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RESEARCH ARTICLE

Continental Contrasts in Climate Extremes That Control Tree Fecundity

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ABSTRACT

In 2023, more than half of olive harvests (*Olea europaea*) across Spain, Greece, and Türkiye were lost to drought. The same year late freeze destroyed 90% of the peach crop (*Prunus persica*) on the Georgia Piedmont and the apple crop (*Malus domestica*) in central New York, Vermont, and southern Quebec. Climate extremes now rank with the costliest threats to agriculture, but their role in forest recovery from diebacks that are happening globally is unknown for lack of tree fecundity estimates in forests. Tolerance of climate extremes could depend on past exposure but constrained by phylogenetic conservatism. We report a continental scale analysis of climate extremes and forest fecundity across North America and Europe showing that responses to late freeze and drought are happening now. Species differences are not explained by the traits typically included in ecological studies and they are weakly associated with phylogeny. Late freeze, that is, freezing temperatures that follow the onset of flower development in spring, is shown to be "normal" in North America, but not Europe, potentially explaining failed seed production due to delayed onset and the resultant shorter growing period by North American transplants dating back at least to the 18th century. Drought has thus far had the greatest impacts in dry forested regions, but here too, species differences are not explained by traditional trait values. If responses have been buffered from drought and late freeze by past exposure, acclimation and local adaptation prove inadequate as extremes intensify.

For affiliations refer to page 13.

Why [do] North American plants carried to Europe … flower so late and do not produce ripe fruit before the frost overtakes them… Pietr Kalm (1770) Travels into North America (Kalm 1770).

1 | Introduction

As large-scale diebacks focus the attention of conservationists on forest regeneration (Curtis et al. 2018; Guldin 2018; Holl and Brancalion 2020), the implications of failed seed production are substantial—unlike agriculture, forest recovery is not mitigated by irrigation or replacement cultivars that come available through selective breeding (Pechan et al. 2023). [More than 90% of forest regeneration depends on native seed production rather than vegetative regrowth, seed addition, or transplants (Clark et al. 2016; FAO 2020)]. All evidence suggests that natural forests should be experiencing reproductive failures like those in agriculture. Similar climates that support temperate mixed forests on both sides of the Atlantic provide an opportunity to examine late freeze in different contexts. Kalm's unanswered 18th-century query highlights a continuing lack of understanding, while suggesting that continental comparisons might shed light on not only worsening drought, but also late freeze.

Quantifying the impact of late freeze requires an index that captures the three-way interaction between timing, duration, and depth of freeze events. [*Depth of freeze* refers to degrees below zero; this is important because previous indices monitor only if subzero temperatures occur, but not their extent]. With advancing spring phenology, freeze damage has become the leading weather risk for orchard practice, and it is impacting forests (Guillaume et al. 2018; Hänninen 2006). As highlighted by 2023 losses (Lutz and Kann 2023; Ministerio de Agricultura 2024; Paddison 2023; Soguel 2023; Soylu 2023; Staff 2023) impacts can accumulate from the time of bud expansion to flowering and early fruit development (Figure 1). Ice and freeze tolerance (supercooling) vary between species, genotypes, and even branches of the same tree (Charrier et al. 2011; Schmitz et al. 2015; Wisniewski et al. 2018). Winter dormancy protects sensitive tissues until a chilling requirement is satisfied, usually measured as hours or days within a low temperature interval (Vitasse et al. 2014). Finding climate indices to quantify freeze effects has been difficult because the time when chilling stops and heating starts is not observable in the field (Clark et al. 2014; Hänninen 2006; Luedeling et al. 2013). Timing is important because the later freeze occurs, the greater the damage. For many species in temperate regions, spring budburst follows an accumulation of chilling days. This chilling delay (CD) is an avoidance mechanism. After a threshold is reached, heating degree days begin to accumulate. A species with a large CD value of 50 days (on the scale used here) is buffered from all but the latest freeze events. Conversely, a species with a low CD value of 10 days experiences early freeze events potentially at a vulnerable time. The effects of freezing temperatures that occur after a species-specific CD are amplified by the heating degree days

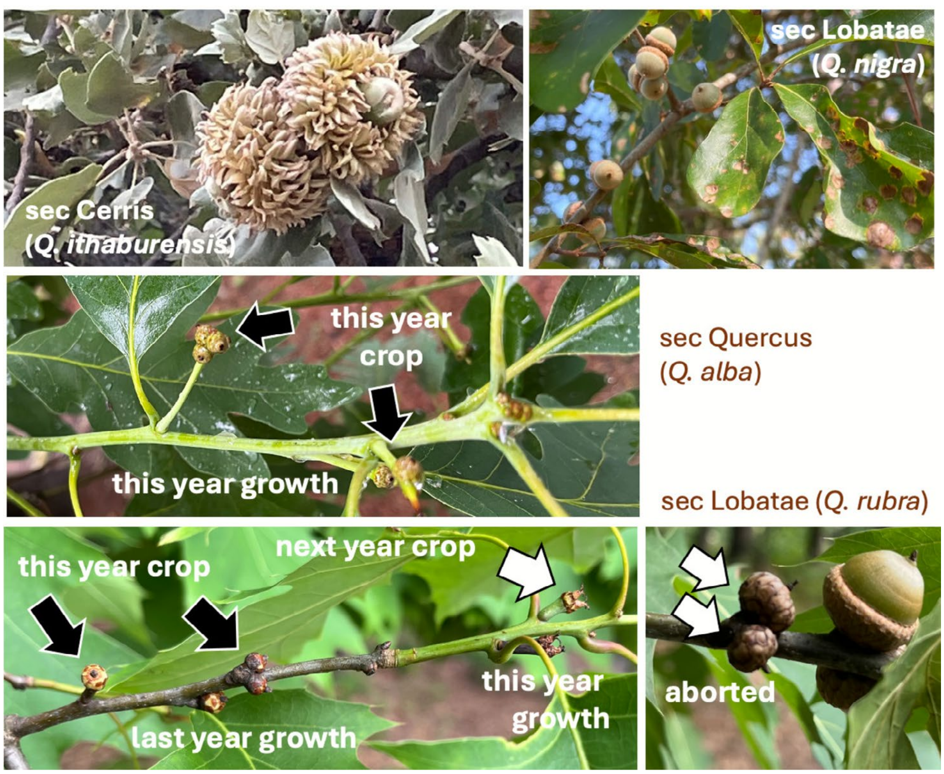

FIGURE 1 | Structural adaptation to drought and seasonal attrition. The exaggerated *Q. ithaburensis* cupule (top left) limits moisture loss by scattering radiation; contrast the moisture-demanding *Q. nigra* (top right). Lower panels show species that develop in one (section Quercus) and two (section Lobatae) years on 5 May 2024, in Durham NC. Following 2 weeks without rain in June, nearly all *Q. alba* and many *Q. rubra* aborted. Aborted fruits that have not yet abscised are shown at lower right with a still-viable fruit. [photos JSC].

that have accumulated to that date and the depth and duration of the freeze event—short exposures cause less damage than long ones (Charrier et al. 2021, 2015). Chilling requirements reported from orchard practice, including extension services and trade publications, are specific to a location and species (or cultivar; Fernandez et al. 2022) and, thus, are hard to generalize (Drepper et al. 2022). Many ecological studies focus on phenology of leaves, often using simulation (Chuine and Régnière 2017; Hufkens et al. 2012). However, we are unaware of direct estimates from forest fecundity data. Site- and species-specific studies are hard to extrapolate due to heterogeneous data and methods (Clark et al. 2019; Drepper et al. 2022), and there is limited calibration to known crop losses (Kaukoranta et al. 2010; Zohner et al. 2020).

If tolerance of extreme weather depends on past exposure, through local adaptation and/or acclimation, then Kalm's puzzlement at delayed fruit development in North American transplants is relevant for the contemporary rise in extreme climates. Commissioned at the behest of mentor Carl Linnaeus, and a colleague of North American botanist William Bartram (Bartram 1791), Kalm was informed by the extensive species transplants of the 18th century (Kalm 1770). Severe winters could not explain why transplants to Europe fail to develop fruit in time; northeastern North American winters were already known to be as long and colder than the European planting sites (Kalm 1770). If delayed development protects freeze-sensitive flowers in North America, then we expect to find differences between the two continents in climate variables like temperature or degree-days.

As with late freeze events, commercial practice offers limited insight on the effects of worsening drought. Seed production in forests does not benefit from expanding irrigation and crop replacements (Brito et al. 2019; Pechan et al. 2023). The associations between tree fecundity and drought in forests have been estimated for few species, each at one to a few sites (Bogdziewicz et al. 2020; Le Roncé et al. 2021). Drawdown in growing season moisture can cause premature bud abscission and abortion of developing fruit (Espelta et al. 2008; Gucci et al. 2009; Liu et al. 2013). Although extremes can happen quickly, effects can lag. The extended memory of drought is held not only in soil moisture deficits that linger from one season to the next, but also in tree condition. Fruits of some genera (e.g., *Acer, Morus, Ulmus*, and some *Prunus*) mature before soils dry in summer. For these early developers growing season moisture deficits may affect reserves for next year's crop rather than the current one (Figure 1). Lag effects may be inevitable for species that require two or more years to develop, including many Pinaceae and Lobatae (red) oaks (Figure 1). Late-developers that fully exploit the growing season for the current year's crop, including many moisture-laden fleshy fruits (*Asimina*, *Cornus*, *Diospyros, Nyssa, Olea*, Rosaceae) and nuts (*Corylus*, Fagaceae, Juglandaceae), suffer attrition during extended summer moisture deficits (Stephenson 1981). For forests, the conflicting interpretations of climate effects from site- and species-specific studies are unsurprising considering the huge variation between individual trees (Clark et al. 2004; Greenberg 2000), including within even-aged monocultures of half siblings (LaDeau and Clark 2006), and the emerging evidence that local adaptation in trees is widespread and occurs fast (Alberto et al. 2013; Hanlon et al. 2019; Scotti et al. 2023; Skrøppa et al. 2010).

To evaluate the impacts of climate extremes, this analysis provides synthetic coverage across species and habitats on two continents and a new approach to late freeze that accommodates the three-way interaction between timing, duration, and depth of freeze, translated into the familiar scale of degree days. The Masting Inference and Forecasting (MASTIF) network integrates data that can be referenced to seed production by each tree-year. Allowing for the dependence between trees and within trees over time, the analysis provides full uncertainty on seed production that can be propagated to continental seed production as predictive distributions (Clark et al. 2021, 2019). We quantified the impacts of extreme moisture deficit (MDEF) and late-freeze degree days (LFDD) on tree fecundity, and we transferred individual responses to biogeographic effects. The fecundity response to extremes is estimated here using a dynamic model that admits combined effects on individuals from a wide habitat range.

We implemented a three-step calibration/prediction approach to integrate extreme climate with habitat, species, and tree condition (species, diameter, shade class), and we projected those responses across continents: (A) fecundity data synthesis across North America and Europe, (B) fitting annual seed production to individual condition (size, shading by neighbors) and habitat, including climate norms and anomalies, soils, topography, and region- and species-specific year effects (e.g., masting variation that is not directly tied to climate anomalies; Clark et al. 2019), and (C) projection of the fitted model across harmonized national forest inventories. To evaluate the role of past exposure, MDEF and LFDD are included in the analysis both as the norm for a tree's location and as annual departures from that norm (anomalies).

2 | Methods

Analysis includes three elements, (A) data synthesis, (B) fecundity modeling, and (C) biogeographic prediction (Figure 2). Methods are detailed in an extended Supplement to (Clark et al. 2019). Data are of two types, seed traps (ST) from mapped inventory plots and crop counts (CC) on trees from both inventory plots and individual trees. These two data types are included because both can be referenced to seed production by an individual tree each year (many mast studies use indices that cannot be referenced to a tree-year). Tree-year reference is required because fecundity varies by orders of magnitude between trees and within the same tree over years. CC observations record the number of fruiting structures along with an estimate of the crop fraction that is observed. Crop counts that are obtained on the same trees year after year constitute a time series in the model. These observations contribute to estimates of year effects and individual effects (Clark et al. 2019) in the model. For opportunistic CC data, which have no individual or year effect, this variation is marginalized into the residual error. Seed traps are observed on inventory plots with mapped trees and traps. Each tree represents a time series linked to seed trap observations by a data model that includes seed dispersal and

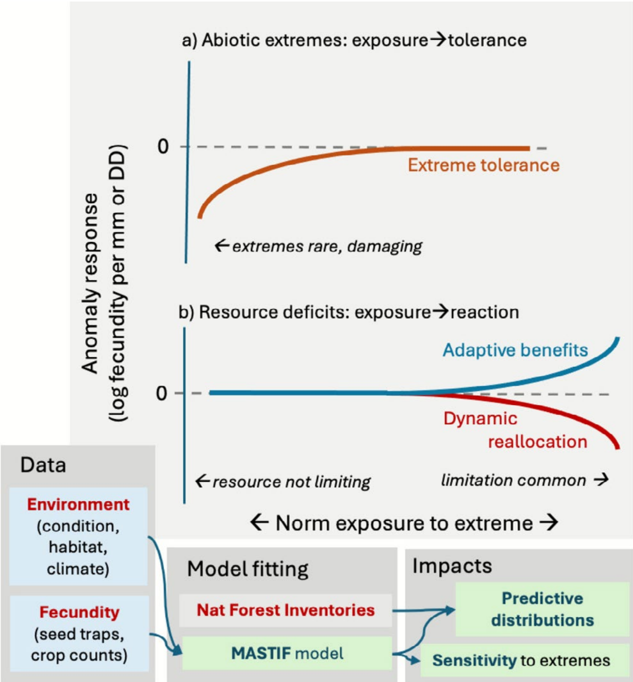

FIGURE 2 | Hypothesized climate-extreme impacts recognize fundamental differences between an abiotic stress (late freeze) and resource deprivation, like moisture. An exposure → tolerance model describes adaptation (including acclimation) to abiotic extremes with increased exposure; negative impacts are severe where past exposure has been limited. Conversely, an exposure → reaction model recognizes impacts that are potentially positive or negative. For a limiting resource (e.g., moisture) minimal effect of anomalies is expected for species from environments where that resource is not limiting. Where limitation is frequent, losses during extremes could be minimized by dynamic cutbacks in demand, such as crop-size reduction through abortion while fruits are still small. Because moisture extremes affect allocation, extremes could reduce growth and/or defense, while tradeoffs with fecundity (Berdanier and Clark 2016) produces a range of responses.

species misidentification. The details for observation error are part of the full model description in the Supplement to (Clark et al. 2019).

The species included in the analysis are those for which there is data coverage sufficient to obtain estimates. The temporal and geographic coverage of observations is reviewed in (Clark et al. 2021; Journé et al. 2022; Qiu et al. 2022) and summarized in Figures 3 and S2. Table S1 lists for each predictor the number of species retained in the fitted model and those that were excluded due to insufficient data distribution.

2.1 | Fecundity Analysis

Annual fecundity of every tree was estimated with a Bayesian hierarchical state-space model to produce species-level coefficients for the main effects and interactions between variables. To summarize the model detailed in (Clark et al. 2019), the data model for ST data describes Poisson counts in traps conditional on dispersal from each tree. The continuous dispersal kernel is estimated with individual fecundity and uncertainty in species identification of fruits in traps. The data model for CC data is beta-binomial for true seeds given counted seeds and crop fraction. The maturation status (mature or not) depends on tree diameter, also estimated for each species. Conditional on maturation, each species has fitted coefficients for main effects of predictors (including norms and anomalies for MDEF and LFDD), interactions, and year effects (Clark et al. 2019). For each species, the conditional fecundity model for tree i at location j (within eco-region r) in year t is

$$\log f_{ij[r],t} = \mathbf{x}'_{ij,t}\boldsymbol{\beta} + \gamma_{r,t} + \alpha_i + \epsilon_{ij,t} \quad (1)$$

where $\mathbf{x}_{ij,t}$ is the design vector holding main effects and interactions, $\boldsymbol{\beta}$ is the corresponding vector of fitted coefficients β_x, where x is the name or index of a predictor, $\gamma_{r,t}$ is the year effect for region r, α_i is the random individual effects, and $\epsilon_{ij,t}$ is random error. There are two sources of zeros in fecundity, i) the tree is immature, or ii) conditional fecundity of a mature tree is lower than the number of seeds held in a single fruiting structure. Eco-regions are used for this quasi-synchronous masting because they approximate the spatial scales described for masting phenomena in the literature. The year effect takes up synchronous variation between trees of an ecoregion that are not explained by interannual climate anomalies (Clark et al. 2019). We use eco-regions defined by WWF to include quasi-distinct biota, climates, and soils. There are 180 and 55 ecoregions in North America and Europe, respectively (Olson et al. 2001).

2.1.1 | Sensitivity Coefficients

Log fecundity is used in Equation (1) due to large variation in seed production between species, individuals, and years. True fecundity is a latent variable in the model with two sources of zeros, (1) a tree is not mature, or (2) conditional fecundity is below the minimum number of seeds contained in a single fruiting structure (Clark et al. 2019). Fitted coefficients $\beta_x = d\ \log(f)/dx$ in Figures 4a, S4, and Appendix S1 are in units of log fecundity mass per unit x, where x is a predictor variable. This is a proportionate response, the numerator being

$$\lim_{df \to 0}\left[d\ \log(f)\right] \to \frac{df}{f}$$

df indicates the differential. For example, a coefficient value of $\beta_{MDEF} = -0.01$ (vertical axis in Figure 4a) indicates a 1% decline for a mm increase in annual mean monthly deficit.

Predictor variables were selected to have known importance for tree condition and to be globally available at all sites over the years spanned by data sets (since the 1950s), including lagged effects and year effects. Moisture deficit is an interaction between temperature T and precipitation P, which combine to give potential evapotranspiration PET. Predictors include tree size, shading by neighbors, temperature norms (linear and quadratic terms), moisture deficit (normed monthly $PET—P$ and annual anomalies, see below), late freeze (norms and annual anomalies), slope, aspect [slope × sin(aspect), slope × cos(aspect)], topographic position, isolation from conspecifics

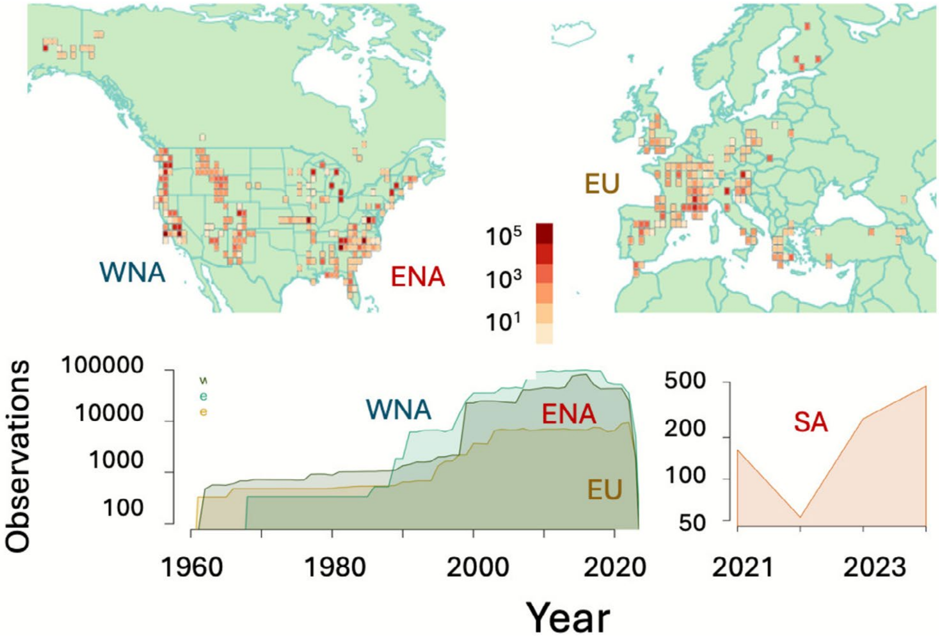

FIGURE 3 | Distribution of tree-years in NA and EU. The 2,874,955 observations shown here omit other regions used in global analyses (Journé et al. 2022; Qiu et al. 2023). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

(in the event of pollen limitation), and pH (Supplement table). Field measurements include tree diameter and the 5-point shading index of the NEON/Forest Inventory and Analysis (FIA) programs. Soil pH and cation exchange, an index of fertility, are estimated for the upper 30 cm at 250 m resolution (ISRIC 2024). Terrain variables (elevation, slope, aspect, position on slope) are 30 m resolution (Farr et al. 2007).

Bayesian analysis combines data with prior knowledge. Prior distributions for predictor variables were flat or truncated at zero. Zero-truncated flat priors have the advantage that they incorporate the known sign of an effect (positive or negative) while leaving the shape of the posterior distribution otherwise dependent on the likelihood (Clark et al. 2013). Predictors with known sign include positive linear and negative quadratic terms for diameter and temperature (they are convex functions). The prior distribution for MDEF is flat, allowing that fecundity may either decrease or increase in dry years. Both outcomes are possible due to potentially many interactions and lag effects that apply to a resource (water) that affects carbon and nutrient acquisition and storage. The prior distribution for LFDD is negative because prior knowledge does not include a path for freeze losses to result in more seed in the same crop. LFDD sensitivity can be arbitrarily close to zero, but not positive.

Variable selection was done with the deviance information criteria (DIC). Predictors were initially screened for each species to include only those with sufficient coverage, gauged by variable range and standard deviation and variance inflation (Table S1). Quadratic terms were only admitted for predictors that were also included as linear effects. The exception is aspect, which only exists as an interaction with slope; there is no main effect of aspect (Table S1). Variance inflation factors (VIF) were evaluated for all variables with sufficient coverage for a species. Any predictors exceeding a value of 10 were sequentially eliminated until none of the remaining predictors exceeded this value. Thus, climate extremes could be omitted for models from some species if those extremes are highly correlated with other predictors. This starting set of predictors was compared using DIC from alternative models that eliminated variables with 95% posterior distributions that include zero. The full set of mean and standard error estimates of lowest DIC models are given in Supplement tables. Additional descriptions for climate extremes follow.

2.1.2 | Moisture Deficit

Extreme drought depends more on duration than daily anomalies. Many indices depend on the availability of high-frequency data and measurements of contributing variables that are not available everywhere, for all years, and measured in the same ways. Our MDEF exploits monthly temperature and precipitation data that are available globally over the more than half-century spanned by our longest tree fecundity data sets. Its simplicity reflects the fact that hydrologic information needed to estimate drainage is limited for most parts of the globe. Additional predictors discussed above (slope, aspect, position on slope) accommodate contributors to local drainage (see above) that locally modify the effects of MDEF.

Moisture deficit is taken as an average over the months included in year t

$$MDEF_t = \frac{1}{m} \sum_{m \in M} PET_{t,m} - P_{t,m}$$

where M is the set of months having greatest influence on the fruiting period for the species, and m is the cardinality (number of elements) of M. The monthly range M differs by species depending on vulnerable fruit development. Because variation in the monthly PET_m—P_m is stored through soil moisture withdrawal and recharge, we included non-growing season months

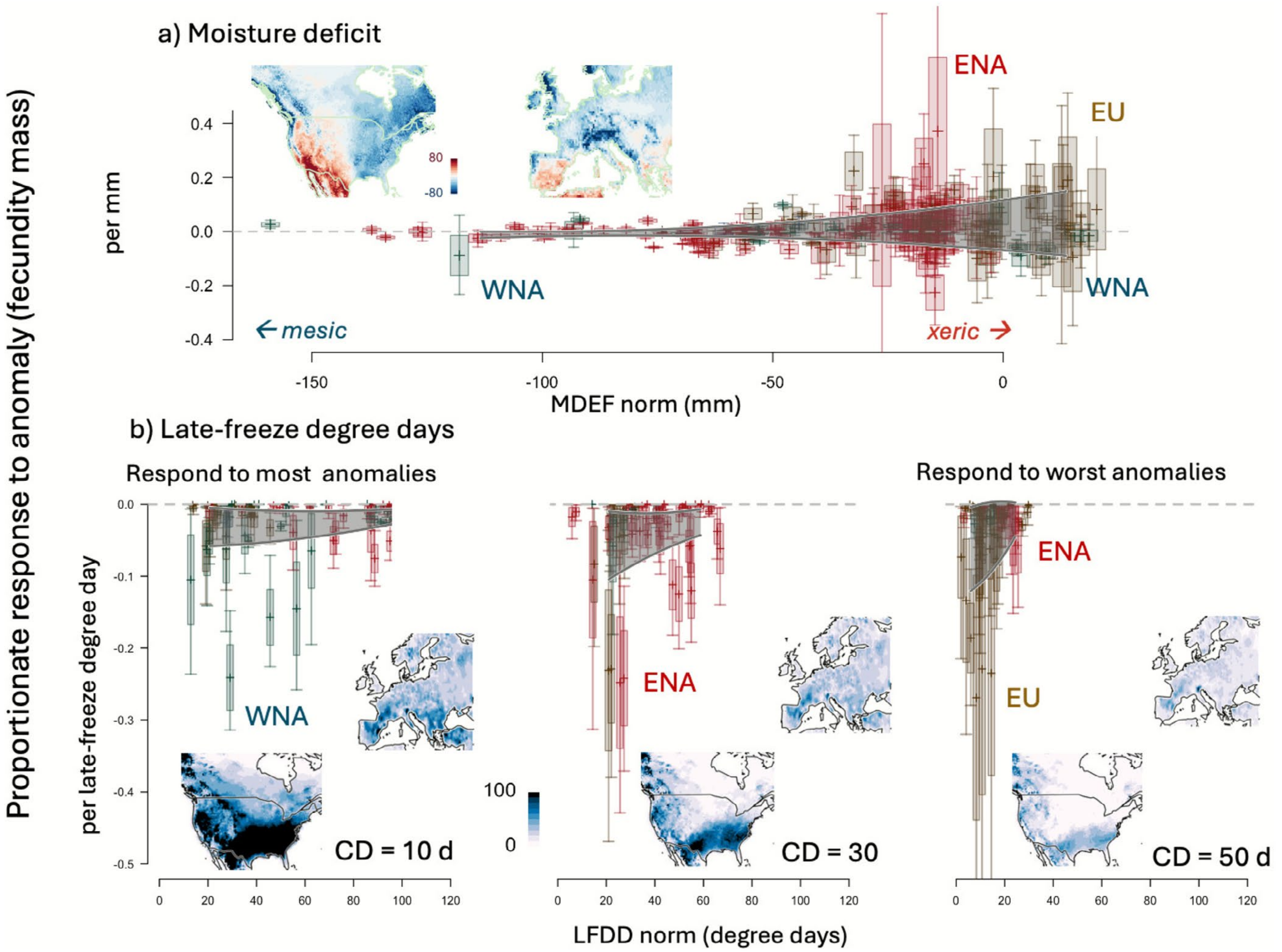

FIGURE 4 | Fecundity responses to extremes differ by region. Coefficients (bars and whiskers) are proportionate fecundity response per unit change in the annual anomalies for MDEF (monthly averaged PET—P in mm) and LFDD (late-freeze degree days). Bars (one per species) span 68% (box) and 95% (whiskers) of posterior distributions. Gray envelopes fit 95% quantiles across species on each panel. Mapped norms are for years 1990 to 2010. (a) Responses to moisture deficits increase in magnitude as moisture becomes more limiting. (b) Responses to late-freeze anomalies diverge between regions. Three panels separate species by the best-fitting CD value: 10, 30, or 50 days. Western North America (WNA) has many species that respond to most anomalies, large and small (CD = 10 days), while Europe (EU) supports species that respond overwhelmingly to the large extremes (CD = 50 days). Eastern North America (ENA) is intermediate (mostly CD = 30 days, but also some 50 days). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

(e.g., snowfall and winter rain come available the next growing season). We include in M the 12 months of the previous year and the development period of the current year, that is, through May for spring seed developers ($m = 15$) or through August ($m = 8$) for others. P and T (used to evaluate PET) combines Terraclimate (Qin et al. 2020) at 4 km, which is available for all years, with CHELSA (Karger et al. 2017) at 1 km that has partial coverage. We combined them with local data using a two-step procedure (Clark et al. 2021). For all locations, we start with regression to project CHELSA forward using Terraclimate, aligned with proximity-weighted interpolation. For montane sites, we follow with calibration to local climate data available from collaborators, LTER, or NEON. This includes the Alps, Appalachians, Rockies, Sierra Nevada, and Cascades. Norms for all climate data include the period from 1990 to 2010, which broadly overlaps with fecundity data, and predates rapid increases in global temperatures of the last decade. Annual anomalies are departures from the local norm.

2.1.3 | Late Freeze

We developed late-freeze degree days (LFDD) to capture the non-linear effects of late freeze on fruit yield that intensify the more developed the crop. Current models can be complex, but they focus on dates for events such as budbreak, leaf unfolding, or flowering (Chuine and Beaubien 2001; Gauzere et al. 2020). We are aware of only a few studies that fit models to fruit yield data, and they are focused on one or a few species at one or a few sites (Augspurger 2013). There apparently are no studies that incorporate the timing, duration, and depth of freeze interaction. A simple date for the last frost (Wang et al. 2025) or a count of degree days before a last frost (Zohner et al. 2020) omits this interaction. For example, the method of Wang et al. (2020) references the difference between an index of wheat productivity in a frost year and the average of "frost-free years". This approach was not used here, because risk is not binary; impact of late freeze is a continuum that depends on timing, duration, and intensity. Xu et al. (2024) assign

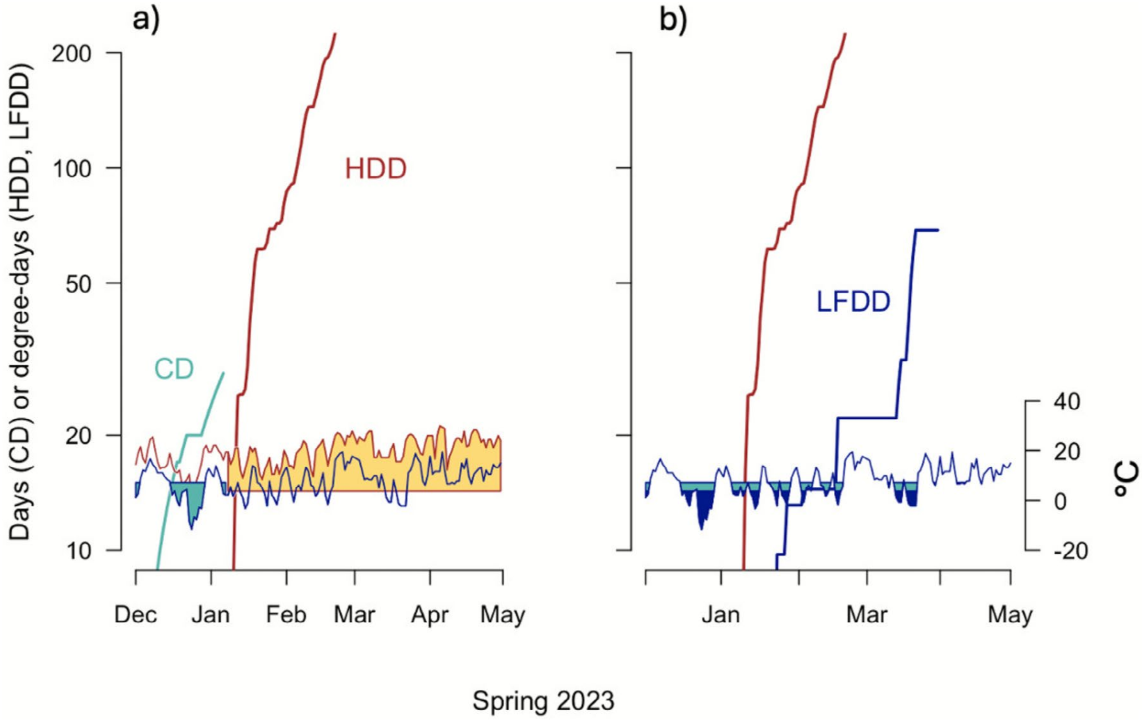

FIGURE 5 | Late-freeze degree days (LFDD), defined in this study, identify peach crop destruction at Warner Robins, GA. (a) Like standard chilling days, the chilling delay (CD) counts cool days until a threshold is passed (Equation (2)): Light blue polygon (bounded above by an upper threshold of 12°C and below by daily $T^{(\min)}$) until the chilling requirement is reached (30 days in this example). Heating degree days (HDD) (yellow polygon) accumulate thereafter (bounded above by daily $T^{(\max)}$). (b) Freezing temperatures cause damage when they occur late, depending on duration and depth of freeze. The LFDD index amplifies sub-zero temperatures (dark blue) by the heating degree days (HDD) that have accumulated to that date. Warm days in January allowed HDD to accumulate early. However, subfreezing temperatures (dark blue) did not contribute much to LFDD until the March freeze that caused LFDD to soar and destroyed much of the peach crop.

an ordinal score for severity to a freeze event (mild, moderate, severe) and record the time when it occurs, but not how it interacts with duration and depth of freeze. Because we require timing, duration, and intensity we use temperature rather than ordinal scores and we allow that timing for each species differs and cannot be defined in advance. The index that follows has the further advantage that units are familiar: degree days.

The concept of LFDD is simple: the duration and depth of a freeze event amplify the heating degree days that have accumulated since the chilling delay (CD) was satisfied. Our model tracks the maximum and minimum daily temperatures reached each day. For our index, the CD for a species is met when sufficient chilling days have accumulated. A chilling day has minimum daily temperature $T^-_{t,d}$ between lower and upper bounds $\left(T_l, T_h\right) = (-1, 12)^{\circ}$C (Lin et al. 2022). The accumulated CDs at day of the year (DOY) d is

$$CD_{d_t} = \sum_{d'=c_0}^{d} 1\left(T_l \le T^-_{t,d'} < T_h\right) \tag{2}$$

where the indicator function $1(\cdot)$ takes the value of 1 when its argument is true and zero otherwise. On day d^c_t, the CD_{d_t} is equal to the CD requirement for the species, $CD = CD_{d^c_t}$, and heating degree days (HDD) begin to accumulate (Figure 5). We begin counting CDs on c_0 = December 1 and continue until the requirement is satisfied on DOY d^c_t. Again, this threshold can differ for each species.

HDDs accumulate after the CD is satisfied on DOY d^c_t,

$$HDD_{t,d} = \sum_{d'=d^c_t}^{d} \left(T^+_{t,d\prime} - T_h\right) \times 1\left(T^+_{t,d\prime} > T_h\right)$$

Thus far, neither HDD nor CD capture the effects of late freeze events (Figure 5), which must account for the increasing impact of freeze degrees with accumulated HDD.

We define freeze degrees as the sub-zero temperatures on DOY d, $FD_{t,d} = -T^-_{t,d'} \times 1\left(T^-_{t,d'} < 0\right)$, and scale it by the heating that has accumulated since the chilling requirement was met,

$$LFDD_t = \sqrt{\sum_{d'=d_{t,c}}^{d_2} FD_{t,d'} \times HDD_{t,d'}} \tag{3}$$

The summation is taken until freezing risk is zero, (d_2 = July 1). It increases with development time, duration, and depth of freeze. LFDD has units of degree days.

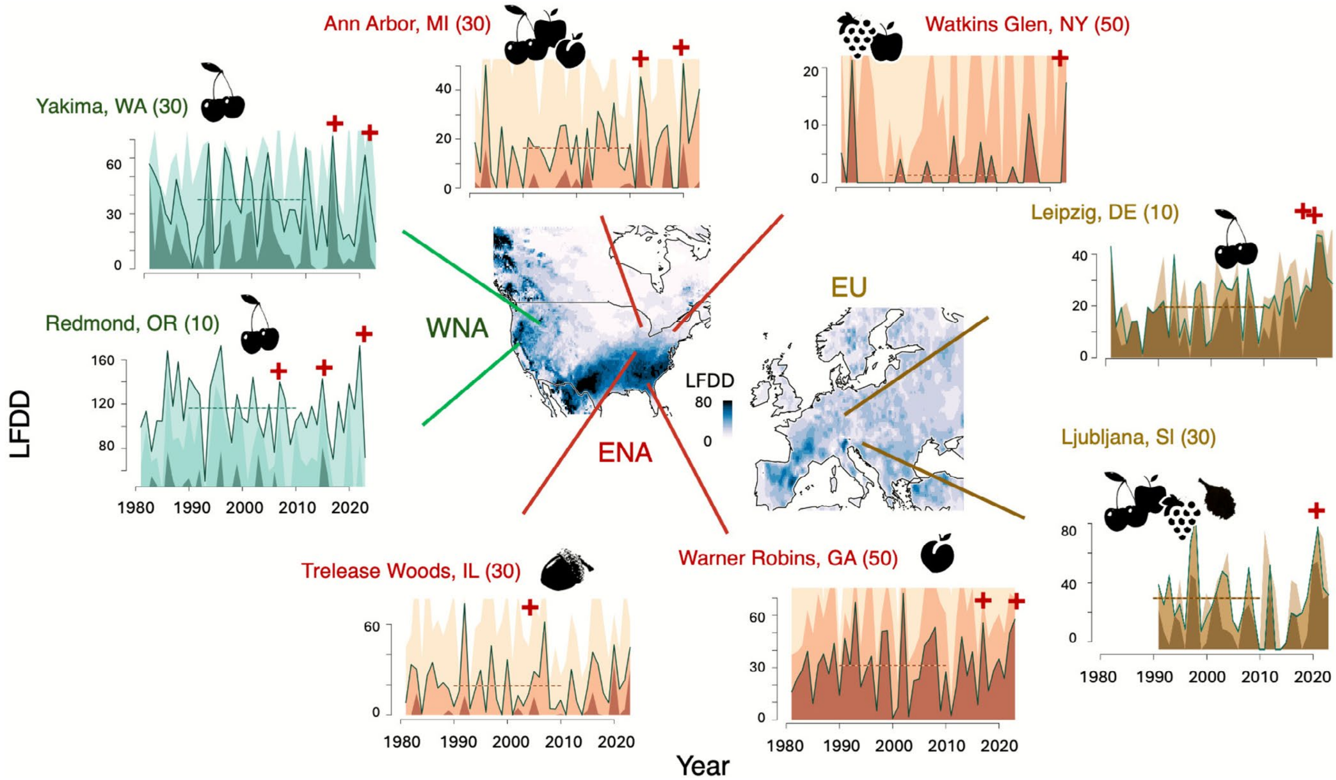

FIGURE 6 | Documented orchard crop losses (red crosses) align with late-freeze degree days (LFDD). Maps (center) show continental contrasts in LFDD norms for a chilling delay (CD) of 10 days with example time series from western North America (WNA, green), eastern North America (ENA, rust), and Europe (EU, brown). The blue shading on maps saturates at LFDD = 80 degree-days. LFDD time-series plots include CDs of 10 (darkest shading), 30, and 50 days (lightest shading). The CD that aligns with crop losses for each location (red crosses) is highlighted with a solid line and written after the location name in parentheses. Red crosses indicate freeze events reported in the literature or media outlets, represented by icons for peach, sweet and sour cherry, apple, grape, and forest species (*Quercus* and *Fagus* shown). Horizontal lines indicate the LFDD norm (1990–2010) for the CD value that is highlighted for crop losses. Horizontal scales are all the same, vertical scales differ. Ljubljana data are available to the European Climate Assessment only after 1990. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

LFDD requires daily data. Unlike moisture deficit, where extremes span extended intervals, late freeze operates over days (or hours), not weeks to months; daily data come from daymet (NA; Thornton et al. 2021) and the European Climate Assessment (EU; Cornes et al. 2019). CD is not readily identified in the model (it is not observed), but can be approximated with model selection (again, lowest DIC). We fit the model with chilling delays spanning a range that has effects on LFDD, including 10 days (high exposure to extreme freeze), 30 days, and 50 days (low exposure). The low value of 10 days generates high LFDD values close to no chilling requirement. The high value of 50 days generates LFDD close to zero over most of NA and EU.

2.1.4 | Climate Norms and Anomalies

Norms were evaluated for the period spanning 1990–2010, because it predates especially erratic climate years of the past decade and covered by substantial data in MASTIF (Figure 3). To highlight the current period, mapped norms and trends for the last 15 years shown included in Figure S1. Anomalies are calculated as annual departures from the norm (i.e., not standardized). While recognizing that the effects of anomalies may depend on the norm (e.g., dry anomalies become more important in dry climates, or vice versa), interaction terms between norms and anomalies were omitted due to the large size of the model and the fact that the expanded data coverage needed to span the full range of combined variables would limit the species that could be examined. This option should be considered as data accumulate in the future.

2.2 | Commercial Losses

Due to the large number of countries involved and the need to include events more recent than could be extracted from many government compilations like USDA's National Agricultural Statistics Service (NASS 2014), Figure 6 includes recent events that are widely reported in the media. We searched on keywords “frost”, “orchard”, “harvest”, “North America”, and “Europe”. We have included representative citations for the years and locations in Figure 6.

2.3 | Biogeographic Prediction

The fitted model includes predictors that are also available for inventory data, including national forest inventories (NFI). Fecundity of each tree has a predictive mean and standard deviation, both of which are propagated to the plot level. NFI plots were obtained from Finland, Poland, Germany, Slovakia, France, Spain, Italy, Austria, Canada, and the United States (Baeten et al. 2013; Bank 2019–2023; Cienciala et al. 2016; Inventaire Forestier National Français 2015; Canada's National Forest Inventory 2024; Bundesministerium für Ernährung und Landwirtschaft 2012; Mäkipää and Heikkinen 2003; Ratcliffe 2020; Sebeň 2017; Service 2024; Villaescusa and Diaz 1998). Additional inventory data come from NEON (USA), CzechTerra (Czech Republic), and MASTIF (international). All living trees > 12 cm diameter were included in predictions. Predictive distributions on a per-area basis were obtained by marginalizing over the posterior distribution of parameters time likelihood (Clark et al. 2021). This prediction step includes 10,639,644 trees (8,180,258 NA; 2,459,386 EU) on 358,780 inventory plots (181,866 NA; 176,914 EU).

2.4 | Trait Analysis and Phylogeny

Traits discussed in (Qiu et al. 2023) were correlated with responses to anomalies. Species-level anomaly responses can be taken as functional traits, with phylogenetic distances between species being Euclidean. Phylogeny comes from (Zanne et al. 2014) and, for *Quercus*, (Hipp et al. 2020). Tests for phylogenetic signal were obtained with the R package phylosignal (Keck et al. 2016).

3 | Results

The model, fitted to 2,874,955 tree-years from 298 wild species (Figure S2) and translated to 10.6 M trees on inventory plots, provides insights in two forms: (i) individual sensitivity to extremes and (ii) biogeographic impacts (Methods; Clark et al. 2021, 2019). Sensitivity is a species-level response of fecundity (log mass per tree per year) to a unit change in MDEF (mm) and LFDD (degree days). Predictive distributions from the fitted model translate tree sensitivity to stand fecundity (kg/ha/year), accounting for the competitive environments and habitats of each tree on forest inventory plots. We begin with the connections between extremes that are destroying orchard crops and the continental contrasts reported in the 18th century, a contrast that may explain their responses to different LFDD norms. We compare orchard crop losses to annual LFDD anomalies. We then show a fundamental difference between responses to late freeze and moisture deficit, where the impact of anomalies depends on the norm.

3.1 | An 18th Century Puzzle Explained

Kalm's 18th century puzzle may be answered by the continental contrasts in late-freeze degree days (LFDD; Figure 6). Eastern North America (ENA) experiences average LFDDs several-fold higher than the highest exposures in EU (maps in Figure 6). The delayed spring development to avoid late freeze should cause North American trees to lag Europe, where there is low risk of starting early. An early start allows full development in advance of low temperatures in autumn. Delayed onset in North America is consistent with acclimation or adaptation to high LFDD. Nonetheless, North American tree species that have habituated to high LFDD have become naturalized in Europe, suggesting the importance of acclimation or local adaptation, a point to which we return below. Mean monthly moisture deficits (MDEF) broadly overlap on the two continents: the wider range in NA (Figures 4a and S3b) includes deserts and thus is less relevant for forest fecundity.

On both continents, change in climate norms is not uniform. The recent trends that are most relevant for the bulk of observations in MASTIF (2010–2024) include increasing MDEF in the North American Southwest and southern and eastern Europe (trends in Figure S1). Where annual MDEF is decreasing, recent concentration of rainfall into few extreme events means lower infiltration and potentially extended intervals between events; the net benefits of decreasing deficit can be smaller than these trends in annual averages suggest. Annual LFDD is increasing in central and eastern Europe, but not in southeastern Europe. Late freeze changes in North America are heterogeneous and have substantial differences between chilling delays.

3.2 | One Index to Identify Commercial Losses

The importance of recent exposure for responses to extremes is consistent with the LFDD values we calculate for crop losses in the literature and media. A short chilling delay of CD = 10 means that trees suffer damage from late freeze that occurs early, that is, after a short chilling delay. Conversely, a long delay of CD = 50 ensures minimal risk and is the best fit for species that do not respond to freeze, even when late. The lower, dark shading in each time series of Figure 6 (CD = 50) describes species that delay, and thus avoid, late freeze; this curve does not record many of the events that contribute to the upper, light shading (CD = 10). One of the rare field studies reporting on multiple species in forests documented damage at Trelease Woods during the late freeze of 2007 (Augspurger 2009). This was an extreme year for trees that require CD = 30 days, but unremarkable for trees that require only CD = 10 days and missing entirely at CD = 50 days (Figure 6). The short CD = 10 days, which exposes trees to the earliest late-freeze anomalies, is shown for sweet cherry (*Prunus avium*) at Redmond OR. The long CD of 50 days at Watkins Glen shows that the 2023 loses came with a spike of less than 20 LFDD; however, this qualifies as extreme against the low norm that is typical of these northern latitudes (Figure 6). The cherry losses at Redmond OR come at much higher LFDD spikes that occur for a species with CD = 10 days against a high norm.

Chilling delays do not reduce the LFDD exposure in central Europe as shown by the nearly identical curves for all CD values at Leipzig and Ljubljana (Figure 6). Recent freeze events have arrived so late (LFDD for all three CD values are increasing in central Europe, Figure S1) that long chilling delays do not offer protection against these recent extremes.

3.3 | Extreme Climate Is a Niche Axis

The effects of climate extremes are modulated by terrain, stand structure and composition, and all other spatial variables in the best-fitting model. Recall that year effects in the model capture quasi-synchronicity between individuals at the ecoregion scale

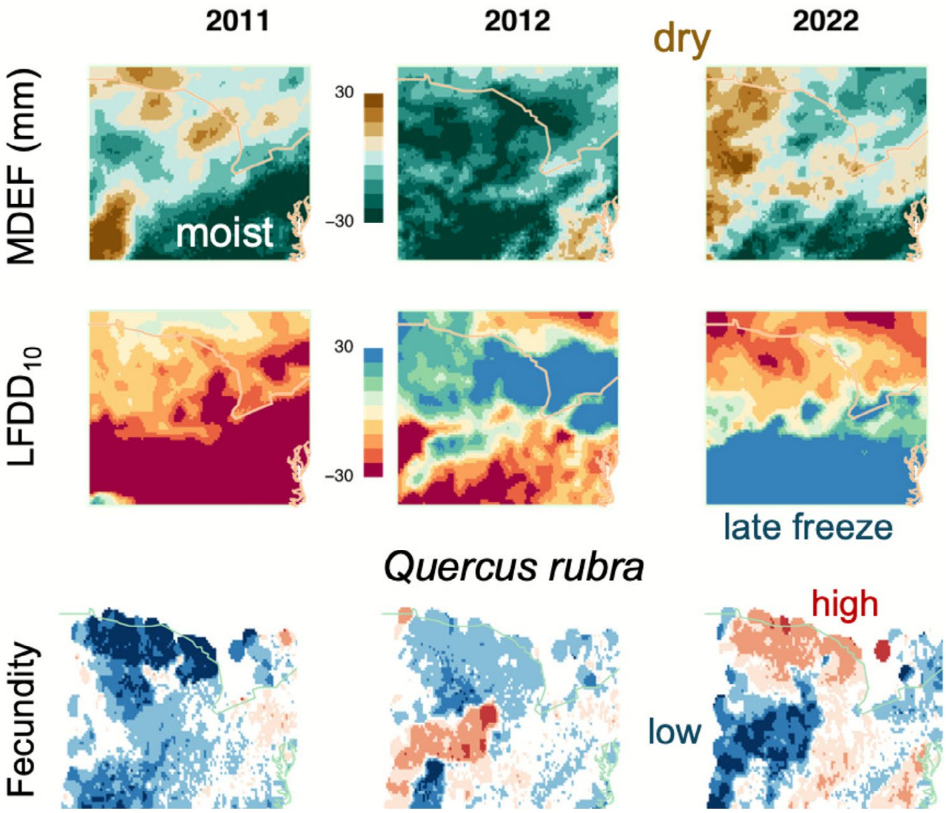

FIGURE 7 | In midwestern North America *Quercus rubra* shows high fecundity (red) mostly associated with moist intervals ($b_{\text{MDEF}} = -0.0377 \pm 0.00216\,\text{mm}^{-1}$; negative MDEF in green). It is weakly sensitive to late freeze that comes early (CD = 10; $b_{\text{LDFF10}} = -0.00178 \pm 0.000767\ \text{DD}^{-1}$; blue LFDD_{10}). In both cases associations are weakened by other variables that also influence fecundity (Table S1). Fecundity maps are local anomalies on a log (proportionate) scale; colors saturate at ±2 SD. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

that is not captured by annual climate anomalies, that is, masting (Equation (1)). For this reason, maps of any one variable are not expected to closely align with fecundity, just as extreme weather is expected to have patchy effects in nature (Augspurger 2013). Annual anomalies in the upper Midwest of North America show shifting combinations of MDEF and LFDD_{10} with *Quercus rubra* fecundity in Figure 7. In addition to being a masting species, *Quercus rubra* fecundity was associated with moist conditions and limited late freeze (negative β_{MDEF} and β_{LDFF}). In addition to MDEF and LFDD_{10} temperature (quadratic terms) and pH (positive) are part of the best fitting model and vary geographically. Combining these influences *Q. rubra* fecundity was low throughout the map in 2011 and most of 2012, despite wet conditions and lack of late freeze. These years were non-mast years (negative anomalies in the year effects for these ecoregions). The year 2012 saw high fecundity in the southwestern portion of the map where moist conditions coincided with lack of late freeze. In 2022 high fecundity in the central portion of the map mostly avoided late freeze that affected the south but included areas of low moisture in the Northwest.

Sensitivity coefficients summarized in Figure 4 (see also a specific example in Figures 7 and S4 for credible intervals) are limited to species that responded to extremes (Table S1) organized by the best-fitting CD (10, 30, 50 days) in Figure 4b. Phylogenetic relationships in sensitivity are highlighted in Figure S9. Crop production for extreme years includes examples for individual species in Figure 8 and the Supplement.

An exposure-tolerance model could describe acclimation and/or adaptation to abiotic extremes like late freeze, with large impacts where exposure has been limited (Figure 2a). This model describes diminishing effects of LFDD that could result from frequent exposure (Figure 4b). However, this general rule plays out differently in the three regions. If the LFDD difference between continents (map inserts to Figure 4b) selected for delayed development in ENA, then long CDs would shorten the time available for fruit development. At the same time, frequent exposure could also select for adaptations that do not suffer the growing-season costs of prolonged delays. The intermediate to long delays estimated for ENA (58% of species for CD = 30, 50) are consistent with high exposure to extremes. A majority of western North America (WNA) species CD = 10 (53%) represents crops that respond to events both early and late. In other words, WNA species are risking the early events, while ENA species delay avoiding early events.

Long delays are estimated from EU data (53% for CD = 50 days), but here the long CD estimate results from near absence of late freeze events in the data (i.e., almost no LFDD). The crop losses from recent LFDD extremes would have occurred even with longer delays because freeze events came so late (e.g., the lack of CD effect on LFDD experienced at Leipzig and Ljubljana in Figure 6). The EU flora that is rarely exposed to late freeze responds to the worst extremes that occur there (right panel in Figure 4b), consistent with widespread orchard losses of the last decade, including examples in Figure 6.

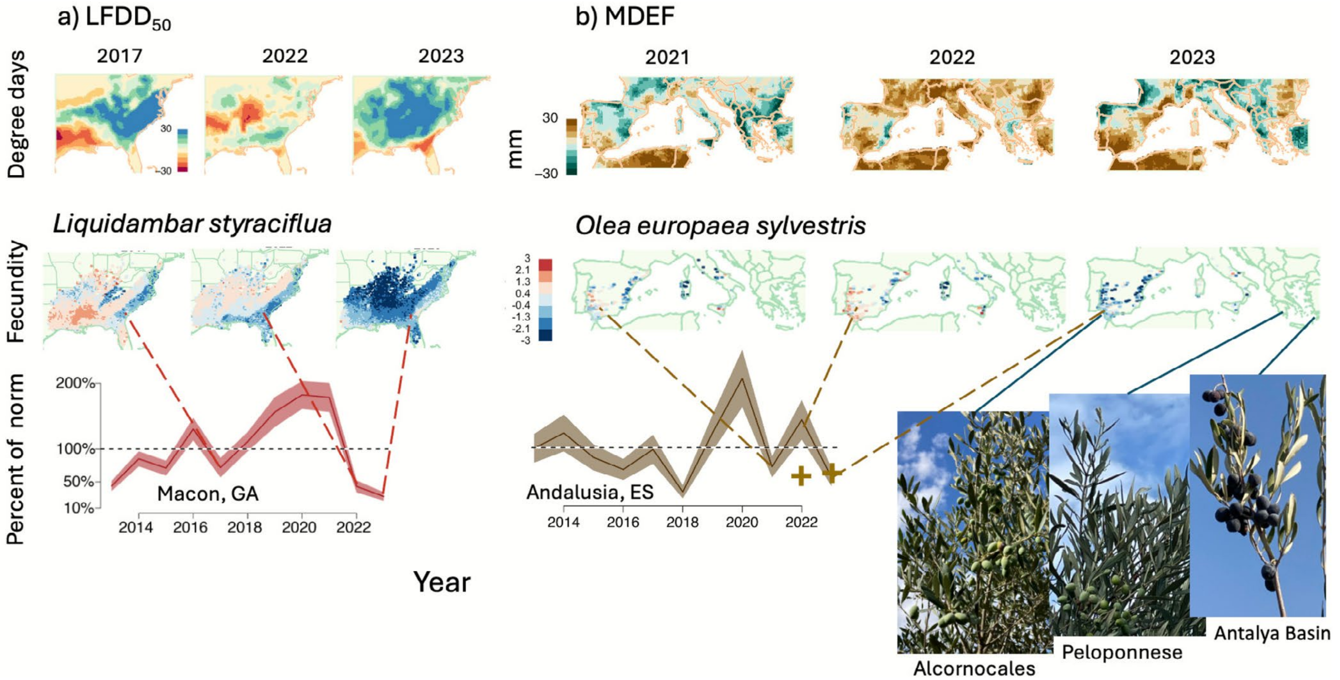

FIGURE 8 | Anomalies associated with commercial losses compared with forests. Examples species show losses in late-freeze years (blue LFDD in a) and drought years (red, brown MDEF in b). Map colors saturate at ±3 SD of the mean on a log (proportionate) scale. Each dot on fecundity maps aggregates seed production (log kg/ha) from inventory plots (Methods). Shaded intervals in time series are 95% for annual crop averages with respect to the mean for both series. (a) Mapped anomalies for sweetgum (*L. styraciflua*) fecundity (center) track mapped LFDD anomalies for the strongest declines in peach-harvest years. (b) Wild olive (*O. europaea sylvestris*) maintains productivity in regions where commercial harvests were hard-hit by drought, with wild crops still above the norm in 2022. Commercial harvests in 2022/2023 are indicated by '+' (Ministerio de Agricultura 2024). Map shading is absent from Greece and Türkiye, which lack inventory data. Photos from three regions of commercial harvest failures show productive wild olive crops in 2023. Map lines delineate study areas and do not necessarily depict accepted national boundaries. [photos JSC].

Large differences in extreme response contribute to niche differences, with some species succeeding where others suffer. Not all commercial crops respond alike, so it is not surprising that wild populations range widely in sensitivity (Figures 4 and S4). These differential species responses reduce covariation between the crops of competing species, focusing competition for disperser mutualists and regeneration sites within rather than between co-occurring species (Clark 2010).

3.4 | Drought Stimulates and Suppresses Seed Production

Consistent with its role as an essential resource, moisture deficit (MDEF) anomalies have impact only for species from regions where moisture is limiting, that is, with high MDEF norms in Figure 4a. The large responses in dry environments are positive for some species and negative for others. Where credible intervals include zero MDEF contributes to the variation in fecundity (it is retained in the best-fitting model), but not in a simple way. An exposure-reaction model allows impacts that are potentially positive or negative (Figure 2b). Positive or negative responses can depend on dynamic allocation to reproduction relative to other activities affected directly and indirectly by moisture and carbon stress at high deficits. Where moisture limitation is frequent, losses during extremes could be minimized by dynamic cutbacks in demand, such as abortion while fruits are small (Figure 1). Because moisture effects on allocation can lag, extremes that reduce growth and/or defense could trade off with fecundity (Berdanier and Clark 2016), producing positive or negative responses in the same or future years. The fact that drought-induced mortality is increasing globally suggests that extremes have already reached the point where allocation tradeoffs are often not enough to avoid lethal effects.

3.5 | Trait Differences or Recent Exposure?

Whether by acclimation or adaptive evolution (Merilä and Hendry 2014), the extreme responses in this study (Figure 4) have developed in ways that could not be inferred from commonly measured traits or phylogenetic distance. We examined traits that are relevant for tree fecundity (fruit type, dispersal and pollination vectors, leaf habit, and dioecy (Qiu et al. 2023)). For these commonly measured traits, we might expect that large seeds, especially moisture-demanding fleshy fruits and nuts, could be particularly prone to extreme drought (Gucci et al. 2009). In this study of 298 species, none of these traits are associated with responses to extremes (Figure S6).

Unlike the commonly measured traits in ecological studies, which tend to be phylogenetically conserved, responses to extremes are not (Table S2, Figure S7). Our study could only include the 298 species that were sufficiently abundant to allow parameter estimates (Table S1). If much of the adaptation to extremes is not observable as measurable traits, then phylogenetic distance might still offer insight on divergent extreme responses. If adaptations accumulate as populations diverge, then distantly related species might show the largest differences in response. Species in this study trace their ancestry to high-latitude early Cenozoic forests that moved south with cooling climates and progressive isolation by the spreading Atlantic Ocean (EU from ENA) and aridification in the North American interior (WNA from ENA). Many genera remain extant in all three floras even as speciation and extinctions changed the composition and diversity of these genera. As biotic and abiotic conditions subjected populations to novel combinations of extreme climate, adaptations could diverge over time. All else being equal, species differences in their capacities to tolerate extremes might be associated with relatedness, suggesting phylogenetic distance as a surrogate for adaptations that are unobserved. Despite the large number of species with wide-ranging phylogenetic distances within and between continents, there is no association between extreme response and relatedness, in aggregate or at the family level; only four of 12 family-level correlations differ from zero, and two of those are negative. There is strong phylogenetic signal in traditional traits, but not in sensitivities to climate extremes (Table S3).

4 | Discussion

As escalating climate anomalies devastate even the commercial orchards that benefit from mitigation efforts, the impacts on forest fecundity threaten to slow or divert recovery from increasing climate-related diebacks. This analysis shows that entire regions are responding to late-freeze events that can be linked to their differential sensitivities.

The continental contrasts in LFDD effects are larger than expected from traditional climate metrics like growing degree days: much of North American forests are subject to a high background of late freeze, while EU is experiencing late freeze as novel. Because these recent events are both late and intense, chilling delays that would reduce risk in North America may not be enough to protect against damage in either continent.

Despite the massive data synthesis, results are limited by coverage of the important environmental gradients and individual condition. Accurate interpretations rely on the observation space in species × size/age × competition × soils × climates. Because there is a spatial scale associated with masting, there is additional need for geographic coverage. Current data do not offer requisite coverage for important variables for many species (Table S1). Fortunately, accumulation of data, which is occurring not only through collaborators but also the iNaturalist project MASTIF (Clark 2019), will continue to expand the variable space that can be evaluated for more species.

The fact that most EU species are best described by the largest CD value (50 days, Figure 4b) could result from the paucity of freeze events after spring development begins. For a species to respond at a CD level, there must be years when events occur after that CD lag and years when they do not. Then there must also be a difference between fecundity in those event and non-event years. Where both happen (events and non-events associated with different fecundity levels) the LFDD model can be identified. Historically, late freeze has not been a part of spring development in EU, and selection between lag values may simply default to the longest value. As data accumulate now that late freeze is increasingly common, the effects in EU may clarify.

Northern hemisphere forests sharing a common ancestry are responding to intensifying extremes in different ways. The 18th century mystery surrounding transplants to Europe may be explained by the extremes that have been the norm in North America, but rare in Europe. Trees transplanted from North America, where late freeze is common, to Europe, where it is rare, could be expected to delay development. Acclimation of these transplants to the European climate might change timing to allow successful fruiting.

Are forests suffering the extreme crop losses documented in orchard practice? Commercial harvests report aggregate yields for municipalities, often as percent losses. The balanced distribution of inventory plots allows us to aggregate individual trees to area-based responses that are comparable with crop statistics. Georgia's 90% peach crop destruction from 2023 late freeze, or 10% of the norm, is comparable to wild *Liquidambar styraciflua* in the same location and year (Figure 8a). However, the maps for *L. styraciflua* differ from mapped LFDD (Figure 8a), which is only one of many influences that affect species in different ways (see also Figures 7, S10, and S11). By contrast, the small-fruited wild olive (*Olea europaea sylvestris*) crop did not suffer to the same degree as the widely publicized commercial olive losses from 2021 to 2023 in Andalusia and other parts of the Mediterranean (Figure 8b). Despite some fluctuations in these years, 2021 was an average year, and 2022 was above average for wild olive. Not until 2023 did the wild-crop yield dip below average. Future studies can exploit this approach to examine commonalities between forest and agricultural impacts.

Wide variation in species responses is not predicted by the trait differences that are typically included in ecological studies. There are clear adaptations to freezing and moisture deficit (Figure 1), many of which are phylogenetically conserved. Despite this, the extreme responses observed here are differentiated by region (Figure 6) rather than by observable traits (Figure S6) or phylogeny (Table S2). The traits that can be observed may not predict responses that are subject to strong and localized selection on metabolic pathways that respond more rapidly than structural traits measured in the field. The evidence for local adaptation in common garden experiments is still limited to few sites and predominantly commercial species, but is broadly consistent with the potential for rapid, local adaptation (Alberto et al. 2013). A small number of genes can determine cold tolerance, and some of the same genes are involved in drought adaptation (Alberto et al. 2013; Thomashow 1999); they are not associated with observable traits like those available from ecological studies. Although trees are long-lived, remarkably high fecundity variation between individuals of a species within the same habitat (Clark et al. 2004; Greenberg 2000) suggests high genetic variation and potential for rapid response to selection (Savolainen and

Pyhäjärvi 2007; Scotti et al. 2023; Skrøppa et al. 2010), fueled by heritable somatic mutations (Hanlon et al. 2019) and low linkage disequilibrium in trees (Alberto et al. 2013). Naturalization of North American transplants to Europe (e.g., *Quercus rubra, Robinia pseudoacacia, Acer negundo, Tsuga heterophylla, Picea sitchensis*) further supports acclimation or rapid adaptation.

The implications of extremes for forest recovery are expected to amplify over time. Crop loss to one drought or late freeze does not in itself represent a threat, because reproductive effort can sometimes be transferred to future years. Low-moisture years affect reproduction primarily in dry areas, but the limited response in mesic areas could be transient as extremes intensify. Species adapted to low-moisture can shed buds and developing fruit as an avoidance mechanism that spares resources for future reproduction (Stephenson 1981). For the species that have thus far avoided the effects of intensifying extremes, this avoidance cannot be indefinite. As drying continues, the moisture-demanding species currently restricted to mesic sites could become most vulnerable.

The fact that climate extremes destroying commercial harvests are having wide-ranging impacts on forest fecundity (Figures 4 and S10) is unsurprising given their close relationships with orchard species or wild progenitors that remain common in the forests of both continents. Eurasian origins include plum, pear, apple, citrus, cherry species, apricot, peach, persimmon, pomegranate, quince, fig, olive, pistachio, walnut, and almond. North American origins include pecan and avocado. Orchard crops have spread and naturalized in surrounding forests (e.g., apple, plum, fig, walnut). Wild and feral populations occur alongside orchards of the same species (e.g., sweet cherry, pomegranate, olive, walnut). Despite continuing introgression from wild genetic pools (Julca et al. 2020), domestic olive is suffering losses that are not yet evident in wild populations from the same regions (Figure 8). Large, moisture demanding fruit of the domestic crop may explain some of this difference (Gucci et al. 2009). Orchard practice raises awareness of the expanding risks, highlighting the need for monitoring fecundity in forests.

The climate anomalies experienced by forests in this study (Figure S1) are continuing and the start of intensifying extremes to come (Wu et al. 2023). The broad similarities between North American and western Eurasian forests, supporting most of the same genera, could foster the expectation that they would respond similarly to apparently similar changes in extremes. This study finds that species responses to extremes now are associated with where they live and not clearly tied to membership in a phylogenetic group. Whether or not rapid local adaptation has buffered fitness against the extremes through 2023, the magnitude of these effects suggests local adaptation as a transient solution as extremes intensify.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Code is available in R package MASTIF on CRAN. Data are deposited at https://doi.org/10.7924/r42v2t66k.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Mapped norms and trends in LFDD (degree days) for three chilling delay values and moisture deficit (mm). **Figure S2:** Species summary by genus and family. **Figure S3:** Broad climate space in North America has especially large coverage at high LFDD. **Figure S4:** Sensitivity of seed production (proportionate mass per tree-year) to annual anomalies. **Figure S5:** Densities taken over all species corresponding to coefficients in Figure S4. **Figure S6:** Cross validation shown as prediction for holdouts versus observed for *Liriodendron tulipifera* at 148 locations in Duke Forest. **Figure S7:** Out-of-sample prediction errors plotted against the predictive mean. **Figure S8:** Trait correlations with sensitivity to climate anomalies. **Figure S9:** Response to extreme anomalies, shown as barplots, do not show phylogenetic structure, including defAnom (MDEF, outer), LFDD50Anom, LFDD30Anom, LFDD50Anom. **Figure S10:** Dry anomalies in ENA (brown MDEF) associate with low fecundity (blue) in *Acer rubrum* and *A. saccharum* (above) and, in EU, with high (red) *A. platanoides* and *A. pseudoplatanus* (below). **Figure S11:** Dry or late-freeze anomalies in ENA and EU for MDEF and LFDD associate with low fecundity (blue) in *Fagus grandifolia* in ENA and F. sylvatica in EU. MDEF and LFDD color maps saturate at ±30 mm and DD, respectively. **Table S1:** Number of species (298 total) with each predictor included in the model and those that are different from zero (see Methods). **Table S2:** Late-freeze events at Warner Robins, GA in 2023. **Table S3:** Phylogenetic signal for five indices, with significant values ($p < 0.05$) in bold font. **Table S4:** File fitlog.csv. Rows are organized by genus and region and then by lowest DIC weighted. **Table S5:** Files parEst.csv and parSE.csv. Posterior mean estimates and standard errors.