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Variation in Climate Shapes Seedling Recruitment Along Resource Gradients in a Northern Hardwood Forest

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ABSTRACT

Climate change is altering forest structure and function globally, directly affecting trees and seedlings through warming and drought, and indirectly through increased mortality and changing understory conditions. However, forest community responses also depend on local characteristics, including species-specific sensitivities and site conditions like soil moisture. Because seedling recruitment is a key demographic bottleneck, evaluating recruitment across local environmental gradients is essential for predicting shifts in forest composition. We hypothesized that warmer, drier conditions would limit recruitment, especially for species associated with mesic sites, whereas xeric species may be pre-adapted to drier conditions. Alternatively, xeric species-site complexes might be more susceptible because they are already under drought stress, whereas mesic sites could buffer drought impacts. We further predicted that forest overstories would buffer understory conditions and ameliorate climate effects on seedlings, particularly in mesic sites with higher canopy cover. We tested these hypotheses by evaluating soil moisture and temperature effects on seedling abundances of 10 tree species, using 26 years of annual seedling censuses from 12 sites spanning soil resource gradients in temperate hardwood forests of Lower Michigan, USA. Recruitment of mesic species-site complexes was generally more sensitive to warmer, drier conditions than that of xeric complexes, with future climates likely to favor recruitment of *Acer rubrum*, *Ostrya virginiana*, *Prunus serotina*, *Quercus rubra*, and *Q. alba*. Overstory buffering effects were strong: seedling abundances were negatively related to canopy openness for mesic and widespread species, but not for xeric complexes. Our results demonstrate that canopy cover can buffer mesic species-site complexes from drought, and that fine-scale environmental variation strongly mediates seedling responses to climate. These findings reveal strong interspecific variation in recruitment sensitivity, emphasizing the importance of local conditions and early life stages in determining forest responses to climate change.

1 | Introduction

Climate change is altering the environmental conditions that define plant habitats, reshaping the distributions and abundances of species at local, landscape, and regional scales (Anderegg et al. 2019; Boisvert-Marsh et al. 2019). Forest resilience to these changes depends not only on whether species can migrate to newly suitable areas, but also on their ability to persist and regenerate under shifting conditions within their current ranges (Aitken et al. 2008; McNichol and Russo 2023; Sharma et al. 2022; Young et al. 2019). As long-lived and often dispersal-limited organisms, trees respond to climate change primarily through variation in demographic processes—especially seedling recruitment and survival—across environmental gradients (Canham and Murphy 2016; Ibáñez et al. 2017; Magee et al. 2021). Local-scale (i.e., within-stand) gradients in soil moisture, fertility, and light availability interact with landscape-scale (i.e., across-forest stands or communities) variation in these factors and regional-scale processes (e.g., climate change in the Great Lakes region), offering a useful framework for assessing

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seedling responses to changing conditions. Monitoring these early life stages along such gradients can reveal how forest communities are changing locally and regionally under climate change.

Responses to climate change are expected to vary considerably among and within species, including across ontogenetic stages (e.g., seedlings versus adults) (Anderson-Teixeira et al. 2013; Meineri et al. 2020; Peltier and Ibáñez 2015). Because seedling recruitment and survival represent major demographic bottlenecks, seedling population responses play a central role in shaping community composition and broader distributional shifts (Canham and Murphy 2016; Clark et al. 2011; Copenhaver-Parry et al. 2020; Vanderwel et al. 2013). Seedling establishment is particularly sensitive to environmental variation, which is intensifying under climate change (Deser et al. 2012; Harper 1977; Silvertown 1987). This heightened sensitivity is reflected in juvenile trees often occupying narrower environmental niches and exhibiting stronger responses to climatic and edaphic stress than adults (Dobrowski et al. 2015; Jackson et al. 2009; Qiu et al. 2021).

Some climate-related changes—such as warmer springs, disturbances, and elevated CO_2—could enhance seedling performance (Classen et al. 2010; Darbah et al. 2008; Wang et al. 2020), whereas drought and heat waves may be detrimental (Bell et al. 2014; Sharma et al. 2022; Woodall et al. 2009). In temperate forests, warmer spring and fall temperatures are extending the growing season (Menzel and Fabian 1999; Piao et al. 2019), but hotter, drier summers can reduce photosynthetic capacity and increase seedling mortality (Badano and Sánchez-Montes De Oca 2022; Elliott et al. 2015; McDowell et al. 2008). However, these effects vary across species and sites (Boisvert-Marsh et al. 2019; Vickers et al. 2019); for example, in the western USA, juveniles occupy moister habitats than adults, where drought limits survival (Dobrowski et al. 2015), suggesting desiccation stress and water limitation can drive recruitment failure along moisture gradients (Sharma et al. 2022).

Although tree species distributions are linked to climate–soil moisture gradients (Niinemets and Valladares 2006), species-specific recruitment responses to soil moisture remain less well understood (Hubbart et al. 2016; Walters et al. 2023). Here, we define *drought* as reduced plant-available water resulting from regional climatic conditions (e.g., precipitation and temperature) and their interaction with landscape- or local-scale edaphic controls on soil moisture, which may impose physiological stress depending on species' traits. Its effects are expected to vary along landscape- and local-scale moisture gradients: drought may exert stronger effects on xeric sites where conditions approach physiological limits, especially for mesic-adapted species (Caspersen and Kobe 2001; Phillips et al. 2016), or may have stronger effects on mesic sites where greater competition, water demand, and less drought-tolerant species increase sensitivity (Clark et al. 2016; Ibáñez et al. 2007). Extreme precipitation events may temporarily alleviate water limitation and aid recruitment on both mesic and xeric sites, but can also increase soil pathogen risk (Bhatti and Kraft 1992; Elad and Pertot 2014; IPCC 2022), offsetting benefits.

Local overstory structure further modulates regional- and landscape-scale moisture effects by altering understory microclimate. Greater canopy cover buffers temperature extremes and evaporative demand, increasing soil moisture and moderating seedling exposure to water stress (Breshears et al. 1997; Copenhaver-Parry et al. 2020; Davis et al. 2019; De Frenne et al. 2019; Dobrowski et al. 2015; McNichol et al. 2024; Villegas et al. 2010). In contrast, canopy openness increases desiccation risk and seedling mortality, particularly for shade-tolerant species, although light-demanding species may benefit from canopy gaps (Badano and Sánchez-Montes De Oca 2022; Bauweraerts et al. 2013; Lin et al. 2014; Magee et al. 2021; Schupp et al. 1989; Walters et al. 2023). Overstory structure also influences belowground resource availability, linking above- and belowground controls on recruitment (Johnson et al. 2017; Qiu et al. 2021). Together, these patterns indicate that both drought and excess moisture are strongly mediated by local- and landscape-scale gradients (Clark et al. 2016; Walter 2018).

Species composition often shifts along landscape-scale environmental gradients, reflected in differential seedling performance and the emergence of species-site complexes (Fortunel et al. 2016; Kobe et al. 2014; Russo et al. 2005). Canopy openness typically declines with increasing soil fertility (Kobe et al. 2014), with nutrient-rich sites supporting greater tree densities, growth, and canopy leaf production (Baribault et al. 2010; Baribault and Kobe 2011) and higher seedling recruitment and growth (Gauthier et al. 2015; Kobe 2006; Kobe et al. 2002; Record et al. 2016). Species' strategies mediate these relationships, with stress-tolerant species dominating less fertile sites, and competitive, fast-growing species performing better on more fertile sites (Grime 1974; Kobe 1996; Schreeg et al. 2005). Such landscape-scale gradients and species-site complexes offer valuable insight into how species-specific differences in recruitment success under similar regional macroclimate shifts may shape future forest composition. Yet long-term seedling recruitment studies remain scarce (Clark et al. 1999), particularly in temperate forests, despite being a critical supplement to forest inventory datasets focused on later life stages (e.g., USDA Forest Inventory & Analysis, Smithsonian Forest Global Earth Observatory Network).

When evaluating climate impacts on seedling recruitment (Clark et al. 1999; Ibáñez et al. 2017), it is essential to account for mast cycles, as interannual fluctuations in seed production—which can vary by orders of magnitude—can mask underlying climate effects. Climate variability could differentially affect recruitment in mast versus non-mast years, especially if temperature or moisture act through density-dependent processes such as pathogen-mediated seed mortality under warm, moist conditions. However, the combined effects of mast cycles, interannual climate variability, and landscape- and local-scale environmental context on seedling recruitment remain poorly understood (Clark et al. 1999; Hubbart et al. 2016).

To examine how climate variation affects early recruitment of 10 tree species differing in their natural distributions, we leveraged 26 years of annual seedling censuses from 12 northern hardwood sites spanning landscape- and local-scale soil moisture,

fertility, and light gradients in northwestern Lower Michigan, USA. Using species-level Bayesian hierarchical models, we evaluated the effects of growing season average and minimum Palmer Drought Severity Index (PDSI) and temperature extremes on early seedling recruitment. In the Great Lakes region, average annual precipitation and temperature have increased (Fei et al. 2017) and are projected to continue rising (IPCC 2022). However, intensifying summer heat and precipitation variability may reduce soil moisture and increase vapor pressure deficit (Peltier and Ibáñez 2015), potentially limiting recruitment. We focus on early seedling recruitment, which we define as the abundance of seedlings < 1 year old (Castro et al. 2004; Caspersen and Saprunoff 2005; Badano and Sánchez-Montes De Oca 2022).

Our global hypothesis is that variation in PDSI and temperature influences recruitment of tree seedlings, with local- and landscape-scale environmental gradients mediating these effects. Plausible arguments can be made for very different effects of local environmental conditions on associated species. Drought and extreme temperatures could exert a weaker influence on recruitment at more xeric than mesic sites, as xeric species may be preadapted to drier conditions. Alternatively, drought and extreme temperatures could exert stronger influence on recruitment at more xeric than mesic sites because of lower resource availability and reduced overstory buffering of understory conditions, compared with the more highly buffered, resource-rich understories of mesic sites.

2 | Materials and Methods

2.1 | Study Sites

Our study was conducted across 12 northern hardwood stands in the Manistee National Forest (~44°12′ N, ~85°45′ W) in Wexford and Manistee counties, northwestern Lower Michigan, USA (Table 1, Figure 1). The forests are second-growth stands between 91 and 126 years in age that established following widespread logging in the early 20th century (Henry 2022; Host et al. 1988). Forests across this landscape vary in species composition in association with three major post-glacial landforms—outwash plain, ice-contact, and moraine—which generate a gradient of increasing water availability and soil fertility (N, Ca) (Baribault et al. 2010; Walters et al. 2023). Outwash plains are lower in moisture and fertility, with well-drained, coarse-deposited sands; ice-contact terrain occurs on more complex, hilly topography, and features finer-grain, more developed soils; and moraines have higher moisture and fertility, well-developed, fine-textured soils, and larger spatial extents (Host et al. 1988). Species composition transitions from *Quercus alba* L. and *Quercus velutina* Lam. dominance on outwash plains, to *Quercus rubra* L. and *Acer rubrum* L. dominance on ice-contact terrain, to *Acer saccharum* Marshall dominance on mesic moraines (Table 1, Figure 2b). The 12 sites occur in a 960 km^2 area (furthest distance between sites: 38.1 km; Figure 1b) and experience a similar regional macroclimate (Baribault et al. 2010). Each site features a 240 × 41-m (0.98 ha) mapped stand censusing adult trees with trunk diameter ≥ 10 cm at breast height (DBH; 1.37 m) with a 200 × 1-m seedling transect in the center (Figure 1c). Because of the presence of roads and topographic variation, Site 4 is divided into two adjacent 120 × 41-m stands and 100-m seedling transects (Baribault et al. 2010).

2.2 | Seedling and Adult Tree Censuses

We monitored seedlings of 10 common tree species in these forests [*A. rubrum*, *A. saccharum*, *Fagus grandifolia* Ehrh., *Fraxinus americana* L., *Ostrya virginiana* (Mill.) K. Koch, *Prunus serotina* Ehrh., *Q. alba*, *Q. rubra*, *Q. velutina*, and *Tilia americana* L.] (Table S1). In 1998, we established a 200 × 1-m seedling transect in the center of each site (Figure 1c), marking transects with PVC along a consistent azimuth every 10 m, from 20 m before the transect origin to 20 m beyond the transect to facilitate stand mapping. We censused seedlings between mid-June and late July of each year's growing season (1998–2023), dividing the transects into 200 1 × 1-m quadrats. In each quadrat, we identified each seedling to species and determined whether they were < 1 year old on the basis of the absence of terminal bud scars. For oaks (*Quercus* spp.), we excluded seedlings that had resprouted from older rootstocks. To analyze early recruitment, we used annual quadrat counts of < 1 year old seedlings (hereafter, seedling abundances).

In the 240 × 41-m stand at each site, in 1998–1999, we identified, tagged, and mapped the locations of adult trees (DBH ≥ 10 cm) relative to the seedling transect. We censused tree DBH at nine intervals (1999, 2005, 2007, 2009, 2011, 2013, 2016, 2019, and 2022), and calculated tree basal area (BA, m^2) each census year using DBH measurements. We estimated tree BA for each study year using BA in the closest census year, or the earlier year if two were equidistant. We calculated species BA per site as the sum of individuals' BA for a species. We also calculated the total basal area of all tree species within a 10-m radius of each understory light measurement location for each census year to evaluate temporal changes in local overstory structure (see Methods: 2.4); these values were not included in seedling recruitment analyses.

Site 8 had a uniform dominance of *A. saccharum*, and thus, when the site was established, a smaller area (180 × 21-m; ~3/8 or 0.375 of the stand) was mapped to represent adult trees on the site. We estimated total site *A. saccharum* BA by multiplying the sum of measured BA by 2.67. To fully characterize seed sources other than *A. saccharum*, in 2024, we comprehensively surveyed the entire stand for trees of all other species and used species' growth increments from previously censused individuals to back-calculate BA for the non-*A. saccharum* trees.

To account for variation in composition and species BA across all sites, we standardized species' annual quadrat-level seedling abundances by dividing by species' BA estimates to derive species-specific seedling recruitment normalized by BA at each site. From 1998 to 2023, we censused 188,821 tree seedlings and 6801 adult trees of 10 focal species across 12 sites. Seedling abundance per species ranged from 967 (*O. virginiana*) to 86,355 (*A. rubrum*), and the number of adult stems ranged from 42 (*O. virginiana*) to 1786 (*A. saccharum*) (Table S1). Across sites and years, mean seedling abundances per quadrat ranged from 0.02 (*Q. velutina*) to 1.38 (*A. rubrum*), and maximum abundances per quadrat ranged from 8 (*O. virginiana*) to 154 (*F. americana*) (Table S1).

TABLE 1 | Summary of 12 forest stands in the Manistee National Forest, Michigan, USA. Site locations, post-glacial landform types (Baribault et al. 2010), stand age since last major anthropogenic disturbance (calculated for 2025 from Baribault et al. 2010), dominant tree species, and mean (±standard deviation) canopy openness, soil volumetric water content (VWC), base cation exchange capacity (CEC), basal area, and stem density. Data for dominant species, basal area, and density are based on average values across nine mature tree censuses at each site across the study. At Site 8, only eight censuses were conducted (none in 1999) and only ~3/8 of the stand area was censused, so these values represent data for a subset of the total stand, converted to a per hectare basis.

Site	Location	Landform/soil type	Stand age (years)	Dominant species	Canopy openness (%)	Soil VWC (%)	Base CEC	Basal Area (m^2/ha)	Density (stems/ha)
1	44°14′ N, 85°56′ W	Outwash	103	Quve, Piba, Pist	9.80 ± 3.31	13.0 ± 1.50	0.20 ± 0.05	23.71 ± 1.66	569 ± 23
2	44°14′ N, 85°57′ W	Outwash	95	Qual, Quve, Acru	11.60 ± 3.66	13.7 ± 1.26	0.16 ± 0.04	24.47 ± 1.62	468 ± 29
3	44°16′ N, 85°53′ W	Ice contact	112	Quve, Acru, Qual	5.09 ± 1.04	15.0 ± 1.46	0.35 ± 0.19	31.90 ± 1.07	505 ± 35
4	44°17′ N, 85°53′ W	Ice contact	126	Qual, Acru, Quve	3.90 ± 1.82	15.1 ± 2.07	0.34 ± 0.22	30.45 ± 3.51	434 ± 64
5	44°19′ N, 85°52′ W	Mesic ice contact	98	Quru, Acru, Pogr	3.86 ± 0.90	13.9 ± 1.78	0.24 ± 0.10	38.09 ± 2.05	644 ± 57
6	44°12′ N, 85°48′ W	Mesic ice contact	105	Acru, Quru, Pogr	4.82 ± 1.24	19.0 ± 5.13	0.51 ± 0.36	38.60 ± 2.64	553 ± 77
7	44°11′ N, 85°40′ W	Poor moraine	94	Acsa, Quru, Acru	1.29 ± 0.36	13.6 ± 1.73	0.40 ± 0.13	33.73 ± 1.95	534 ± 28
8	44°20′ N, 85°29′ W	Poor moraine	92	Acsa, Acru, Osvi	1.37 ± 0.32	14.9 ± 2.01	0.84 ± 0.45	29.61 ± 0.67	892 ± 93
9	44°22′ N, 85°50′ W	Intermediate moraine	95	Acsa, Quru, Fagr	1.20 ± 0.49	16.6 ± 2.25	0.27 ± 0.15	41.63 ± 2.04	638 ± 53
10	44°15′ N, 85°45′ W	Moraine	99	Acsa, Tiam, Fagr	1.31 ± 0.37	15.3 ± 2.69	2.14 ± 0.99	40.82 ± 1.53	577 ± 53
11	44°13′ N, 85°40′ W	Moraine	91	Acsa, Tiam, Fram	1.00 ± 0.36	16.7 ± 2.55	3.37 ± 0.79	35.57 ± 2.50	482 ± 66
12	44°13′ N, 85°45′ W	Moraine	107	Acsa, Tiam, Acru	0.96 ± 0.20	15.7 ± 2.01	2.31 ± 1.01	33.73 ± 4.65	472 ± 95

Abbreviations Of dominant tree species: Acru = *Acer rubrum*, Acsa = *Acer saccharum*, Fagr = *Fagus grandifolia*, Fram = *Fraxinus americana*, Osvi = *Ostrya virginana*, Piba = *Pinus banksiana*, Pist = *Pinus strobus*, Pogr = *Populus grandidentata*, Qual = *Quercus alba*, Quru = *Quercus rubra*, Quve = *Quercus velutina*, Tiam = *Tilia americana*.

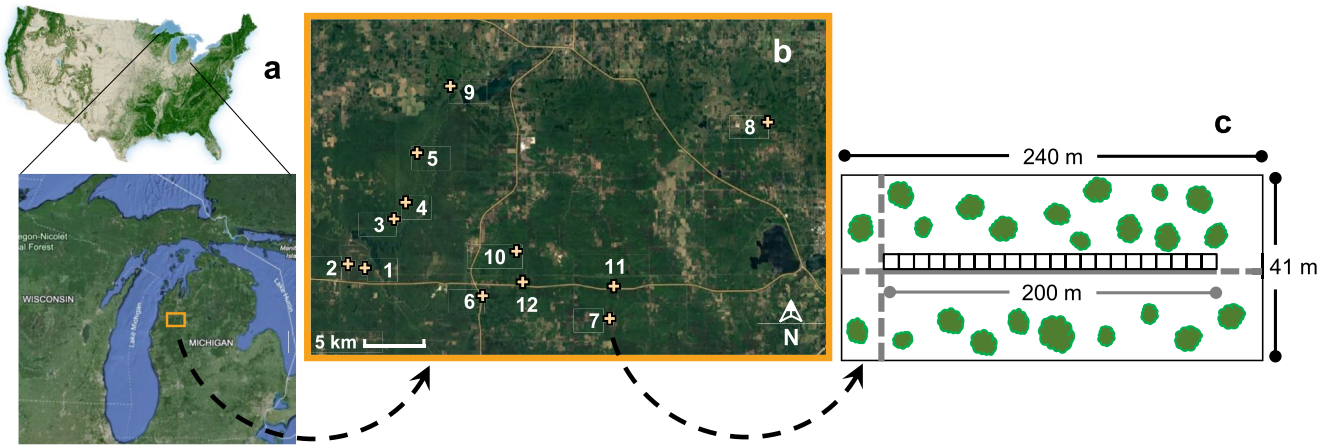


FIGURE 1 | Study location, distribution of 12 forest stands in the Manistee National Forest, Michigan, U.S., and sample layout of a stand and seedling transect. (a) Location of the Manistee National Forest in the northwestern Lower Peninsula, Michigan (image modified from Google Earth), with respect to a map showing the distribution of forest cover in the continental U.S. (taken from the U.S. Forest Service's Forest Atlas of the U.S.); (b) locations of the 12 mapped forest stands sampled for adult trees and seedlings in the Manistee National Forest [image modified from Google Maps; site coordinates shown in WGS84 (EPSG:4326)]; (c) schematic of one of the 240 m by 41 m mapped forest stands, with green polygons representing adult trees, and the 200-m seedling transect situated at the center of the stand.

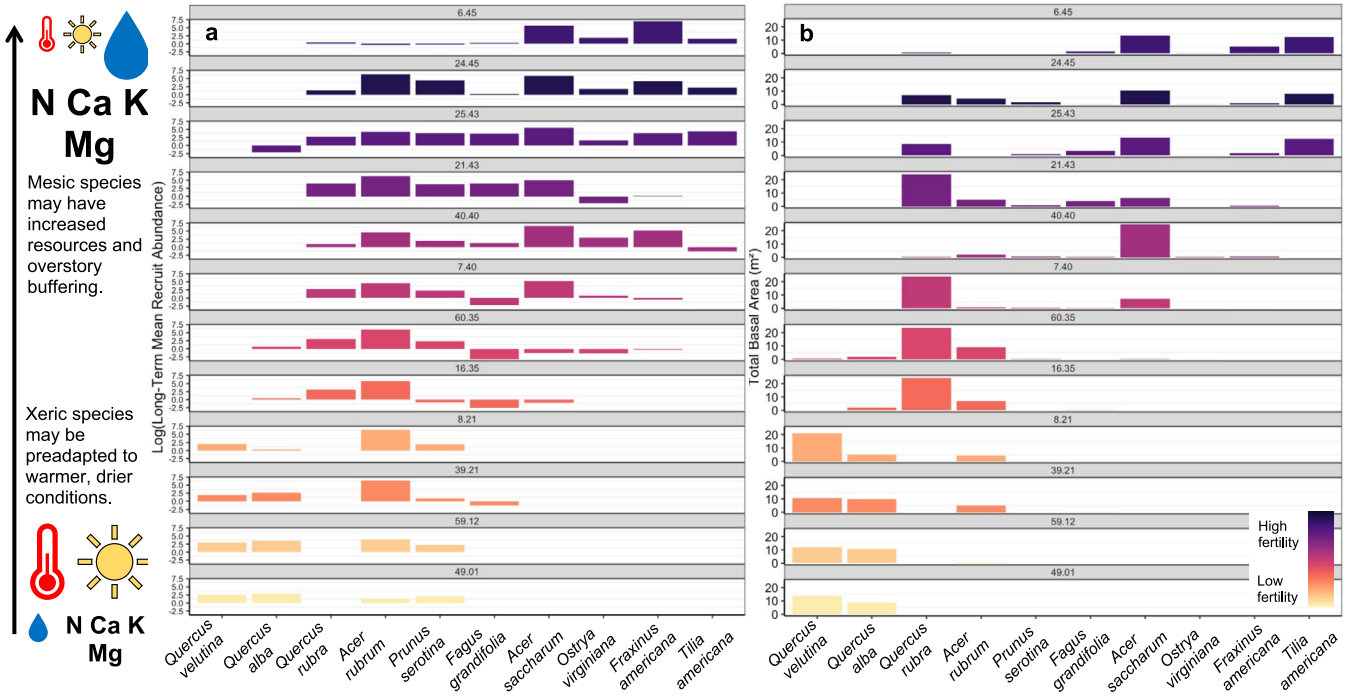


FIGURE 2 | Landscape-scale variation in mean seedling recruit abundances versus total adult tree basal area across 12 sites in the Manistee National Forest, and conceptual depiction of hypotheses. (a) The log-transformed long-term mean abundance of recruiting seedlings (averaged across 1998–2023) and (b) total adult tree (DBH ≥ 10 cm) basal area (representative data from the 2011 tree census) for 10 tree species (*x*-axes) occurring on 12 sites (panels with gray labels) spanning a local environmental gradient from xeric, low-fertility (yellow-orange colors; bottom panels) to mesic, high-fertility conditions (pink-purple colors; top panels). Species are ordered left to right from those dominant on xeric to mesic sites, and the environmental gradient is depicted along the *y*-axis, along with hypotheses regarding potential responses of species' seedling recruitment to climate change on mesic versus xeric sites. Seedlings were censused in 200 × 1-m transects, and adult trees were censused in a 240 × 41-m stand.

2.3 | Site-Specific Mast Cycles

To account for annual variation in species' reproductive output associated with mast cycles (Clark et al. 1999) and better isolate climate effects on recruitment, we determined site-specific mast years on the basis of standardized deviations in annual seedling production from long-term means, following an approach modified from LaMontagne and Boutin (2009). We calculated annual deviates by subtracting the long-term mean standardized abundance from the focal

year's standardized abundance and dividing by the standard deviation (SD). We then used the absolute value of the lowest standard deviation as a threshold: years with annual deviates above this value were classified as mast years, and those below it as non-mast years. For species-site combinations with consistently low abundance (sum of standardized abundances across years <100 for *A. rubrum*, *A. saccharum*, *F. grandifolia*, *F. americana*, *O. virginiana*, *P. serotina*, *T. americana*, or <15 for oaks: *Q. alba*, *Q. rubra*, *Q. velutina*), all years were denoted as non-mast because of the rarity of trees and seedlings. Across species, mast years comprised approximately 3%–24% of site × year observations (typically ~10%–18%), on the basis of 64–285 observations per species (Table S1). This classification should be interpreted operationally as identifying years of relatively high versus low seedling density, rather than as a direct measure of seed production, and was used to account for strong episodic variation in recruitment.

2.4 | Measurement of Local-Scale Environmental Gradients

2.4.1 | Canopy Openness, Soil Moisture, and Nutrients

Understory light availability (canopy openness, %) was measured in August 2004 as diffuse non-interceptance using a LAI 2000 (LI-COR Biosciences, Lincoln, NE, USA) at 30 cm aboveground at 2-m intervals along the seedling transects (Baribault and Kobe 2011). Although canopy structure can change over time and light environments may have shifted during the study, adult tree mortality was minimal at most sites (aside from *F. americana* loss at mesic sites due to the alien insect emerald ash borer, EAB, *Agrilus planipennis* Fairmaire). Moreover, basal area within a 10-m radius of light measurement locations showed strong rank stability from 1999 to 2022 (Figure S1, Table S2), indicating that relative differences in understory light levels were stable through time.

Soil moisture (volumetric water content, VWC, %) was measured twice in April–May 1999 to 30 cm depth by time domain reflectometry (Environmental Sensors Inc., Sidney, BC) at 10-m intervals along transects (Baribault et al. 2010) and averaged to derive relative soil moisture indices. Soil nutrient concentrations were measured in September 2011 and can be considered a relative nutrient availability index. Along the 200-m seedling transect at each site, three 15-cm soil cores were collected every 10 m, combined, dried samples, and analyzed for concentrations (ppm) of calcium (Ca), potassium (K), and magnesium (Mg) using ICP spectrometry (Optima 2100DV ICP Optical Emission Spectrometer, Perkin-Elmer, Shelton, CT, USA) (Rozendaal and Kobe 2016). To summarize site fertility, we calculated an integrated index of base cation exchange capacity (CEC): base CEC (milliequivalent, meq, per 100 g soil) = (ppm Ca/200) + (ppm K/390) + (ppm Mg/120), where 200, 390, and 120 represent the meq/100 g soil for base cations of Ca, K, and Mg, respectively. We used linear interpolation to estimate canopy openness, VWC, and base CEC at 1-m intervals, for each quadrat-site combination. Across quadrats and sites, canopy openness was negatively correlated with VWC ($r=-0.22$, $p<0.001$) and base CEC ($r=-0.44$, $p<0.001$), whereas VWC and base CEC were positively correlated ($r=0.24$, $p<0.001$). These relationships indicate that closed-canopy quadrats were generally more mesic and fertile, consistent with the underlying local environmental gradients in these forests (Baribault et al. 2010; Walters et al. 2023).

2.4.2 | Climatic Variables

The PDSI is a standardized metric of cumulative moisture balance that integrates precipitation, atmospheric demand, and soil water storage to quantify sustained departures in water availability, with values typically ranging from −4 (drier) to 4 (moister) (Dai 2011; Palmer 1965). Because our objective was to characterize growing season water availability relevant to seedling recruitment, we used the self-calibrating formulation (sc-PDSI), which adjusts model parameters to local soil moisture and improves comparability among sites (Wells et al. 2004). Calculating site- and year-specific PDSI identifies periods of water deficit that reflect both regional climatic drivers and local soil water balance, aligning with our definition of drought as reduced water availability from either source.

Using site latitudes and longitudes, we obtained 1 × 1-km gridded daily total precipitation (mm/day) and minimum and maximum air temperature (°C, at 2-m height) from 1998 to 2023 from NASA Daymet (Thornton et al. 2022) using the 'daymetr' package in R 4.2.1 (Hufkens et al. 2018; R Core Team 2022). We averaged daily minimum and maximum temperatures to estimate daily means and computed monthly mean temperatures during growing season (May to September) using the 'dplyr' package (Wickham et al. 2023). These temperature data were used to characterize regional interannual climate variability and were assumed to be shared among quadrats within a site. Monthly potential evapotranspiration (PET) was estimated using the Thornthwaite method (Thornthwaite 1948) in the 'SPEI' package (Beguería and Vicente-Serrano 2023). To incorporate local soil controls on water availability, we calculated available soil water content (AWC, mm) for each quadrat by converting measured VWC to depth-integrated storage (300 mm). Because AWC was derived from quadrat-level measurements, resulting drought estimates incorporated local heterogeneity in soil water holding capacity. Monthly PET, cumulative monthly precipitation, and AWC were used to calculate monthly sc-PDSI for each quadrat-site-year combination using the 'scPDSI' package (Zhong et al. 2018). For each year, we derived minimum and mean growing season PDSI and minimum and maximum growing season temperatures.

2.5 | Statistical Analyses

We conducted all analyses in R (R Core Team 2022), reading in data with the 'data. table' and 'readxl' packages (Barrett et al. 2023; Wickham and Bryan 2023), and summarizing and visualizing data with the 'dplyr', 'ggplot2', 'stats', and 'viridis' packages (Garnier et al. 2023; R Core Team 2022; Wickham 2016; Wickham et al. 2023). We developed species-specific hierarchical regression models in a Bayesian framework to examine the effects of minimum and mean growing season PDSI, minimum and maximum growing season temperature, and masting on standardized seedling abundances in quadrats nested within sites and years. Temperature represented site-level conditions (characterizing landscape-scale variation) shared among quadrats within each site-year, whereas quadrat-level PDSI

incorporated local variation in soil water availability through AWC. Our models implemented a Gamma-normal distribution (Alzaatreh et al. 2014):

$$\begin{cases} Y \sim \text{normal}(\theta, \text{precision}) \\ \theta \sim \text{gamma}\left(r, \frac{p}{1-p}\right) \end{cases} \quad (1)$$

where precision $= 1/\text{SD}^2$, θ is seedling abundance, r controls the shape of the Gamma distribution, and p indirectly influences the rate of the Gamma distribution, representing the typical probability of successful establishment per opportunity. To account for zero-inflation from quadrats with zero seedlings, we added a zero indicator as a multiplier on θ. We estimated r and SD for non-mast and mast years (m), and SD for zeroes and non-zeroes (ind), rewriting the Gamma-normal distribution as:

$$\begin{cases} Y \sim \text{normal}\left(\theta * Z, \frac{1}{\text{sd}\left([ind], [m]\right)^2}\right) \\ \theta \sim \text{gamma}\left(r[m], \frac{r[m]}{\ln(mu)}\right) \end{cases} \quad (1.1)$$

where Z is a Bernoulli-distributed zero-inflation indicator, mu is the response variable representing non-zero standardized seedling abundances, $ind = 1 + 1{*}Z$, and Z can be written as:

$$Z \sim \text{bern}(p.zi) \quad (2)$$

where $p.zi$ is a zero-inflation probability. We estimated separate effects of covariates for zero-inflated (logistic regression) (3) and count (normal regression) (4) components in non-mast and mast years, with each regression modeled hierarchically as quadrats q within sites s within years y, and the following equations representing the most complex models:

$$\begin{aligned} \text{logit}\left(p.zi_{qsy}\right) = \quad & \alpha_o[m] + \alpha_1[m] * \text{PDSI}_{qsy} + \alpha_2[m] * \text{temp}_{sy} \\ & + \alpha_3[m] * \text{PDSI}_{qsy} * \text{temp}_{sy} \end{aligned} \quad (3)$$

$$mu_{qsy} = \beta_o[m] + \beta_1[m] * \text{PDSI}_{qsy} + \beta_2[m] * \text{temp}_{sy} + \beta_3[m] * \text{PDSI}_{qsy} * \text{temp}_{sy} \quad (4)$$

where α_o and β_0 are intercepts, α_n and β_n are estimated parameters, temp is temperature, and the hierarchical notation denotes the scale at which variables were measured and therefore modeled. We standardized PDSI and temperature values by subtracting the mean and dividing by SD, and used the following prior distributions:

$$\alpha_o \sim \text{norm}(0, 1); \alpha_n \sim \text{norm}(0, 1)$$

$$\beta_o \sim \text{norm}(0, 0.5); \beta_n \sim \text{norm}(0, 0.5)$$

$$r \sim \text{unif}(0.1, 5)$$

$$\text{sd} \sim \text{norm}(0, 4)\text{T}(0.001, 1)$$

where the prior for sd [2,m] (non-zeroes) was truncated (T) between 0.001 and 1 to avoid extreme values, and the prior for sd[1,m] (zeroes) was set at 0.001. To assess model fit, we calculated year- and site-specific Bayesian posterior p-values, representing the probability of future observations being more extreme than the data (Gelman 2005). We ran models for 55,000 iterations (burn-in and samples) following 1000 adaptive iterations, with three chains and a thinning interval of 10. To assess the impact of minimum and mean growing season PDSI and minimum and maximum growing season temperature, we evaluated 13 candidate models for each species, including main and interactive effects of covariates and a null model (Table S3). We compared models using the Watanabe-Akaike information criterion (WAIC) (Watanabe 2010), a Bayesian approach that estimates out-of-sample expectation by calculating a log pointwise posterior predictive density and penalizing additional parameters (Gelman et al. 2014). We plotted predicted standardized seedling abundances with respect to climate variables in the best candidate model for each species, using median parameter estimates with 95% credible intervals (2.5% and 97.5% quantile estimates). To visualize species' responses to future climates, we back-transformed mast year parameter estimates for PDSI, temperature, and their interactions, averaged parameter estimates from zero-inflated and count model components, computed weighted averages for interaction terms, and plotted estimates for PDSI versus temperature for each species. We ran models in R with the 'rjags' and 'parallel' packages (Plummer 2023; R Core Team 2022) and JAGS software version 4.3.0 (Plummer 2003), using the High Performance Computer Center at Michigan State University, East Lansing, Michigan, USA. We assessed model convergence, fit, and Gelman-Rubin statistics using the 'coda' and 'kableExtra' packages (Plummer et al. 2006; Zhu 2024).

To evaluate the influence of overstory buffering on recruitment and its variation across sites (at sites with ≥25 seedlings per species), we correlated the quadrat-level observed standardized seedling abundances with canopy openness using the 'stats' package. To assess variation in site-specific effect sizes (correlation coefficients) and quantify overall buffering effects, we ran a random-effects meta-analysis with the 'metafor' package (Viechtbauer 2010). We plotted site-specific effect sizes and 95% confidence intervals for mesic and xeric species-site complexes, and widespread species. Statistical significance was evaluated at $\alpha = 0.05$.

3 | Results

3.1 | Overview

We observed higher seedling abundances (Figure 2a) and adult basal area (Figure 2b) on mesic than xeric sites, though these patterns varied across species. Seedlings exhibited broader landscape-scale distributions than their conspecific adults (Figure 2), occurring on four (*Q. velutina*, *T. americana*) to 12 (*A. rubrum*, *P. serotina*) sites, whereas adult trees occurred on three (*T. americana*) to 10 (*A. rubrum*) sites.

Seedling abundances differed sharply between mast and non-mast years, with mast year predicted abundances being ~10 times (*A. rubrum*, *P. serotina*) to >100 times (*F. americana*, *Q. rubra*) greater than in non-mast years. For mesic-site species, non-mast year abundances were <0.2%–2.5% of mast-year abundances (*A. saccharum*, *F. grandifolia*, *F. americana*, *O. virginiana*, and *T. americana*; Figure 3a–i). Among widespread species, non-mast year abundances were 0.7%–10% of mast year abundances (*A. rubrum*, *P. serotina*, and *Q. rubra*; Figure 3j–o), and for xeric-site

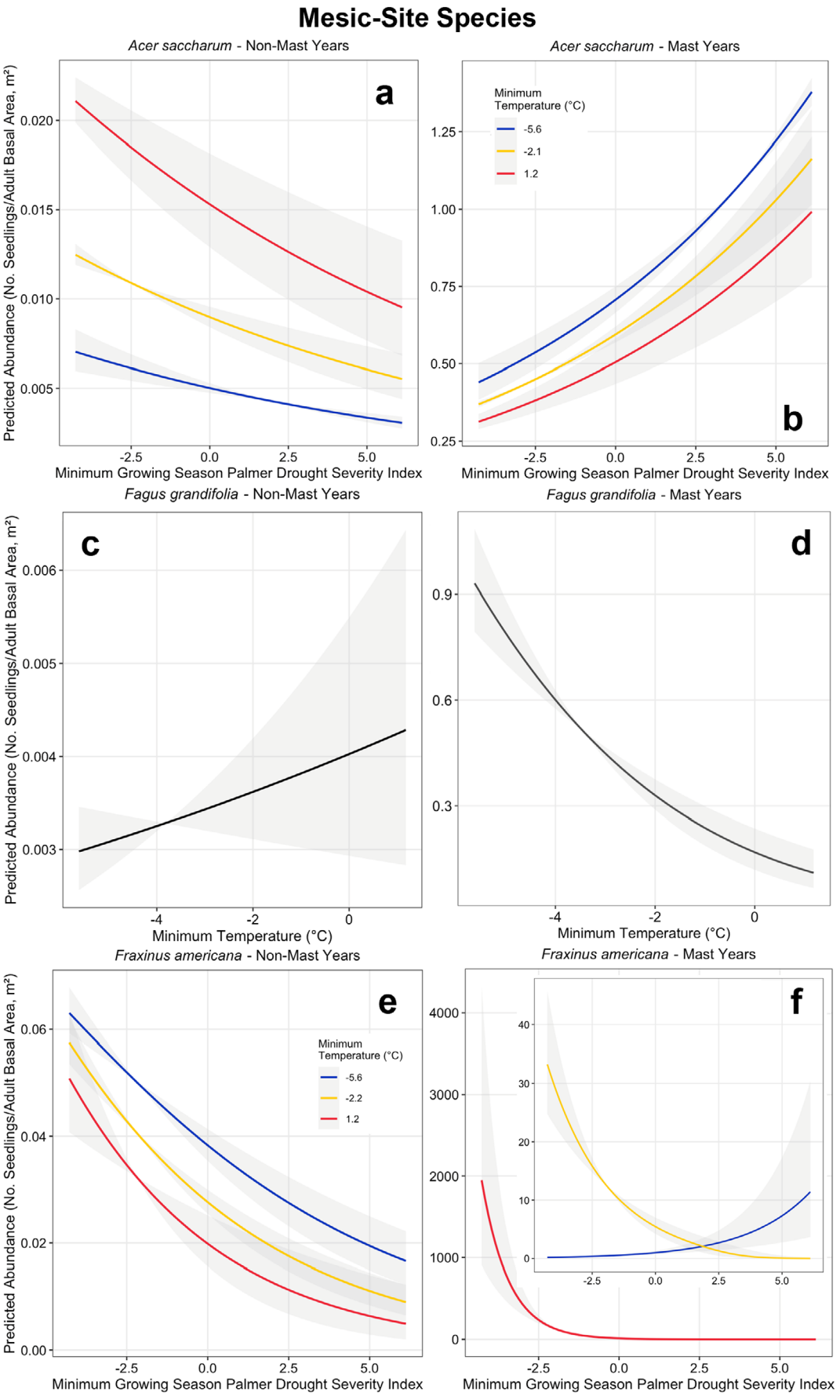

Mesic-Site Species
Acer saccharum - Non-Mast Years
Acer saccharum - Mast Years
a
b
Minimum Temperature (°C)
-5.6
-2.1
1.2
Predicted Abundance (No. Seedlings/Adult Basal Area, m²)
Minimum Growing Season Palmer Drought Severity Index
Fagus grandifolia - Non-Mast Years
Fagus grandifolia - Mast Years
c
d
Minimum Temperature (°C)
Fraxinus americana - Non-Mast Years
Fraxinus americana - Mast Years
e
f
-5.6
-2.2
1.2

FIGURE 3 | Predicted abundances of tree seedlings with respect to variation in climate for 10 tree species abundant in the Manistee National Forest, Michigan, U.S. Standardized predicted seedling abundances (number of seedlings divided by species' site-level adult basal area; *y*-axes) of (a–i) species dominant on mesic sites, (j–o) species widespread across sites, and (p–s) species dominant on xeric sites. Panels show (a, b) *Acer saccharum*, (c, d) *Fagus grandifolia*, (e, f) *Fraxinus americana*, (g, h) *Ostrya virginiana*, (i) *Tilia americana*, (j, k) *A. rubrum*, (l, m) *Prunus serotina*, (n, o) *Quercus rubra*, (p, q) *Q. alba*, and (r, s) *Q. velutina* versus mean or minimum growing season Palmer Drought Severity Index (PDSI; *x*-axes, a, b, e–s) for minimum, mean, and maximum temperature scenarios (blue to red lines) of minimum (a, b, e–i, l–s) or maximum (j, k) temperature, or versus minimum temperature (*x*-axes, c, d), with the indicated climate variables representing those in the best candidate model for each species. Figures in the left-hand column (a, c, e, g, i, j, l, n, p, r) are predicted abundances in non-mast years, whereas the right-hand column figures (b, d, f, h, k, m, o, q, s) are predicted abundances in mast years (note that mast versus non-years correspond to years of relatively high versus low densities; see Table S1 for a summary of site by year mast years for each species). Predicted curves (lines) are based on the median parameter estimates, with their associated 95% credible intervals (shown in gray). Minimum, mean, and maximum temperatures shown for each species, and the range of PDSI on the *x*-axes in (a, b) and (e–s), are based on values across the study period (1998–2023) for the sites on which each species occurs. PDSI was not included in the best candidate model for *F. grandifolia*, and there was no effect of PDSI or temperature on *T. americana* seedling abundances during mast years (results not shown). See Table S4 for parameter estimates for each model.

species, 0.8%–1.4% of mast year abundances (*Q. alba* and *Q. velutina*; Figure 3p–s).

Annual seedling abundances were strongly influenced by growing season PDSI and temperatures, as well as by masting, with the relative importance of these factors and their interactions varying across species (Figures 3, 4 and Table S4). The best candidate model for each species had strong support (WAIC value ≤38 units lower than competing models). Across all models, year- and site-wise Bayesian *p*-values ranged from 0.49 to 0.51, indicating good fit, and Gelman-Rubin statistics for estimated parameters were ≤1.1, indicating convergence.

3.2 | Effects of PDSI on Seedling Abundances

Wetter conditions (i.e., higher PDSI) were often associated with higher seedling abundances during mast years (Figure 3). Among mesic-site species, *A. saccharum* and *O. virginiana* (at higher minimum temperatures) had greater abundances in wetter conditions (Figure 3b,h). Among widespread species, *A. rubrum* and *P. serotina* showed similar positive responses (Figure 3k,m), as did the xeric-site species *Q. alba* and *Q. velutina* under lower minimum temperatures (Figure 3q,s). During non-mast years, wetter conditions were also associated with higher seedling abundances for the mesic-site species *O. virginiana* (except at lower minimum temperatures; Figure 3g) and *T. americana* (Figure 3i), and *A. rubrum*, *Q. alba* and *Q. velutina* (except under higher minimum temperatures; Figure 3j,p,r).

In contrast, wetter conditions were associated with *lower* seedling abundances during mast years only for the mesic-site species *Fraxinus americana* (at higher minimum temperatures; Figure 3f) and the widespread species *Q. rubra* (at lower minimum temperatures; Figure 3o), whereas in non-mast years, *A. saccharum*, *F. americana*, *P. serotina*, and *Q. rubra* had lower abundances under wetter conditions (Figure 3a,e,l,n).

3.3 | Effects of Temperature on Seedling Abundances

Temperature influenced seedling abundances for most species, with effects roughly split between positive and negative responses across species and between mast versus non-mast years. Most species responded more strongly to variation in minimum temperatures, except for the widespread species *A. rubrum*, for which higher maximum temperatures corresponded to lower seedling abundances in non-mast years (Figure 3j) but had no effect in mast years (Figure 3k).

During mast years, warmer conditions (i.e., higher minimum temperatures) corresponded with higher seedling abundances for the mesic-site species *F. americana* (under drier conditions) and *O. virginiana* (Figure 3f,h), the widespread species *P. serotina* and *Q. rubra* (under wetter conditions; Figure 3m,o), and the xeric-site species *Q. alba* (Figure 3q). During non-mast years, warmer conditions promoted higher abundances for the mesic-site species *A. saccharum*, *F. grandifolia*, and *O. virginiana* (Figure 3a,c,g), and for *Q. alba* (Figure 3p).

However, warmer temperatures were nearly as often (8 of 17 cases) associated with lower seedling abundances. During mast years, *A. saccharum*, *F. grandifolia*, and the xeric-site species *Q. velutina* had reduced seedling abundances under warmer conditions (Figure 3b,d,s), whereas during non-mast years, warmer conditions corresponded to lower abundances for *F. americana*, *P. serotina*, *Q. rubra*, *Q. velutina*, and the mesic-site species *T. americana* (Figure 3e,i,l,n,r).

3.4 | Predicted Effects of Future Climates on Seedling Abundances

To explore potential effects of future climates, we plotted species according to the sensitivity of their seedling abundances to growing season PDSI and temperature, characterized by estimated coefficients for these variables (Figure 4). Projected regional increases in annual precipitation and temperature (IPCC 2022), corresponding with wetter, warmer growing seasons, would likely favor recruitment of *A. rubrum*, *O. virginiana*, *P. serotina*, *Q. alba*, and *Q. rubra* (upper right quadrant, Figure 4), and limit recruitment of *A. saccharum* and *F. grandifolia* (lower right quadrant, Figure 4), *Q. velutina* and *T. americana* (lower left quadrant, Figure 4), and *F. americana* (upper left quadrant, Figure S2). Only *F. americana* responded positively to warmer and drier conditions—a likely scenario if higher temperatures and greater variability in precipitation reduce growing season

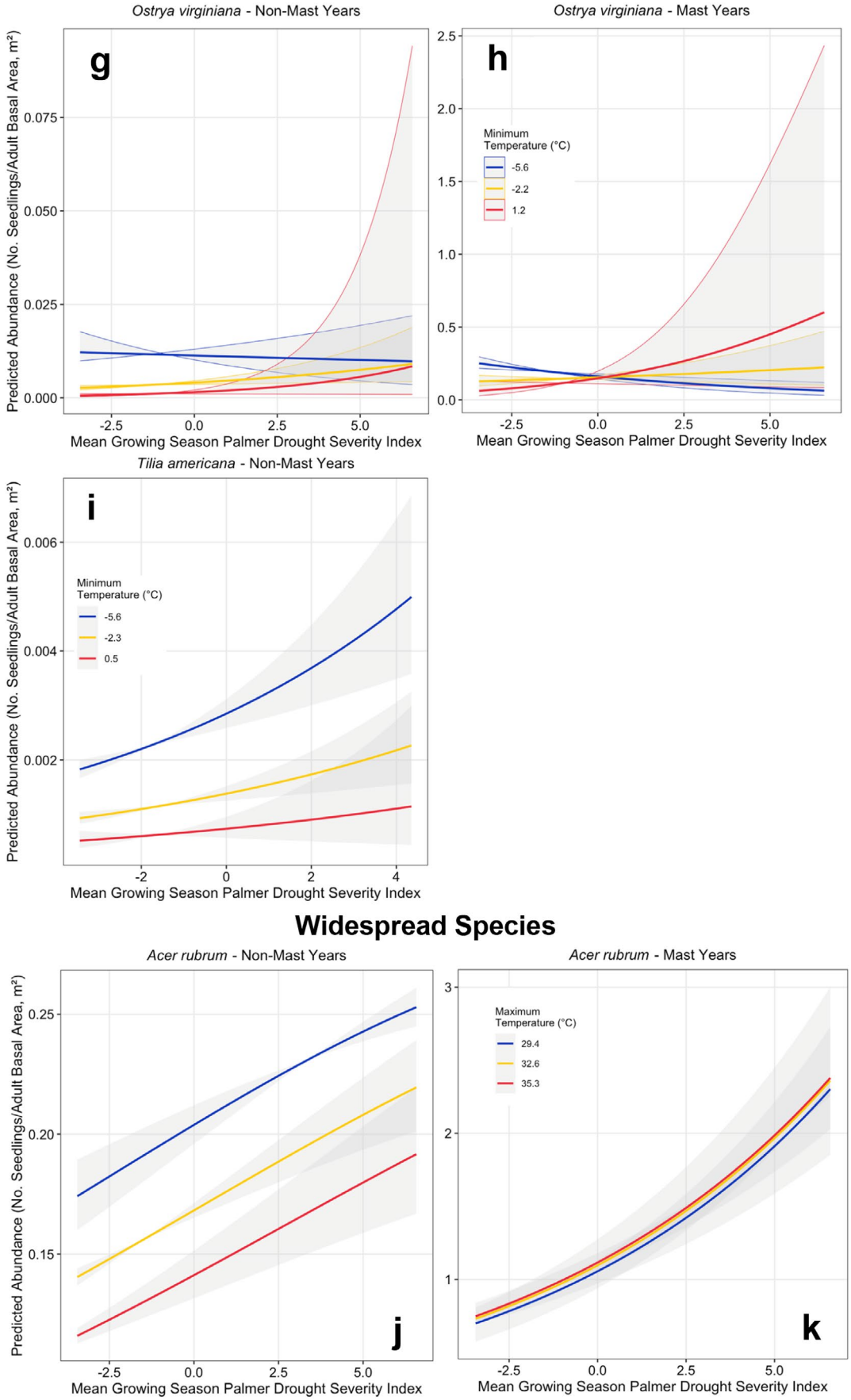


FIGURE 3 | (Continued)

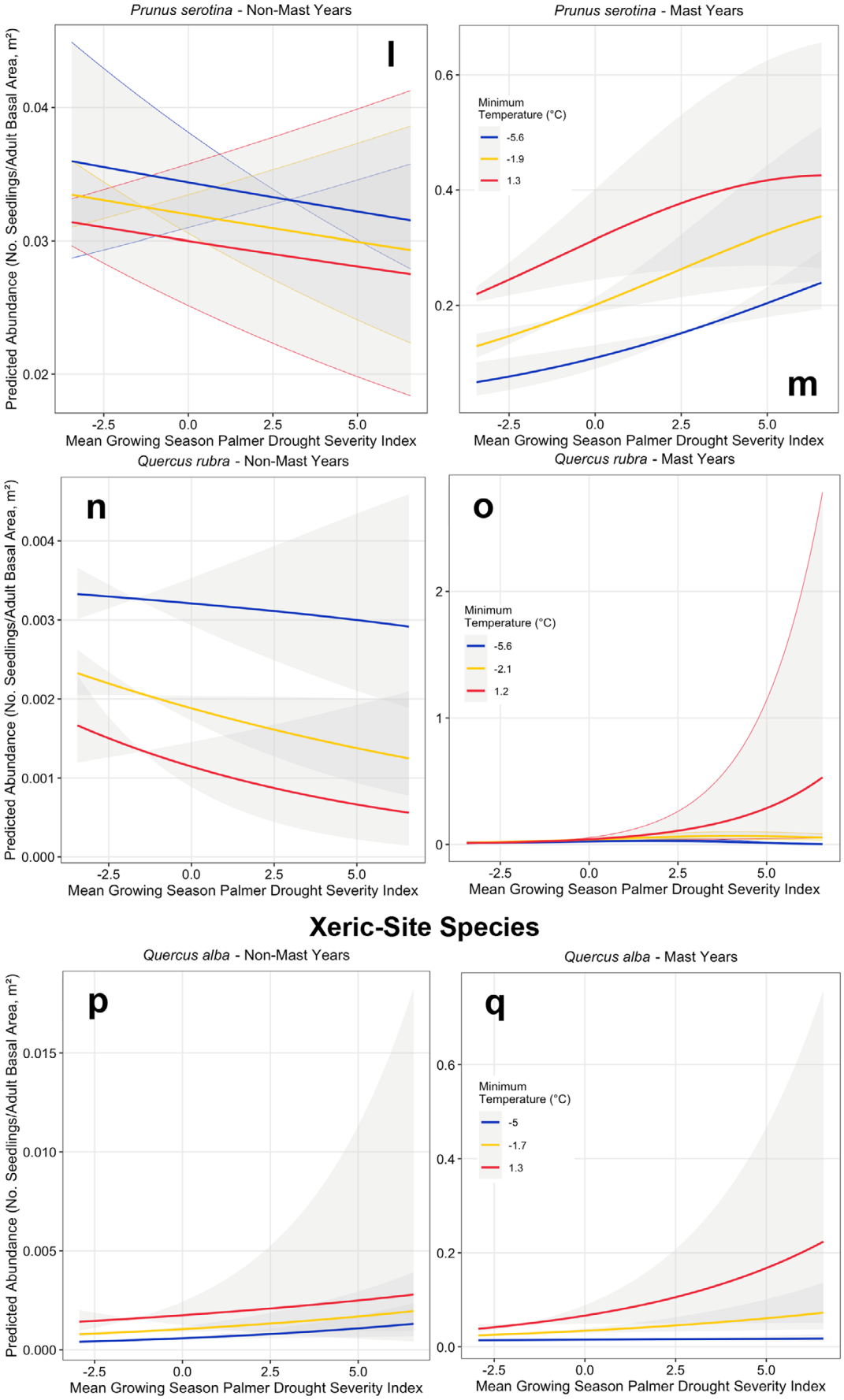


FIGURE 3 | (Continued)

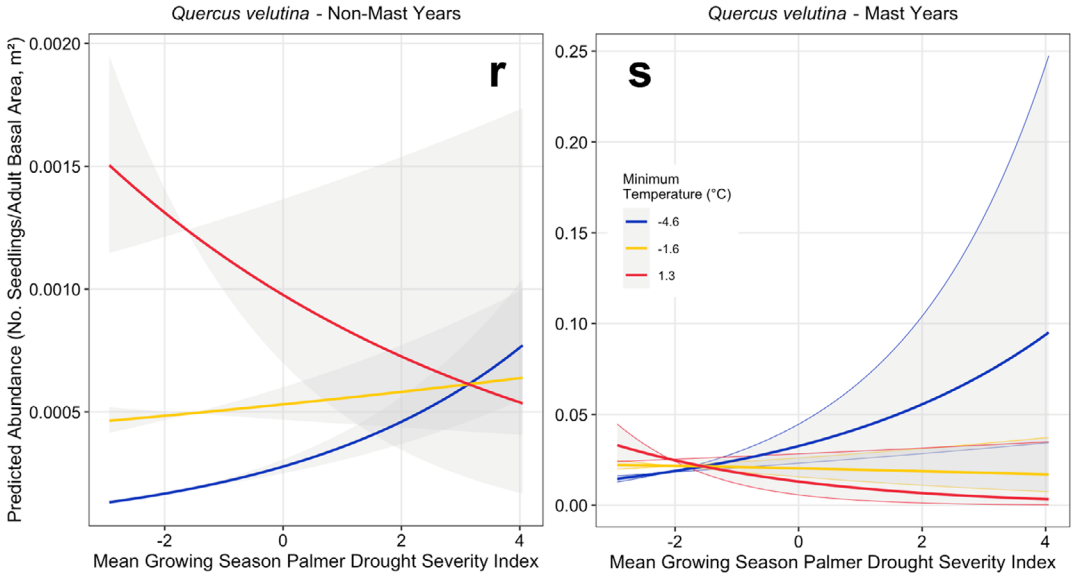


FIGURE 3 | (Continued)

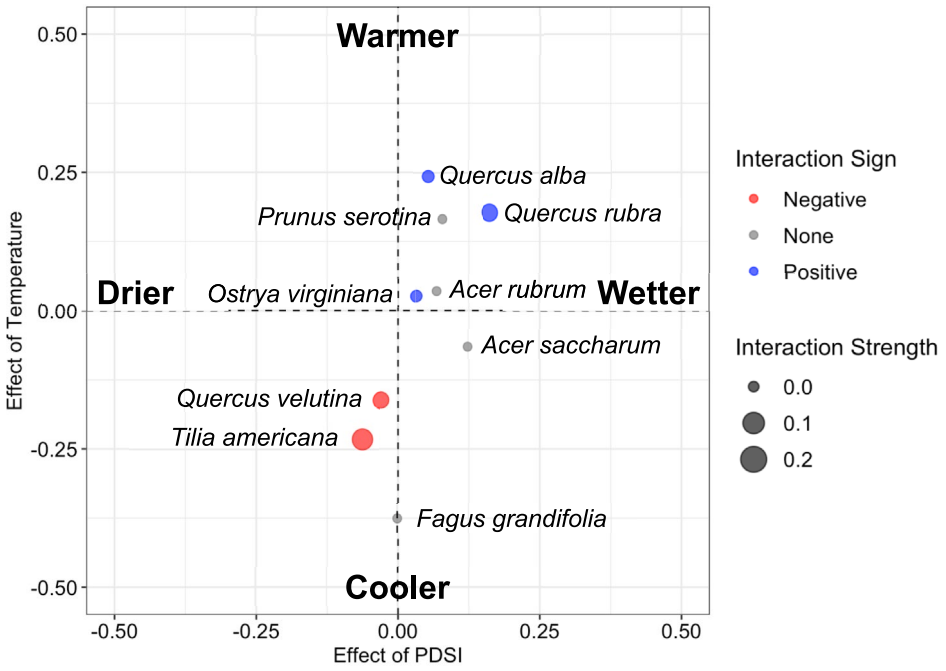


FIGURE 4 | Effects of growing season climate on predicted abundances of seedlings in the Manistee National Forest. Position of nine tree species (points) on the basis of the median parameter estimates of the Palmer drought severity index (PDSI, *x*-axis; higher values indicate wetter conditions) versus temperature (*y*-axis), with the color and size of points denoting the sign and strength of the interaction between PDSI and temperature as indicated by the legend. Parameter estimates are from mast years for each species and were averaged between the zero-inflated and count components of each model prior to plotting; weighted averages were computed using the 95% credible intervals for the interaction term to give more influence to estimates with smaller uncertainty. One species, *Fraxinus americana*, was excluded from this visualization because of large parameter estimates associated with high adult tree mortality but is shown in Figure S2.

soil moisture and humidity (Peltier and Ibáñez 2015). Although cooler future climate conditions are highly unlikely, cooler conditions would favor the recruitment of *F. grandifolia* regardless of moisture, *Q. velutina* and *T. americana* under drier conditions, and *A. saccharum* under wetter conditions. Interactions between PDSI and temperature generally reinforced rather than diminished main effects.

3.5 | Effects of Overstory Buffering on Seedling Abundances Were Strongest for Mesic Species-Site Complexes and Species Widespread Across Sites

We observed increased overstory buffering (higher seedling abundances with lower canopy openness) for species dominant at mesic sites and widespread across sites, but not for species at

xeric sites (Figure 5, Table S5). On the six more mesic sites spanning moraines (Sites 7–12), seedling abundances decreased with openness for *A. saccharum*, *F. americana*, and *O. virginiana* at all sites (all $p < 0.05$), and for *F. grandifolia* and *T. americana* at all except Sites 9 and 12, respectively (Figure 5a). These relationships indicate strong buffering effects at mesic sites, with significant variation across sites for all species but *O. virginiana* ($p = 0.345$; Table S5), and significant across-site buffering for all species. For species widespread across all sites, *A. rubrum*, *P. serotina*, and *Q. rubra*, we also found a predominance of buffering effects (seedling abundance decreases with higher canopy openness); however, *A. rubrum* seedling abundance increased with openness at Sites 2 and 12, and there was no relationship between seedling abundance and canopy openness for *A. rubrum* at Site 4 and for *P. serotina* at Sites 1, 2, and 4 (Figure 5b). In contrast, on the six more xeric sites spanning outwash plains to ice contact (Sites 1–6), we did not document buffering effects, observing significant increases in seedling abundances with greater openness for *Q. alba* and *Q. velutina*, except at Site 2 for *Q. alba* and Site 4 for *Q. velutina* (Figure 5c).

4 | Discussion

Our study, on the basis of 26 years of seedling data across prominent landscape- and local-scale environmental gradients, provides strong evidence that seedling responses to climate are mediated by these gradients. At the landscape scale, seedling abundances of mesic species-site complexes were generally more sensitive to increasing drought severity and warmer conditions than those of xeric species-site complexes. At the local scale, overstory buffering moderated these climate effects, particularly for mesic species-site complexes and widespread species at mesic sites, but not for xeric species-site complexes. This supports our hypothesis that mesic species-site complexes are more susceptible to warming and drying in the absence of buffering, whereas xeric species-site complexes are preadapted to warming. We defined drought as the combined influence of regional climatic conditions and landscape- and local-scale edaphic controls on soil moisture. At our sites, a lack of lateral flow and stable soil properties support the inference that differences in local soil moisture measurements reflect persistent relative differences among sites. Consequently, landscape- and local-scale moisture gradients provide a consistent framework for interpreting seedling responses, whereas regional climate modulates the overall intensity of drought; the degree to which climatic drought is alleviated may depend also on temporal variability in rainfall. Our results underscore the importance of accounting for landscape- and local-scale environmental variation (Abiem et al. 2023; Jin et al. 2018; Kobe 1999; Kobe et al. 2014), alongside monitoring tree seedling dynamics, to understand how climate change will shape forest communities.

By pairing long-term seedling monitoring with spatial variation in soil resources and canopy conditions, we capture how temperature and moisture interact with landscape and local context to shape early seedling recruitment—a perspective rarely achievable in tree demographic studies. Recruitment of *A. rubrum*, *O. virginiana*, *P. serotina*, *Q. alba*, and *Q. rubra* seedlings was enhanced by warmer and wetter conditions, whereas *A. saccharum*, *F. grandifolia*, *F. americana*, *Q. velutina*, and *T. americana* recruitment was diminished, primarily because of increased temperature. If forests experience longer periods of drought combined with warming, our results suggest that recruitment of all species will decline, with *F. americana* as a possible exception, though its mortality due to EAB (Sun et al. 2024) will likely minimize its future role in these communities. These findings reflect recruitment-stage sensitivity, not long-term population success, as later survival and growth may alter species' trajectories.

We presented results as seedling recruitment, which represents the integrated outcome of several key demographic processes: seed production, seed survival, germination, and early seedling survivorship. Although this makes our study more phenomenological than mechanistic, it provides a comprehensive view of how climate variation affects forest regeneration at the earliest seedling life stage. Changes and variability in climate and other stressors (e.g., disturbances, biotic interactions) can constrain these processes (Badano and Sánchez-Montes De Oca 2022; Brown and Wu 2005; Copenhaver-Parry et al. 2017; Muller-Landau et al. 2002), potentially reducing population persistence (Copenhaver-Parry et al. 2020; Kueppers et al. 2017; McNichol and Russo 2023). Because we analyzed growing season climate effects on recruitment in the same year, we likely captured climate influences on seed survival and germination prior to our censuses but not on prior-year adult tree reproductive output. An important caveat is that we only examined seedlings during their first growing seasons. Consequently, fully understanding climate impacts on future forest composition will require robust annual data on seed production, coupled with tracking seedling survival through the sapling stage and beyond, especially under interactions with high deer browse pressure (Henry and Walters 2023).

Observed species differences in recruitment are consistent with variation in germination responses. Species with greater recruitment under warmer, wetter conditions (*A. rubrum*, *O. virginiana*, *P. serotina*, *Q. alba*, and *Q. rubra*) require consistently moist seedbeds or are sensitive to frost during germination (Bell 1975; Hutnick and Yawney 1961; Lewin 1974; Marquis 1973; Sander 1965). In contrast, species that declined with warming (*A. saccharum*, *F. grandifolia*, *F. americana*, *T. americana*, and *Q. velutina*) often exhibit strong dormancy requirements, narrow temperature thresholds, or complex stratification needs (Brinkman 1965; Fowells 1965; Marquis 1975; Williams and Hanks 1976), which may limit successful germination under warmer conditions. Species with delayed germination or persistent seed reserves (e.g., *Prunus serotina*) may also buffer interannual climate variability. These differences suggest that germination strategy contributes to the climate sensitivities observed in early recruitment.

We observed contrasting temperature effects on predicted seedling abundances in mast versus non-mast years for four species—*A. saccharum*, *F. grandifolia*, *P. serotina*, and *Q. rubra*. Warmer temperatures were associated with lower *A. saccharum* and *F. grandifolia* abundances in mast years but higher *A. saccharum* abundances and weak effects on *F. grandifolia* in non-mast years. Conversely, *P. serotina* and *Q. rubra* had higher seedling abundances in warmer conditions during mast years but lower abundances in non-mast years. Although we lack data to test mechanisms, our results suggest that *A. saccharum* and

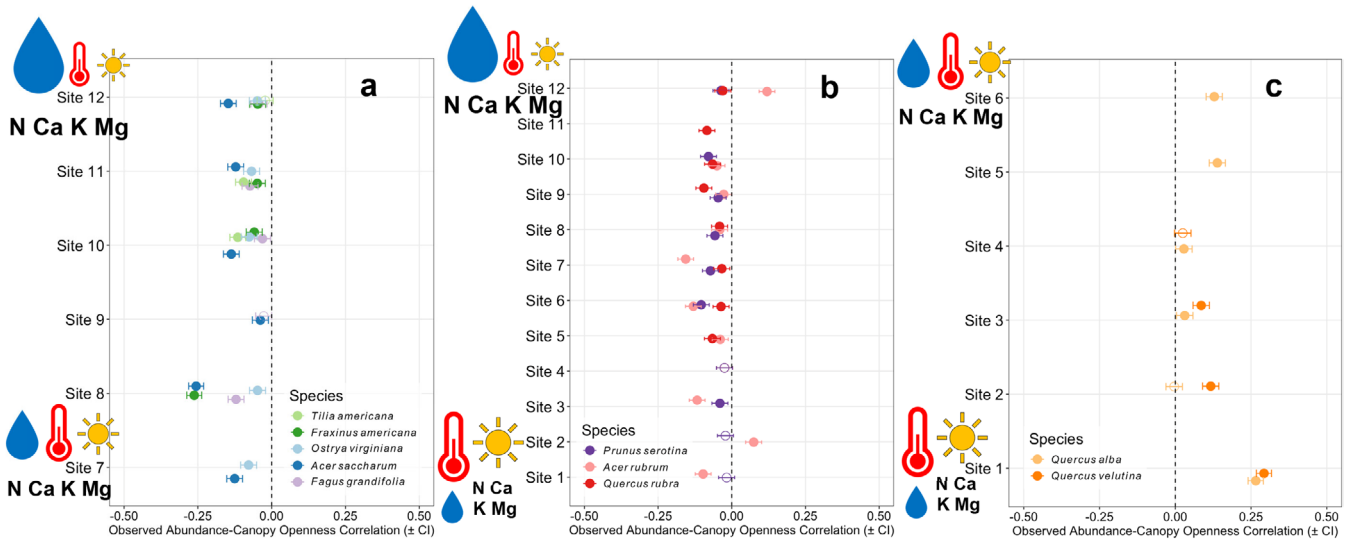


FIGURE 5 | Strength of overstory buffering effects on observed seedling abundances for 10 tree species across 12 sites in the Manistee National Forest, Michigan, U.S. Correlation coefficients (±95% confidence intervals) from relationships between the observed standardized seedling abundances (number of observed seedlings divided by species' site-level adult basal area) versus canopy openness (%) (*x*-axis) at sites (*y*-axis) at which ≥25 seedlings per species occurred across the study period (1998–2023) for (a) species dominant on mesic sites (Sites 7–12), (b) species widespread across sites (Sites 1–12), and (c) species dominant on xeric sites (Sites 1–6). In each panel, sites are ordered from the bottom to top of the *y*-axis from more xeric, low-fertility to more mesic, high-fertility conditions. On the legend and figure, species are color-coded from green to orange from those dominant on mesic to xeric sites. Shapes indicate whether the site-level effect of buffering was significant (filled circles) or not significant (open circles). All species except for *Acer rubrum* exhibited significant overall effects of buffering across sites. Significance was evaluated at $\alpha = 0.05$. See Table S5 for summary statistics associated with random-effect meta-analyses for each species.

F. grandifolia may experience stronger density-dependent effects of factors such as soil pathogens than *P. serotina* and *Q. rubra* under warmer conditions in mast years. Higher temperatures could simultaneously enhance recruitment and pathogen activity, with negative effects of soil pathogens outweighing temperature benefits for *A. saccharum* and *F. grandifolia* when seedling densities are high. In contrast, during non-mast years when density-dependent disease transmission is lower, temperature benefits may outweigh negative effects of pathogens for *A. saccharum* and be relatively neutral for *F. grandifolia*. For *P. serotina* and *Q. rubra*, it remains unclear why temperature effects are positive during mast years but negative during non-mast years; further work is needed to identify mechanisms driving these responses. Although contrasting effects of climate variables in mast versus non-mast years are interesting, predicted standardized seedling abundances during mast years were orders of magnitude higher than non-mast years. Thus, mast year conditions likely dominate recruitment dynamics and long-term regeneration potential; accordingly, we focus our discussion on results from mast years.

We found that recruiting seedlings occupied broader landscape-scale distributions across sites than conspecific adults, a pattern that may initially appear to contradict studies showing greater environmental sensitivity of seedlings (Canham and Murphy 2016; Dobrowski et al. 2015; Jackson et al. 2009; Qiu et al. 2021). However, because we analyzed seedlings in their first growing season, many likely still were supported by cotyledon reserves and had not yet experienced strong environmental filtering. We therefore expect the landscape-scale distributions of these seedlings to narrow as they age. Small climatic changes can drive substantial shifts in the locations of suitable habitat (Iverson et al. 2008; Iverson, Peters, et al. 2019; Loarie et al. 2009), especially in regions with limited topographic relief (Clark et al. 2016), such as northwestern Lower Michigan. Yet strong overstory buffering effects observed in our study suggest that some species—particularly those dominant at mesic sites or widespread across landscape-scale gradients—may maintain higher seedling abundances in buffered understory environments even as regional macroclimate changes (De Frenne et al. 2019; Dobrowski et al. 2015; Zellweger et al. 2020). We acknowledge that some local changes in irradiance likely occurred over the course of the study; however, we feel that our buffering results remain robust for two reasons. First, we detected strong relationships between canopy openness and seedling abundance even without direct measurements of canopy openness later in the study, which we would have expected to be weaker because of regression dilution (Berglund 2012). Second, adult tree basal area surrounding the light-measurement locations—which is tightly linked to canopy openness—showed strong relative rank stability across the study period. This relative stability in overstory structure is likely the reason why canopy openness–seedling abundance relationships remained detectable.

4.1 | Species With Recruitment Favored Under Projected Future Climates: *A. rubrum*, *O. virginiana*, *P. serotina*, *Q. alba*, and *Q. rubra*

Assuming that continued increases in annual temperature and precipitation in the Great Lakes region (Fei et al. 2017; IPCC 2022) translate to wetter, warmer growing seasons, our

results suggest that recruitment of *A. rubrum*, *O. virginiana*, *P. serotina*, *Q. alba*, and *Q. rubra* may be favored in future northern hardwood forests, particularly in years of high seed production. These species occur near their northern range limits in Michigan (Burns and Honkala 1990; Iverson, Peters, et al. 2019; Iverson, Prasad, et al. 2019) and likely near their environmental tolerance thresholds (i.e., minimum temperatures and rainfall requirements) (Sheth and Angert 2014; Slatyer et al. 2013), making them poised to benefit from longer, wetter growing seasons.

A. rubrum and *O. virginiana* recruitment increased under warmer, wetter conditions, consistent with their affinities for more mesic sites and climates and intermediate shade tolerance (Lewin 1974; Burns and Honkala 1990). Both species are also projected to exhibit high regional adaptability to climate change (Iverson et al. 2008; Iverson, Prasad, et al. 2019), consistent with our findings. Similarly, *P. serotina*, which is sensitive to late frosts and relies on moist soils for regeneration (Hough 1965), benefited from warmer, moist growing seasons. Its greater abundance in shaded quadrats suggests that local overstory buffering may further promote establishment by maintaining favorable soil moisture.

Both *Q. alba* and *Q. rubra* also showed increased recruitment in warm years, consistent with their need for moist germination conditions and reduced frost exposure (Bell 1975; Minckler 1965; Sander 1965, 1979). *Q. alba* and *Q. rubra* are likely to have high adaptability to future Great Lakes climates (Iverson, Prasad, et al. 2019), aligning with their positive recruitment responses. However, *Quercus* seedling recruitment and survival are constrained by forest mesophication favoring more shade-tolerant species (e.g., *A. rubrum*) (Alexander et al. 2021; Woodbridge et al. 2022), intense deer herbivory (Dey 2014; Henry and Walters 2023), and pest damage to acorns (Gibson 1972; Minckler 1965) across northern hardwoods and eastern deciduous forests (Dey 2014; Webster et al. 2018). Reflecting these pressures, early seedling recruitment observed over 26 years appears insufficient to replace adult *Quercus* (Table S1).

4.2 | Species With Recruitment Constrained Under Projected Future Climates: *A. saccharum*, *F. grandifolia*, *F. americana*, *T. americana*, and *Q. velutina*

In contrast, *A. saccharum*, *F. grandifolia*, *F. americana*, *T. americana*, and *Q. velutina* showed reduced recruitment under warmer, wetter conditions, suggesting that projected future climates may constrain their regeneration under existing canopy and soil environments. These findings align with projected regional declines of these species in Great Lakes forests due to climate change and other disturbances (Iverson, Peters, et al. 2019; Iverson, Prasad, et al. 2019).

Recruitment of *A. saccharum*, *F. grandifolia*, and *T. americana* declined with increasing temperature, whereas effects of wetter conditions were positive for *A. saccharum*, neutral for *F. grandifolia*, and negative for *T. americana*. All three species are projected to continue becoming more dominant farther north (Boisvert-Marsh et al. 2014; Iverson et al. 2008; Iverson, Peters, et al. 2019; Woodall et al. 2009). *A. saccharum* and *F. grandifolia*, both cold-adapted and highly shade-tolerant (Burns and Honkala 1990; Kobe et al. 1995; Logan 1973), benefited from overstory buffering and cooler temperatures—consistent with shade-tolerant juveniles occupying cooler microsites than adults (Dobrowski et al. 2015). Reduced recruitment under warmer conditions aligns with observed declines in seedling performance for *A. saccharum* (Iverson et al. 2008; Peltier and Ibáñez 2015; Prasad et al. 2020), and only moderate climate adaptability for *F. grandifolia* (Iverson et al. 2008; Iverson, Prasad, et al. 2019). Adult *F. grandifolia* trees face pressure from beech bark disease (*Cryptococcus fagisuga* Lindinger and *Neonectria* spp.) (Reed et al. 2022; Stephanson and Ribarik Coe 2017), with some mortality at our sites, whereas the arrival of beech leaf disease (*Litylenchus crenatae* mccanni) in southeastern Michigan could threaten juveniles (Reed et al. 2022), making northern expansion contingent on escaping pests. *T. americana*, which prefers mesic sites and cold winters (Burns and Honkala 1990), also declined under warmer conditions but responded positively to overstory buffering, consistent with its shade-tolerant regeneration niche (Ashby 1960; Fowells 1965).

F. americana was the only species to show increased recruitment under warmer, drier conditions. This response may reflect regeneration on well-drained mesic sites, where flooding is less limiting (Wright 1965), or the potential for this species to regenerate on dry sites with higher nutrient availability, as observed in the northeastern U.S. (Swain 2020). However, these results are uncertain given extensive EAB-driven adult mortality (> 93% from 2016 to 2019), which introduced standardization bias and inflated predicted abundances (Figure 3f). Declining seed viability, complex requirements for warm and cold seed stratification, and continued EAB impacts (Klooster et al. 2014; Marshall 2020; Sun et al. 2024) suggest that future recruitment and landscape-level persistence will depend on the resilience of surviving seedlings and saplings.

Q. velutina recruitment increased under cooler, drier conditions, contrary to expectations on the basis of its southern distribution (Little Jr. 1979). At our sites, *Q. velutina* occurs in disjunct populations on xeric, low-fertility soils just beyond the northern limit of its primary geographic range (Little Jr. 1979). These populations may be acclimated to cooler, drier environments and less tolerant of excess light and drought (Brinkman 1965), which could explain reduced recruitment under warmer, wetter conditions. Because early recruitment may respond to different conditions than later survivorship, the mismatch between the southerly distribution of *Q. velutina* and its negative regeneration response to warming warrants further study.

5 | Conclusions

Leveraging 26 years of annual censuses across landscape-level variation in soil moisture, we found that growing season climate strongly influences early recruitment of 10 dominant tree species. Seedling abundances of mesic species-site complexes were generally more sensitive to warmer, drier conditions than those of xeric species-site complexes, and these climate effects were further shaped by local gradients in soil resources and light. Overstory buffering played a key role: canopy cover supported recruitment of mesic species and widespread species within

mesic sites, consistent with the importance of sheltered understory microclimates in mediating drought stress. By focusing on early seedling recruitment, our study complements existing forest inventory datasets focused on later tree life stages, offering a more comprehensive assessment of how future climates may affect regeneration and shape forest composition and diversity in northern temperate forests. Our results highlight substantial interspecific variation in recruitment sensitivity and underscore the importance of landscape- and local-scale resource gradients and early demographic bottlenecks in shaping forest responses to climate change.

Author Contributions

Bailey H. McNichol: conceptualization, methodology, investigation, writing – original draft, visualization, writing – review and editing, data curation, formal analysis. **Richard K. Kobe:** conceptualization, methodology, investigation, writing – review and editing, data curation, funding acquisition, supervision, resources, project administration.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study will be made available in the Dryad Data Archive at https://datadryad.org/.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Taxonomy, distribution, and recruitment and adult summary for the 10 species censused for seedling recruitment from 1998 to 2023 in the Manistee National Forest, Michigan, U.S. Columns denote the number (no.) of sites with recruitment; total no. of seedling recruits censused across the study period; total no. of adult trees (diameter at breast height ≥ 10 cm; censuses in 1999, 2005, 2007, 2009, 2011, 2013, 2016, 2019, and 2022); standardized mean ± standard deviation (SD) no. and maximum no. of recruits per quadrat (1 m^2); and, for each species, the no. of site × year observations and the no. and percentage classified as mast years (i.e., relatively high seedling density). Site 8 was not censused in 1999, and only ~3/8 of the stand is mapped, the total number of *Acer saccharum* stems (the dominant species at Site 8) is an underestimate. **Figure S1:** Basal area (BA) in 10-m radius plots in 1999 and 2022 across 11 sites in the Manistee National Forest. Each panel shows BA in 1999 and 2022 for all 10-m plots at a given site, with lines connecting the values for each plot across the two census years. Green lines indicate plots where BA increased from 1999 to 2022, whereas dark blue lines indicate plots where BA decreased. Panels are ordered from xeric, low-fertility sites (top-left) to mesic, high-fertility sites (bottom-right). BA was summed in 10-m radius plots surrounding the locations where canopy openness measurements were taken along each transect. Site 40.40 was excluded because of incomplete adult tree censuses along the transect. See Table S2 for a summary of the relative rank stability on the basis of the BA of plots within sites. **Table S2:** Percentage of 10-m radius plots at each site for which the within-site basal area (BA) rank changed by less than 10% between 1999 and 2022. For each site, BA was summed in 10-m radius plots surrounding the locations where canopy openness measurements were taken along each transect. Plots were ranked within each year from highest to lowest BA, and rank change was calculated as the absolute difference between the rank of a plot in 1999 versus 2022. A plot was classified as stable if its rank shifted by less than 10% of the total number of plots at that site. See Figure S1 for a visual summary of changes in plot BA from 1999 to 2022. **Table S3:** List of the 13 candidate Bayesian hierarchical regression models tested for each species. Model forms presented have been simplified to just indicate the main and interactive effects of covariates evaluated in each candidate model; see Methods for details

about the zero-inflated versus non-zero components of models. Std. abundance = standardized abundance of recruits (number of seedlings/conspecific adult basal area, m^2); [M] = masting index variable; PDSI = Palmer Drought Severity Index; * = interaction term (both main effects and their interaction were tested in models with *). **Table S4:** Parameter estimates from the best candidate models of seedling recruitment for 10 tree species abundant in the Manistee National Forest. Species, best candidate model, and parameter estimate for the intercept (Int), Palmer drought severity index (PDSI), temperature (Temp), and their interaction (PDSI*Temp) for zero-inflated (ZI) and non-zero (count) components of the model, in non-mast years (top portion of table) and mast years (bottom portion of table). Values are the median (50% quantile) and the lower and upper bounds of the 95% credible interval (CI; 2.5% and 97.5% quantiles), in parentheses, from the posterior distributions of parameter estimates. Values in bold represent 95% CIs that do not overlap with zero, and all values have been back-transformed from model outputs. See Table S3 for the full list of candidate models. **Figure S2:** Effects of growing season climate on predicted abundances of seedlings of 10 tree species abundant in the Manistee National Forest. Position of each tree species (points) on the basis of the median parameter estimates of the Palmer drought severity index (PDSI, *x*-axis; higher values indicate wetter conditions) versus temperature (*y*-axis), with the color and size of points denoting the sign and strength of the interaction between PDSI and temperature as indicated by the legend. Parameter estimates are from mast years for each species and were averaged between the zero-inflated and count components of each model prior to plotting; weighted averages were computed using the 95% credible intervals for the interaction term to give more influence to estimates with smaller uncertainty. **Table S5:** Summary statistics from random-effects meta-analyses evaluating the effects of overstory buffering on seedling abundances of 10 tree species in the Manistee National Forest. Species, overall effect size (correlation coefficient, *r*) across sites and its lower and upper confidence intervals (CI), *Z* value, and *p*-value. Heterogeneity statistics, which indicate variation in buffering effects across sites, are: $\tau 2$, the variance in effect sizes across sites; I^2, the percent of total variation due to heterogeneity; and the Q-statistic and associated *p*-value, which tests for significant heterogeneity in buffering effects between sites. Values in bold are for effect sizes and measures of between-site heterogeneity significant at $\alpha = 0.05$.