT models fitted highly nonlinear responses when initially attempted.

4. Results

4.1. Archaeological Sites Versus Tree Relative Abundances, 3005 BCE–1745 CE

Three of the five taxa showed a significant difference at any timestep in relative abundance (based on 24 km resolution estimates) between grid cells with or without an archaeological site: oak, pyrophilic, and pine (Table S1). Oak had the highest number of significant test results: 19 out of 20 tests were significant ($p < 0.05$), including the 13 most recent timesteps, starting in 1255 BCE. Median oak relative abundance per timestep ranged from 74 to 82% for cells with an archaeological site, versus 44–67% without (Figures 2 and 3; Table S1). For combined pyrophilic, 17 out of 20 tests were significant, including the eight most recent timesteps starting in 5 BCE. Median pyrophilic relative abundance per timestep ranged from 86–91% with a site, versus 66–82% without; oak accounted for the majority of pyrophilic vegetation. Pine produced three significant results, including for the most recent timestep (1745 CE) and three of the four most recent timesteps. Chestnut and hickory yielded no significant results. This analysis did not include coastal regions with high Indigenous populations and high percentages of fire-adapted vegetation, such as Martha's Vineyard and eastern Cape Cod, due to its omission in the 24 km resolution dataset.

When analysing lower elevations, oak and combined pyrophilic abundances were often modestly higher where archaeological sites occurred (Table S2). The median oak abundance ranged from 74–82% for cells with a site, versus 70–77% without. The median pyrophilic abundance ranged from 86–91% for cells with a site, versus 82–88% without. The oak abundance was significantly ($p < 0.05$) higher at 7 out of 20 timesteps, and the pyrophilic abundance was significantly higher at 4 out of 20 timesteps; both these taxa yielded significant results for the most recent timestep. Only two other tests were significant: one for pine and one for hickory.

4.2. Indigenous Geography Versus Tree Relative Abundances, Circa 17th–18th Centuries

Circa 17th–18th centuries, oak showed higher relative abundance (at 8 km resolution) at Indigenous sites (median 62–64% versus 55–63%) using any representation of Indigenous geography (Table S3), and when performing tests both within all of southern New England or just lowlands. However, the oak results were significant ($p < 0.05$) only when testing across all of southern New England. Hickory showed significantly higher relative abundance at Indigenous sites (median 7% versus 5%) when testing across southern New England using any representation of Indigenous geography; it was higher when testing within the lowlands using two of three representations of Indigenous geography, but not significantly so. The pyrophilic vegetation combined showed significantly higher relative abundance at Indigenous sites (median 87% versus 84–85%) when testing across southern New England using any representation of Indigenous geography but was not higher when testing within lowlands. Pine showed a higher relative abundance at Indigenous sites (median 6% versus 4–5%) when testing across southern New England using any representation of Indigenous geography but was significant only when using one representation of Indigenous geography; it was generally not higher when testing within lowlands. Chestnut showed higher abundance away from Indigenous sites rather than at Indigenous sites.

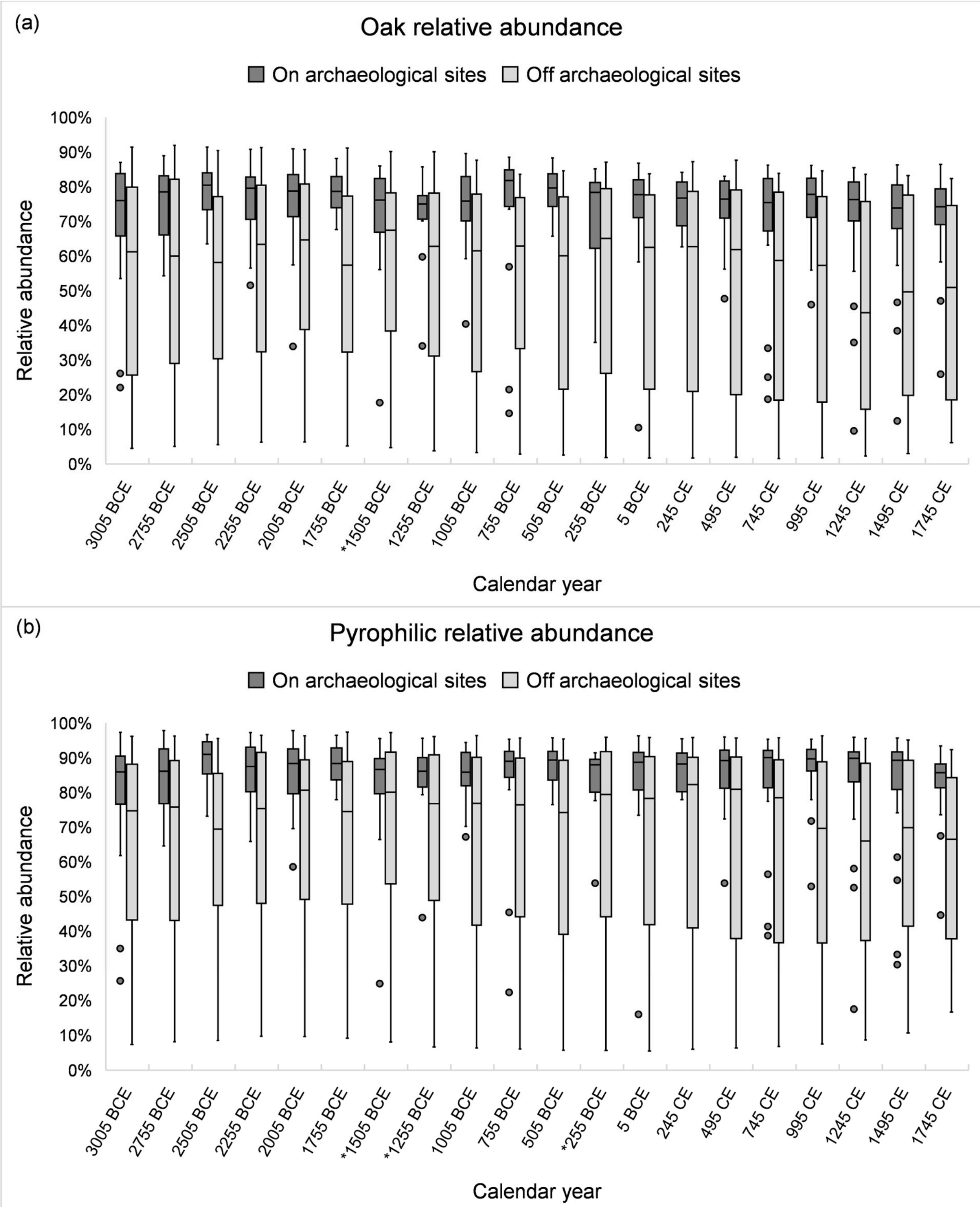

Figure 3. (**a**) Oak (*Quercus* spp.) and (**b**) pyrophilic vegetation relative abundance from 3005 BCE to 1745 CE (4955–205 years before present), in archaeological site presence and absence locations at 24 km resolution. Non-significant differences are indicated with an asterisk on the *x*-axis labels.

4.3. Relationships Between Oak Abundances, Indigenous Settlements, and Climate, 505 BCE–1495 CE

BRT models at 24 km resolution suggested the combined importance of temperature and Indigenous settlement, and also somewhat precipitation, in shaping the geographic distribution of oak relative abundance in the 2000 yr preceding the European colonisation. Models including the proxy for Indigenous settlement (i.e., an interpolation based on

CARD data) improved upon climate-only models (Table 2): the models that ranged in percent deviance explained (based on cross-validation data, relative to null model) from 79.0 to 83.5%, and were 0.2–5.5 percentage points higher than corresponding climate-only models. Results in this section hereafter pertain to models including the Indigenous proxy.

Table 2. Parameters and results of boosted regression tree models relating oak abundances to climate predictors and a proxy of Indigenous settlement (24 km resolution), 505 BCE–1495 CE. "with CARD-based proxy" = models with climate predictors and proxy for Indigenous settlement based on CARD data [52]; "with climate only" = models with only climate predictors. CV = cross validation, SE = standard error, RMSE = root-mean-square error.

	Oak, 505 BCE		**Oak, 5 BCE**		**Oak, 495 CE**		**Oak, 995 CE**		**Oak, 1495 CE**	
	with CARD-Based Proxy	**with Climate Only**	**with CARD-Based Proxy**	**with Climate Only**	**with CARD-Based Proxy**	**with Climate Only**	**with CARD-Based Proxy**	**with Climate Only**	**with CARD-Based Proxy**	**with Climate Only**
Number of trees	2500	1400	1950	2100	3600	1000	3100	500	1200	3900
Learning rate	0.005	0.020	0.020	0.020	0.010	0.030	0.010	0.040	0.030	0.010
Training data correlation	0.958	0.950	0.979	0.970	0.983	0.968	0.983	0.963	0.987	0.973
CV mean deviance	0.014	0.017	0.014	0.016	0.013	0.014	0.013	0.015	0.011	0.015
CV deviance SE	0.002	0.003	0.004	0.003	0.003	0.003	0.004	0.003	0.003	0.002
CV D squared	0.997	0.996	0.997	0.997	0.997	0.997	0.997	0.997	0.998	0.997
CV mean correlation	0.903	0.878	0.868	0.761	0.770	0.909	0.909	0.871	0.901	0.817
CV correlation SE	0.014	0.036	0.065	0.107	0.128	0.019	0.034	0.047	0.033	0.077
CV RMSE	0.113	0.127	0.109	0.124	0.109	0.111	0.106	0.115	0.099	0.118
Deviance: % explained relative to null, training	91.6	90.0	95.8	93.9	96.5	93.6	96.6	92.7	97.3	94.5
Deviance: % explained relative to null, CV	79.0	73.8	80.1	76.3	81.9	81.5	82.4	80.1	83.5	78.0

Temperature was the most important predictor, with relative importance values from 60 to 68% (Table 3). Based on the response curves across all models, oak abundance markedly increased around 7.75–8.50 °C and levelled around 8.50–9.25 °C, increasing approximately 50 percentage points. Response curves plotting predicted abundance versus temperature were interpretable with Pearson's *r* between predicted values and predictor values = 0.9. The Indigenous settlement proxy (ranging from 0 to 1) was the second-most important, ranging from 25–32%. It showed generally positive relationships, with increases around a value of 0.2–0.4, but response curves were the least interpretable of all predictors (Pearson's *r* = 0.5–0.9). Precipitation importance ranged from 0 (excluded from model) to 10%. Oak relative abundance was generally positively correlated with mean annual precipitation, with increases in abundance starting at around 115–120 cm, and these response curves were somewhat interpretable (Pearson's *r* = 0.7–0.9). The inclusion of the Indigenous settlement proxy variables made precipitation response curves more interpretable compared to those from climate-only models.

Table 3. Relative importance for predictors in models of oak relative abundance (24 km resolution) 505 BCE–1495 BCE. "with CARD-based proxy" = models with climate predictors and proxy for Indigenous settlement; "with climate only" = models with only climate predictors.

	Oak, 505 BCE		**Oak, 5 BCE**		**Oak, 495 CE**		**Oak, 995 CE**		**Oak, 1495 CE**	
	with CARD-Based Proxy	**with Env. Only**	**with CARD-Based Proxy**	**with Env. Only**	**with CARD-Based Proxy**	**with Env. Only**	**with CARD-Based Proxy**	**with Env. Only**	**with CARD-Based Proxy**	**with Env. Only**
	with CARD-Based Proxy	**with Climate Only**	**with CARD-Based Proxy**	**with Climate Only**	**with CARD-Based Proxy**	**with Climate Only**	**with CARD-Based Proxy**	**with Climate Only**	**with CARD-Based Proxy**	**with Climate Only**
Mean annual temperature	63.1	79.6	68.2	79.9	62.7	84.2	66.1	87.8	59.7	83.1
Mean annual precipitation	6.5	20.4	0.0	20.1	9.1	15.8	8.6	12.2	10.2	16.9
Indigenous settlement proxy	30.4	---	31.8	---	28.3	---	25.3	---	30.1	---

4.4. Relationships Between Relative Abundance, Indigenous Settlement, and Environment, 17th–18th Centuries

For models of the geographic distribution of circa 17th–18th century relative abundances, including any distance-based proxy of Indigenous land use generally resulted in slight improvements in performance metrics based on training and cross-validation data (Table 4). When examining metrics of all four models trained per taxon, taxa from best fitting to least fitting the cross-validation data were: pyrophilic (81.4–84.1% of deviance explained in cross-validation data explained, relative to null model), oak (71.8–73.7%), hickory (48.0–49.6%), chestnut (45.8–48.9%), and pine (45.0–47.5%). The relative importance for the three proxies possessed the following values, from greatest to least importance to each taxon: oak (2–7%), pyrophilic (1–8%), hickory (2–4%), chestnut (1–4%), and pine (2%). When response curves were not highly irregular, elevated abundance of these taxa generally occurred within 20–25 km of Indigenous settlement. Models that included "distance to nearest 17th-century village site" [50] were generally the best-fitting and possessed the most interpretable response curves: this predictor was the most important of the three proxies. These model results are summarised below.

Across models that included the "distance to nearest 17th-century village site" predictor, mean annual temperature was the most important predictor on average, with relative importance values ranging from 5–51% (Table 5). It was the most important predictor in models for combined pyrophilic (51%), oak (50%), and hickory (17%) abundances. It also generally had the clearest relationships with relative abundance, being positively correlated with each taxon (Figures S2–S6). The importance of distance to village was second-most important for oak and combined pyrophilic, and was eighth-most important (by median relative importance), with relative importance values ranging from 2–8% across all taxa. It too exhibited clearer relationships with relative abundance for most taxa. Relative abundances for taxa were generally higher 0–16 km from 17th-century village sites for oak and pyrophilic, and 0–19 km for chestnut; the relationships between distance and hickory and pine abundance were highly irregular (Figures S2–S6).

Table 4. Parameters and results of boosted regression tree models of relative abundance (8 km resolution). Four models were trained per taxon: "with 17th c. village sites" = models that included distance to nearest 17th-century village site [50], "with dated arch. sites" = models that included distance to nearest radiocarbon-dated archaeological site [52], "with notable Contact arch. sites" = models that included distance to nearest notable 16th–18th century archaeological site [51], and "env. only" = models that included only environmental predictors. CV = cross validation, SE = standard error, RMSE = root-mean-square error.

	Chestnut				**Hickory**				**Oak**				**Pine**				**Pyrophilic**			
	with 17th c. Village Sites	**with Dated Arch. Sites**	**with Notable Contact Arch. Sites**	**with Env. Only**	**with 17th c. Village Sites**	**with Dated Arch. Sites**	**with Notable Contact Arch. Sites**	**with Env. Only**	**with 17th c. Village Sites**	**with Dated Arch. Sites**	**with Notable Contact Arch. Sites**	**with Env. Only**	**with 17th c. Village Sites**	**with Dated Arch. Sites**	**with Notable Contact Arch. Sites**	**with Env. Only**	**with 17th c. Village Sites**	**with Dated Arch. Sites**	**with Notable Contact Arch. Sites**	**with Env. Only**
Number of trees	1200	1000	1000	1400	3100	2700	1100	600	2700	1200	3900	1700	1100	800	1500	1400	2700	2200	3100	2800
Tree complexity	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Learning rate	0.040	0.030	0.040	0.050	0.010	0.010	0.020	0.050	0.010	0.030	0.010	0.030	0.020	0.040	0.020	0.020	0.040	0.050	0.040	0.050
Training data correlation	0.942	0.910	0.923	0.957	0.895	0.885	0.875	0.886	0.949	0.957	0.959	0.967	0.892	0.917	0.914	0.908	0.994	0.994	0.995	0.996
CV mean deviance	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.015	0.016	0.016	0.016	0.008	0.008	0.008	0.008	0.012	0.013	0.013	0.014
CV deviance SE	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.002	0.001	0.001	0.001	0.001	0.002	0.001	0.002	0.002
CV D squared	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	1.000	1.000	1.000	1.000	0.999	0.999	0.999	0.999	1.000	1.000	1.000	1.000
CV mean correlation	0.715	0.707	0.687	0.697	0.711	0.695	0.702	0.717	0.854	0.848	0.845	0.849	0.689	0.675	0.695	0.680	0.917	0.904	0.910	0.897
CV correlation SE	0.020	0.024	0.026	0.030	0.021	0.021	0.028	0.026	0.014	0.019	0.017	0.013	0.026	0.026	0.025	0.027	0.011	0.011	0.008	0.012
CV RMSE	0.042	0.042	0.043	0.042	0.039	0.040	0.039	0.039	0.122	0.124	0.126	0.126	0.089	0.091	0.089	0.091	0.107	0.114	0.112	0.117
Deviance: % explained relative to null, training	87.7	81.6	84.1	90.8	79.0	77.0	75.4	77.4	89.7	91.3	91.7	93.2	78.3	82.9	82.4	81.2	98.9	98.9	99.0	99.1
Deviance: % explained relative to null, CV	48.9	48.7	45.8	47.7	49.3	48.0	49.6	49.4	73.7	73.0	71.9	71.8	46.7	45.0	47.5	45.7	84.1	82.4	82.9	81.4

Notable and interpretable modelled relationships by taxon (from best to worst fit on cross-validation data) were as follows (see also Figures S2–S6): Pyrophilic relative abundance increased sharply (roughly 70 percentage points) at 8 °C and levelled at around 9.5 °C; it increased (roughly 15 percentage points) from 16 km to 0 km from 17th century village sites; it increased in gently sloping terrain averaging between 2 and 8°; and it increased atop coarser-grained soils with percent passing sieve number 200 <40%. Oak also increased sharply (roughly 50 percentage points) beginning at 8 °C and levelling at around 9.5 °C; it increased (roughly 15 percentage points) from 16 km to 0 km from 17th century villages; and it grew in all but the most extreme temperature ranges. Hickory increased around 8.5 °C and levelled around 10.5 °C; it increased with soil pH from 5.5 to 6.5; it increased in fine-grained soils but with low clay content; and it increased as the terrain slope increased from 2 to 7°, then levelled in abundance. Chestnut increased in soils with percent clay from 10% to 13% then levelled in abundance; it increased as the terrain slope increased from 2 to 7° then levelled; it increased markedly in the areas dominated by inceptisols; and it increased from 8 to 10.5 °C then levelled. Pine, the poorest-fitting model, generally had response curves that were challenging to interpret: it increased where the annual temperature range was less than 26 °C (likely coastal pitch pine communities) and greater than 31 °C; and it increased atop coarser-grained soils with percent passing sieve number 200 < 35%.

Table 5. Relative importance for predictor predictors in models (8 km resolution) of relative abundance (8 km resolution). Shown are models that included "distance to nearest 17th-century village site" variable. Predictors are sorted from most important to least important, based on median relative importance values. Three most important predictors per model are bolded.

Group	Predictor Code	Predictor	Chestnut	Hickory	Oak	Pine	Pyrophilic	Median
Climate	bioclim01	Annual mean temperature	8.4	**17.3**	**49.9**	5.5	**50.8**	17.3
Climate	bioclim07	Temperature annual range (July minus January)	4.3	5.8	**6.7**	**15.4**	3.6	5.8
Terrain	slope	Terrain slope angle	**11.2**	6.3	4.0	4.3	**5.7**	5.7
Soil	clay	Percent clay	**14.1**	**7.4**	2.7	5.3	1.6	5.3
Soil	sieve200	Soil passing sieve #200 (fine)	2.8	6.4	2.5	**11.7**	3.8	3.8
Soil	inceptisol	Inceptisol order	**9.5**	4.8	2.3	2.4	3.6	3.6
Soil	bd	Bulk density	3.2	5.5	2.7	**9.5**	3.6	3.6
Indigenous	dist_vill_site	Distance to nearest 17th-century village site	3.5	3.0	**7.0**	1.7	**8.1**	3.5
Soil	ph	pH	3.3	**7.4**	3.1	6.6	1.5	3.3
Soil	sieve10	Soil passing sieve #10 (coarse)	6.8	3.3	1.6	6.1	2.0	3.3
Soil	rockdep	Depth to bedrock	5.4	3.4	2.5	3.2	1.2	3.2
Climate	bioclim15	Precipitation seasonality (coefficient of variation)	3.2	3.1	4.3	8.1	2.5	3.2
Soil	aws	Available water supply	4.1	3.3	1.9	2.7	1.5	2.7
Soil	histosol	Histosol order	2.5	3.9	1.5	5.3	1.4	2.5
Soil	om	Organic matter content	5.4	2.2	1.8	2.0	2.7	2.2
Soil	ksat	Permeability rate	5.9	5.8	2.2	2.2	1.7	2.2
Soil	entisol	Entisol order	2.2	3.4	1.0	2.9	1.8	2.2
Climate	bioclim12	Annual mean precipitation	4.0	1.7	2.1	3.8	2.1	2.1
Soil	mollisol	Mollisol order	0.1	4.7	0.3	1.0	0.5	0.5
Soil	ultisol	Ultisol order	0.1	1.1	0.1	0.3	0.1	0.1

4.5. Relative Influence of Indigenous Land Use Along a Climate Gradient

Linear regression suggested that distance to the nearest 17th-century village site was as much or more important than the temperature in shaping relative abundance patterns in cooler areas (Table 6; Figure 1b). Within areas with 7–8 °C mean annual temperature, oak relative abundance was significantly correlated with distance to nearest village but was not significantly correlated with temperature; distance to nearest village was also the most important predictor (as judged from standardised residuals) in this temperature range. Both predictors were significant, yet distance to village held slightly greater importance in shaping oak relative abundance within the 8–9 °C temperature range. For combined pyrophilic, distance to village was nearly significant where the temperature was significant, but the predictors held roughly equal importance between 7–8 °C. Both predictors were significant and held roughly equal importance for pyrophilic relative abundance between 8–9 °C. Other models of oak and pyrophilic fit the training data poorly, and oak was significantly correlated only with temperature between 9–10 °C and pyrophilic between 9–10 °C. Models of chestnut, hickory, and pine showed poorer fit to the training data (all R^2

values < 19%) than models of oak and pyrophilic with models sometimes yielding illogical regression coefficients.

Table 6. Summary of regression models relating relative abundance with mean annual temperature and distance to nearest Indigenous village site, within 1 °C temperature ranges (Figure 1b). Significant relationships ($p < 0.05$) are bolded. SE = standard error.

Taxon	Temp Range	R^2	Term	Coefficient (Standardised)	Coefficient (Unstandardized)	SE	Statistic	*p*-Value
Oak	7–8 °C	19.7%	(Intercept)	0.000	0.172	0.197	0.872	0.388
			Mean annual temp (°C)	−0.043	−0.008	0.025	−0.313	0.756
			Distance to nearest village site (km)	−0.451	−0.004	0.001	−3.298	**0.002**
Oak	8–9 °C	44.5%	(Intercept)	0.000	−2.264	0.507	−4.463	**<0.001**
			Mean annual temp (°C)	0.374	0.332	0.057	5.786	**<0.001**
			Distance to nearest village site (km)	−0.422	−0.023	0.004	−6.528	**<0.001**
Oak	9–10 °C	5.2%	(Intercept)	0.000	−0.350	0.254	−1.380	0.169
			Mean annual temp (°C)	0.234	0.103	0.026	3.882	**<0.001**
			Distance to nearest village site (km)	0.053	0.002	0.002	0.877	0.381
Oak	10–11 °C	1.0%	(Intercept)	0.000	0.816	0.421	1.937	0.057
			Mean annual temp (°C)	−0.058	−0.020	0.041	−0.490	0.625
			Distance to nearest village site (km)	−0.087	−0.004	0.005	−0.731	0.467
Pyrophilic	7–8 °C	15.1%	(Intercept)	0.000	−0.712	0.451	−1.579	0.121
			Mean annual temp (°C)	0.291	0.119	0.057	2.069	**0.044**
			Distance to nearest village site (km)	−0.205	−0.004	0.003	−1.456	0.152
Pyrophilic	8–9 °C	49.7%	(Intercept)	0.000	−2.865	0.556	−5.149	**<0.001**
			Mean annual temp (°C)	0.425	0.435	0.063	6.907	**<0.001**
			Distance to nearest village site (km)	−0.416	−0.026	0.004	−6.762	**<0.001**
Pyrophilic	9–10 °C	3.9%	(Intercept)	0.000	0.199	0.199	0.997	0.320
			Mean annual temp (°C)	0.198	0.068	0.021	3.264	**0.001**
			Distance to nearest village site (km)	0.087	0.003	0.002	1.440	0.151
Pyrophilic	10–11 °C	0.3%	(Intercept)	0.000	0.833	0.288	2.894	**0.005**
			Mean annual temp (°C)	0.012	0.003	0.028	0.097	0.923
			Distance to nearest village site (km)	−0.049	−0.001	0.004	−0.407	0.685

5. Discussion

Utilising datasets that afforded novel comparisons [45,52,71], results support our hypotheses for southern New England. Specifically, (1) for millennia, pyrophilic vegetation was consistently more abundant near the Indigenous settlements; (2) pyrophilic vegetation circa 17th–18th centuries was correlated with distance to Indigenous settlement; and (3) effects of Indigenous land use were most discernible in cooler areas. Indigenous settlements were geographically and temporally pervasive in oak-dominated landscapes of southern New England, and climate-modulated Indigenous land use likely shaped the geographic patterns of fire-adapted vegetation. This interpretation is bolstered when mapping charcoal records (Figure 1b) and historical descriptions [40] that recorded or described fire in locations corresponding with Indigenous settlement in warmer areas (Figure 1a). Varied datasets—such as pollen-based and land-survey-based relative abundance estimates, and different representations of Indigenous settlement—produced similar results in this study. The results affirm the notion that oak forests are a landscape managed for millennia by Indigenous people [11] in southern New England.

5.1. Higher Abundance of Pyrophilic Vegetation near Indigenous Settlement Over Millennia

The results revealed a consistently and often significantly greater abundance of fire-adapted (mainly oak) taxa near Indigenous settlements (Tables S1–S3). The relative abundances near Indigenous settlements were high for the last five millennia (Figure 3) for oak (median 74–82% from pollen-based reconstructions) and combined pyrophilic (median 86–91%), supporting the notion that Indigenous burning maintained fire-tolerant taxa through climatic changes that would have otherwise benefitted taxa adapted to cooler and/or moister climates [11,85]. These results occurred using different representations of Indigenous settlements, using pollen-based and land survey record-based estimates of relative abundance, analysing at two different resolutions (8 km and 24 km), and analysing various timesteps. Abundances of fire-tolerant vegetation showed greater consistency over time where Indigenous settlements existed and with greater fluctuations elsewhere (Figure 3), suggesting that the sustained presence of Indigenous settlements over millennia stabilised oak-dominated forests. For example, during the regional cooling of the Little Ice Age circa 13th–19th centuries, pyrophilic abundance was still 86–90% in the cells with archaeological sites, versus 66–70% in the cells without. Abundance decreased from previous timesteps in cells without archaeological sites during this time (Figure 3). Indeed, the results show a slight decreasing trend in pyrophilic and oak abundance throughout the region where there were no archaeological sites, perhaps suggesting post-glacial infilling of more mesic species away from Indigenous settlement. The drop in pyrophilic abundance from 1495 to 1745 CE may manifest the effects of an Indigenous depopulation and reductions in cultural burning (Figures 2 and 3).

Results imply that Indigenous settlements maintained the fire-adapted vegetation in various portions of southern New England over millennia. This result may be one reason why another modelling study discovered lower importance of distance to Indigenous sites circa 1500–1700 CE in models of relative abundance across the northeastern US [46], because the pattern observed at European-American arrival may have been the product of shifting settlement over millennia. Fossil charcoal throughout pyrophilic forests of southern New England lowlands (Figure 1b), in a region where lightning ignitions are uncommon [11], provides physical evidence that anthropogenic fire served as a control on vegetation in warmer low-elevation regions.

While our analysis found significantly higher relative abundances for oak and combined pyrophilic where Indigenous sites existed, fewer significant results occurred for pine, hickory, and chestnut. Beyond the methodological reasons—such as a lower accuracy of estimates for the less abundant taxa [71]—cultural and ecological reasons may exist. Leaf litter of northeastern US hickory species have poor (e.g., Carya *glabra*, *Carya tomentosa*) to intermediate (e.g., Carya *ovata*) flammability, suggesting that some hickory species evolved to dampen rather than encourage fire [7]. Non-significant results for chestnut are more challenging to explain, because chestnut possesses fire-adaptive traits [86]. Oak has the most flammable litter of northeastern tree taxa [7], so the sustained pressure of fire over millennia may have given oak a competitive advantage and subsequent dominance over taxa with intermediate flammability in leaf litter.

5.2. Relationships Between Climate, Indigenous Land Use, Soil, and Vegetation

BRT models suggest interlinkages between Indigenous land use, climate, and soil in shaping compositional patterns in southern New England, particularly for oak and combined pyrophilic vegetation. Models saw modest increases in predictive performance when Indigenous proxies were included (Tables 2 and 4); these increases, along with the importance measures of Indigenous land use proxies, were slightly greater than a comparable study of the northeastern US using BRT modelling [46].

Temperature was the most important predictor, being strongly and positively related to oak abundances in the 24 km and 8 km resolution BRT models, and with pyrophilic abundances in the 8 km resolution models. In addition to being directly related to the physiology and phenology of trees [87], warmer temperatures have direct effects on fire frequency, such as by drying fuels and lengthening fire seasons [88]. Results support previous characterizations of southern New England: oak was more abundant in warmer low-elevation areas coinciding with higher fire frequency (Figure 1b) likely by Indigenous peoples [34]. The modelled rapid increase in oak (and combined pyrophilic) abundances with temperature suggests that cultural burning caused a conversion to oak-dominated conditions in areas dry enough to burn, coinciding with a mean annual temperature of approximately 8 °C, a value suggested by the 24 km and 8 km resolution models. Curiously, 24 km resolution models for oak improved in fit from 505 BCE to 1495 CE (Table 2), perhaps suggesting that millennia of Indigenous burning in warmer areas created a regional-level compositional pattern along a fire-temperature gradient. Correspondence between high temperatures, Indigenous land use, fire, and/or high oak abundance is also similar to two previous modelling studies of the 18th century: fire in central Pennsylvania was most common in warm areas near Indigenous settlement [89], and fire-maintained oak savannas in western New York State were most probable in warmer/drier areas near Indigenous villages [48].

We link increasing temperature with increased Indigenous fire frequency, along with direct physiological and phenological effects, as the drivers of increasing oak abundance. All three proxies of Indigenous land use were moderately correlated with the mean annual temperature, with absolute Pearson's r values ranging from 0.58 to 0.65, almost requiring the omission of one predictor in these pairs due to collinearity. This same observation was noted in another study of the northeastern US [46]. Thus, temperature also partially represents patterns in Indigenous land use. We did not link temperature solely with increased drought as a driver of oak abundance, because recent research has suggested that eastern North American oak species, including white oak (*Quercus alba*), are more drought-sensitive than neighbouring species [90,91].

Moreover, linear regression suggested that Indigenous land use was most distinguishable from environmental controls in cooler areas with mean annual temperatures of 7–9 °C (Table 6). For example, areas with temperature 8–9 °C plus Indigenous settlement exhibited pyrophilic abundance values of 80–100% in central Massachusetts, but areas within this same temperature range without Indigenous settlement showed values of only 0–20% in western Massachusetts and northwestern Connecticut (Figure 1b). This temperature range may therefore represent an important transition: difficulty of combustion in regions cooler than 7–8 °C may have precluded widespread cultural burning, whereas burning in regions warmer than 8–9 °C may have facilitated large conflagrations and also may have obscured correlations between vegetation and distance to settlement. Other studies support these temperature-related transitions: few fires were recorded from 1701 to 1750 in central Pennsylvania where temperature was around 7 °C, but as many as 14 fires were recorded where temperature was around 10 °C [89,92].

Regionally, distance to Indigenous settlement was the second most important for oak and combined pyrophilic, suggesting that while Indigenous burning occurred throughout warm areas, it was concentrated within roughly 16 km. This catchment estimate matches some previous studies [47] but is larger than estimates such as 6 km [93] and smaller than 10–50 km [46]. Our models suggest that Indigenous land management occurred within catchments; but coupled with other results (e.g., Figure 2), these catchments were both widespread and shifting, with potential to shape compositional patterns for much of lowland southern New England. However, 16 km catchments would have covered most pyrophilic-dominated areas circa 17th–18th centuries (Figure 1).

BRT models of 17th–18th century relative abundances also manifested relationships with soil and terrain. Oak-dominated pyrophilic vegetation was more abundant in gently sloping terrain and atop coarser soils (Figures S1 and S6). Coupled with understandings of Indigenous horticulture [43,56,59,60], these results suggest that cultural burning occurred in warmer areas too sloping and rocky for agriculture. Aside from these relationships, BRT models generally found fewer strong and/or interpretable relationships with any predictors except temperature and distance to Indigenous sites. These findings support the ideas that oak taxa (e.g., white oak) are soil generalists [94], and that climate and disturbance are most influential in shaping species distributions [95]. Moreover, models of pyrophilic relative abundance yielded the best performance, suggesting that within the region, vegetation responses were based on fire-adaptive traits, with oak and pine being highly adapted [7]. Given the lack of landscape conditions for grassland creation (i.e., high wind speeds and less topographically complex terrain) [96], results suggest that southern New England contained woodlands, savannas, and barrens rather than extensive treeless areas, aligning with ethnohistorical accounts of open but treed environments prior to European settlement [28,38–40].

5.3. Methodological Considerations

Results reaffirm the importance of using disaggregated data to capture spatial heterogeneity in Indigenous settlement and vegetation patterns, and to detect correlations over geographic space between vegetation and Indigenous sites. Previous work discovered no correlation between oak abundances and population nor charcoal over time when aggregating population and vegetation data across southern New England, using the number of archaeological sites as a proxy for population [30]; similar approaches have been used for northeastern US studies [36]. However, in our interpretation of CARD data, we found that fire-tolerant vegetation was consistently higher near disaggregated archaeological sites. Interpreting the aggregated data on pollen, fire, and archaeological sites can lead to incorrect conclusions regarding the relative effects of climate and Indigenous land use on Holocene vegetation dynamics [58].

Finer-resolution analysis at smaller extents may uncover relationships between Indigenous settlement and vegetation better than continental-extent, coarser resolution analysis. Whereas others [37] discovered weak or intermittent population-vegetation relationships when using highly smoothed estimates of human population density and vegetation across North America, we used simple locations of archaeological sites as a sample of finer-scale distribution of Indigenous settlements across a smaller study area. These choices, along with the use of a different estimate of relative abundance from pollen samples [71], yielded significant results in this study. Models that assessed correlations between vegetation and Indigenous settlement generally uncovered meaningful relationships when resolution was finer and extent of analysis was smaller [47,48,80,97], versus when the opposite of both were true [46].

BRT models of circa 17th–18th century relative abundances showed the strongest relationships with Indigenous settlement when distance-based land use proxies were based on historical [50] rather than archaeological [51,52] records. Studies generally found human-vegetation correlations when combined historical-archaeological records were used [47,48,80,97], versus those that used just archaeological records [30,37]. Indeed, underscoring this issue is the fact that Indigenous archaeological sites have been poorly preserved in southern New England, due to the absence of regional surveys, burying from sedimentation on alluvial terraces, and historical disturbance [43]. Despite advantages of archaeological site data (e.g., scholarly rigour and radiocarbon dating), the archaeological record in southern New England may be incomplete enough to weaken the correlations between vegetation and settlement using such data. This study acknowledges additional issues of archaeological data quality including incompleteness: variation in modern human population density, intensity of agriculture, and differences in academic focus across the region may have created bias in archaeological site distribution [98] thus impacting results.

6. Conclusions

Indigenous settlements were associated with fire-tolerant vegetation in southern New England throughout the later Holocene especially the last 3000–5000 YBP. Indigenous settlements in southern New England were spatially extensive within areas dry enough to burn, and exerted influence upon the regional distribution of pyrophilic vegetation. Fire-tolerant vegetation in the region was most abundant in areas > 8 °C mean annual temperature, within 16 km of major Indigenous settlements, on coarse-grained soils, and on sloping terrain. Results manifested the importance of analysis of disaggregating geographic data on Indigenous settlement to reveal human–climate–vegetation relationships. This study contributed to the debate over human–climate–vegetation relationships and to a growing body of literature suggesting worldwide maintenance of fire-tolerant vegetation by past Indigenous cultures. Mimicking the past cultural burning—including by incorporating Indigenous perspectives—may help restore barrens, savannas, and woodlands of oak and other rare fire-tolerant vegetation in southern New England.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land14030525/s1. Explanation of boosted regression trees, Tables S1–S3, and Figures S1–S6, [99,100].

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