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RESEARCH ARTICLE

The Importance of Tree Regeneration for Maintaining Mountain Forest Ecosystem Services Under Global Change

Fecundity and terrain-climate interactions that shape tree niche differences across North America and Europe

Lauren Jenkins[1] | Taylar Bankston[2] | Miao Hu[1] | Inés Ibáñez[3] | Roland Kays[4,5] | Georges Kunstler[6] | Jordan Luongo[1] | Sierra McMurry[5] | Kira Meyer[1] | Emily V. Moran[7] | Miranda D. Redmond[2] | Chantal D. Reid[1] | Tong Qiu[1] | Shiqi Zheng[1] | James S. Clark[1,8]

[1]Nicholas School of the Environment, Duke University, Durham, North Carolina, USA; [2]Department of Environmental Science, Policy and Management, UC Berkeley, Berkeley, California, USA; [3]School for Environment and Sustainability, University of Michigan, Ann Arbor, Michigan, USA; [4]North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA; [5]Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, North Carolina, USA; [6]UR LESSEM, Université Grenoble Alpes, INRAE, Saint-Martin-d'Hères, France; [7]Department of Life and Environmental Sciences, UC Merced, Merced, California, USA and [8]Department of Statistical Science, Duke University, Durham, North Carolina, USA

Correspondence
Lauren Jenkins
Email: lauren.jenkins@duke.edu

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Abstract

1. If niche differences contribute to biodiversity, then landscapes must vary and species must respond differently to that variation. Terrain, through its effects on solar radiation and moisture, is an important contributor to habitat variation, but its effects on demography are largely unknown. Understanding fecundity responses to this landscape heterogeneity could provide insights on niche differences and on how terrain buffers climate change effects. Here, we use a hierarchical Bayesian state-space model to quantify how topographic features buffer tree fecundity from intensifying climate change. We estimate the effects of slope, aspect and drainage on tree fecundity across North America and Europe while accounting for individual condition and climate.
2. We analysed 2,874,955 tree-years from 292 species across forest inventory plots spanning mountainous regions in North America and Europe. We fitted species-specific fecundity responses to terrain variables and climate interactions, then constructed predictive distributions of terrain effects at landscape scales. We quantified community-level hypervolume to assess how diversity in fecundity responses across species relates to topographic heterogeneity.
3. Topography influences tree fecundity, with terrain as an important contributor for most species. In dry portions of their ranges, tree species in southeastern North America and south-central Europe increase fecundity towards northeast aspects, while highest fecundity of species in southwestern North America shifts towards south-facing aspects. Terrain-sensitive species (terrain explains >20% of fecundity variance) are most abundant in southwestern North America (~42% of species), but southeastern North America shows the strongest terrain effects on

fecundity and highest per-species fecundity variance, despite having the gentlest slopes. Community hypervolume is exceptionally high in southeastern United States. Whether this variation maintains diversity depends on how fecundity combines with other demographic rates.

4. *Synthesis*: Fine-scale terrain variation creates reproductive differences through species-specific fecundity responses. The effectiveness of topographic heterogeneity as a climate refuge depends on regional landscape structure and species sensitivity to terrain. In topographically diverse regions, species may buffer climate change through fine-scale redistribution to favourable microsites. Quantifying these differences helps identify factors limiting reproduction and habitat features with greatest potential as local refuges.

KEYWORDS
aspect, forest biodiversity, global change ecology, slope, terrain climate interactions, topographic refugia, tree fecundity

1 | INTRODUCTION

Landscape biodiversity is shaped by environmental variation that drives population dynamics and can allow for niche partitioning among species. Of the three demographic rates, growth, survival and fecundity, forest ecologists have traditionally overlooked fecundity, focusing instead on the first two (but see Grubb, 1977; Hille Ris Lambers & Clark, 2003). Growth responses are documented across light gradients, nutrient availability and water stress (Allen et al., 2015; Poorter et al., 2019). Survival differences can emerge in response to drought, extreme temperature, fire and pathogen pressure (Allen et al., 2015; Bagchi et al., 2010; Davis et al., 2019; Schwantes et al., 2017; Swinfield et al., 2012). The regeneration niche, from seed production through dispersal, germination and seedling establishment, is a foundation for population success (Clark et al., 1998; Grubb, 1977; Ward et al., 2025), yet the contribution of fecundity to species differences remains largely unknown despite growing evidence from continent-wide data synthesis that it responds to environmental gradients (Clark et al., 2021, 2026a, 2026b). Here, we synthesize tree fecundity across montane regions of North American and Europe to assess how terrain-climate interactions shape reproductive niches and species diversity.

Terrain analysis is defined here as the translation of species responses to terrain, as fitted distributions, to landscapes that differ in environmental variation they offer, as predictive distributions. Slope and orientation (aspect) of the Earth's surface control solar radiation available for photosynthesis and, along with drainage, determine moisture availability through their effects on evaporative demand (Ackerly et al., 2020; Dobrowski, 2011; Fridley, 2009; Pradhan et al., 2023; Whittaker, 1956; Figure 1a). If a demographic rate is limited by moisture in dry climates and by solar radiation in wet climates (Nemani et al., 2003), then terrain can potentially mediate climate effects. In the Northern Hemisphere, south-facing slopes receive high solar radiation, stimulating the radiation-limited trees that can be especially common in wet climates. Southwest aspects have high radiation late in the day, when soil moisture is drawn down and stomata close (Måren et al., 2015); this late-day drying raises leaf temperatures, increases heat stress (Buckley, 2005; Urban et al., 2017; Wang et al., 2026) and reduces nitrogen availability (Clark, 1990). In dry climates, northeast exposures with high moisture and protection from heat stress may offer microclimatic refuge (Figure 1b). Topographic position further influences drainage, from dry ridgelines to moist coves and bottomlands (Whittaker, 1956), as well as snow depth and duration and soil properties (Ford & Hille Ris Lambers, 2020). Together, these terrain properties can affect vegetation cover and composition (Choler et al., 2025), even in regions with modest relief (Oosting, 1942; Figure 1a). As such, we use terrain analysis to quantify the fecundity effects of slope, aspect, topographic position and interactions with climate.

Whether terrain effects impact tree fecundity, and how they interact with climate, motivates three hypotheses: (1) species responses to slope and aspect go beyond the traditional N–S (or NE–SW) dichotomy due to multiple limitations from moisture, light and heat stress, (2) responses to terrain can shift from heat stress and moisture limitation in dry climates to radiation limitation in moist climates and (3) regions of high species diversity align with high response diversity, providing the foundation for broad exploitation of niche space. Because trees can experience different limitations across seasons, the 'optimal' solar exposure need not align strictly with N–S (or NE–SW) aspects but may instead favour intermediate aspects that balance these competing limitations (Hypothesis 1). For this reason, terrain analysis includes a slope × aspect interaction. Because the influence of solar exposure on tree performance can shift with climate (Ackerly et al., 2020; Verbyla & Fisher, 1989), we also use a three-way interaction between moisture deficit × slope × aspect (Hypothesis 2).

If fecundity contributes to niche differentiation and thus diversity (Hypothesis 3), then (i) terrain must offer environmental

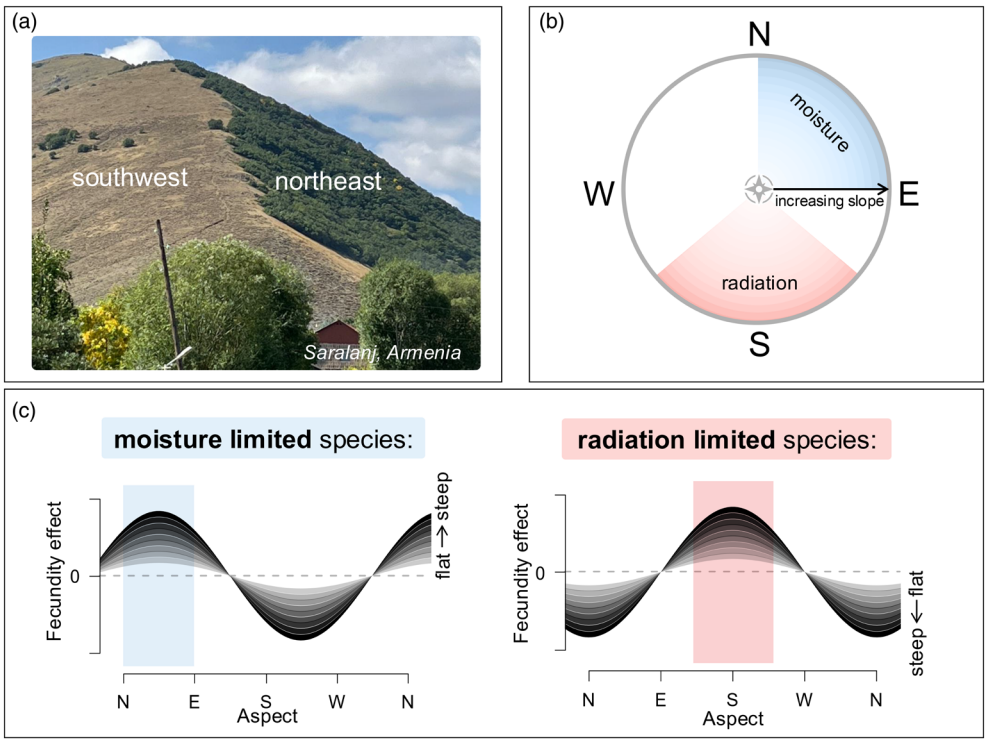

FIGURE 1 Influence of aspect on solar radiation, heat stress and moisture availability, and hypothesized fecundity effects. (a) Saralanj, Armenia, showing vegetation differences on northeast (right) and southwest exposures (left). (b) In the Northern Hemisphere, northeast aspects receive low insolation and retain moisture (inset blue), while south aspects receive high insolation (inset red). Aspect effects are most intense on steep slopes (distance from the origin). (c) Species limited by moisture and/or heat stress in a dry climate (left) may reach high fecundity on cool, moist northeast aspects (inset blue). Species limited by radiation in a moist climate (right) may show high fecundity on south aspects (inset red). Hypothesized effects increase with steepness, where darker shading indicates steeper slopes. Image credit: James S. Clark.

variation (E) and (ii) species must respond (R) differently to that variation through their demographic rates. However, simply showing that species differ in their demographic responses to the environment (R) is not enough to demonstrate that those differences are meaningful. Additionally, the mere presence of environmental variation (E) does not by itself establish that species exploit it in different ways. To properly assess this, terrain analysis combines environmental variation (E)×response (R), or E×R. E×R is high when terrain variation is high, and species have divergent and strong responses to that variation. We use community hypervolume H_E (Clark, 2016), a measure of environmental space that the community of species exploits, to quantify how E×R differs between mountainous regions that support different levels of species diversity.

The interactions between climate and terrain have direct application to contemporary climate changes. For example, with increasing aridity, maximum reproduction of moisture-demanding species could shift to northeast exposures, while heat-tolerant species persist on southern exposures. Many species could become increasingly reliant on local topographic features such as cool pockets and drainage areas. Local adaptation, which can be rapid in trees despite long lifespans (Aitken et al., 2008; Alberto et al., 2013; Sekely et al., 2024), can lead to fine-scale genetic differences across varying terrain (Eckert et al., 2015), potentially reinforcing fecundity-based differentiation patterns.

This synthesis of tree fecundity across North America and Europe provides the first quantitative assessment of how terrain-climate interactions influence fecundity while accounting for individual condition (species, size, canopy exposure). Such community-level patterns emerge from evolutionary patterns that have shaped each region's flora differently. Contemporary differences in diversity across these regions reflect a shared but divergent evolutionary history rooted in Palaeocene/Eocene circumpolar forests (Axelrod, 1983). Woody plant genera largely overlap across continents, while the species in those genera have diverged. Species-level divergence occurred as global cooling and drying forced populations to lower latitudes where they were isolated by a widening north Atlantic Ocean and aridifying North American interior (Axelrod, 1958; Basinger et al., 1994; Loidi Arregui & Marcenò, 2022). Geographic isolation, along with distinct regional climate and terrain, contributed to the regional differences in modern tree diversity. Contrasting relief between our study regions in North America and Europe suggests evolutionary opportunities for divergent fecundity responses.

Terrain variation both within and between continents allows comparisons of closely related species responses to diverse terrain-climate interactions. Unlike most terrain studies, effects of slope and aspect are directly fitted to data, not assumed to operate in a specific orientation (e.g. north–south/east–west) (Clark, 1990; Clark et al., 2021). The formal interaction between climate, slope

and aspect provides estimates that can be directly integrated into predictive models, including models of future climate change. To address our three hypotheses, we evaluate (i) the prevalence, magnitude and direction of fecundity responses to terrain across species, (ii) how these responses vary across regions that differ in climate and topographic complexity and (iii) regional contrasts in community-wide hypervolume of responses.

2 | STUDY REGIONS

Our study regions encompass montane woody vegetation across North America and Europe, providing broad geographic and taxonomic coverage. In North America, well-sampled montane areas include the Appalachians, Sierra Nevada, Cascades and Rocky Mountains, while European coverage spans the Pyrenees, western Baetic Cordilleras (Andalusia), Alps and northern Balkan Peninsula. Sampled areas represent a range of climates, from wet-temperate to temperate mixed forests, dry steppe, Mediterranean scrub, boreal forests and alpine treelines. From the two continents, we compare terrain analysis from three regions with differing species diversity: southwestern North America (SWNA), southeastern North America (SENA) and south-central Europe (SCEU) (Figure 2).

The three terrain analysis regions differ in species diversity but overlap in climate space. Vegetation is dominated by temperate forests (SENA, SCEU), scrublands (SWNA, SCEU) and montane forests (all regions) (Figure 2). Climates with woody vegetation overlap between North America and Europe, though North American deserts are excluded due to the lack of woody plants. SENA receives high rainfall and supports mixed conifer and hardwood forests from the coastal plain to montane zones. SWNA and SCEU both span low-elevation winter-rain (Mediterranean) climates, with vegetation ranging from shrublands to mixed conifer and deciduous forests to alpine zones. Both continents are warming rapidly, though changes in moisture have been heterogeneous (Clark et al., 2026a, 2026b). Of the three regions, SENA supports the highest species richness and Shannon diversity, while SWNA and SCEU show lower and more similar diversity levels despite differing in richness (Table 1; full species list is provided in Table S1).

All three regions show increasing terrain heterogeneity (Equation S4b) with elevation (Figure 3). SWNA exhibits the most equitable distributions of slope, aspect and topographic position, including the rugged Sierra Nevada with elevations exceeding 3000 m. Slope grid averages are from 0.2 to 0.4 m/m across all aspects (Figure 3, top row). Topographic position values, broadly distributed around zero, indicate a mix of ridges, valleys and intermediate slope positions (Figure 3a). Slopes are not uniformly distributed across aspects (Figure 3b). By contrast, SENA has maximum elevations near 1000 m, comparatively shallow slopes (grid averages from 0 to 0.2 m/m) and topographic position values clustered near zero. Steepest slopes dominate southeast aspects (Figure 3, middle row). Like SWNA, SCEU extends to 3000 m in elevation, but topographic position is variable and positively skewed due to extensive forelands below 1000 m. Shallow slopes dominate north aspects (Figure 3, bottom row).

3 | METHODS

The study includes three elements (Figure 4): (1) data on fecundity and predictors, (2) model fitting to estimate sensitivity to terrain-climate interactions and (3) translating the fitted model to inventory plots as

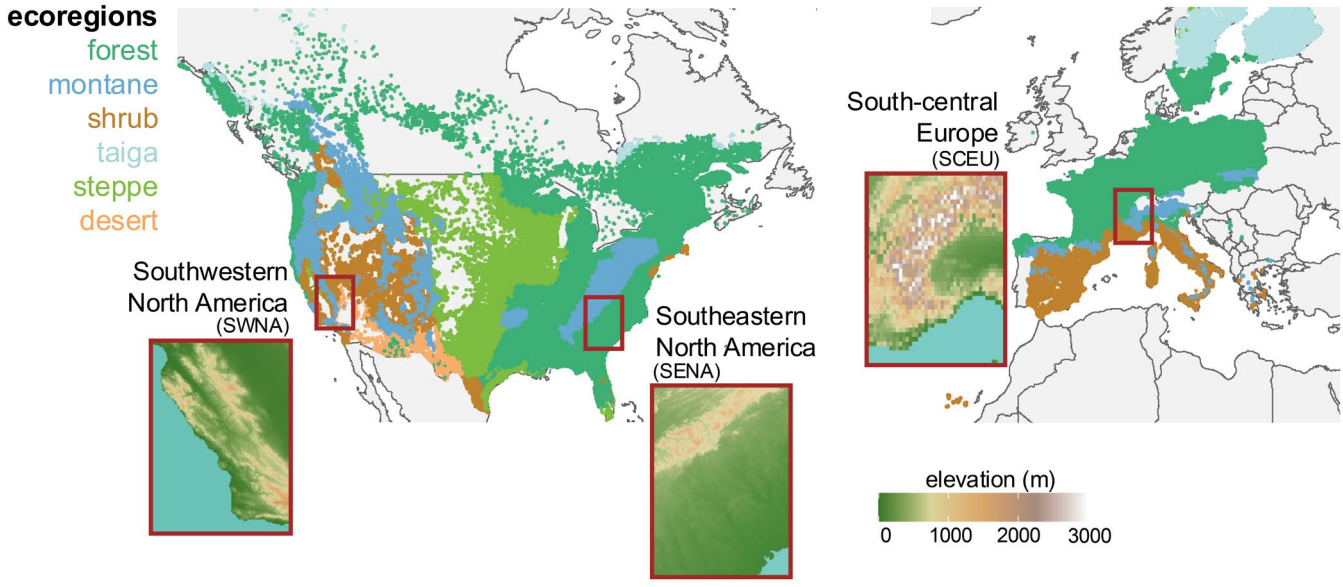

FIGURE 2 Forest inventory plots and ecoregions across North America and Europe. Each dot represents an inventory plot, highlighting ecoregions. Insets show elevation for three terrain analysis regions: Southwestern North America (SWNA), southeastern North America (SENA) and south-central Europe (SCEU). Unshaded areas indicate either absence of forests (e.g. California's Central Valley, Italy's Piedmont) or lack of available inventory plot data (e.g. United Kingdom, Netherlands, Switzerland, Austria, Portugal and eastern European countries).

TABLE 1 Summary of study and terrain analysis regions in Figure 2. Mean and median values include 80th percentile (0.1, 0.9) in parentheses, evaluated over locations and species.

	Species		Terrain	
Study region	Richness[a]	Diversity[b]	Model variance[c]	Terrain fraction[d]
Southwestern North America	77	1.49 (1, 3.83)	0 (0, 6.39)	0.0571 (0.026, 0.494)
Southeastern North America	206	3.62 (1, 8.67)	3.84 (0.144, 34.5)	0.0454 (0, 0.265)
South-central Europe	156	1.66 (1, 3.80)	1.13 (0, 3.91)	0.0432 (0, 0.176)

[a]Number of tree species on inventory plots within the region.

[b]Mean Shannon–Wiener diversity per inventory plot.

[c]Median value across species and grid cells for terrain analysis region ($V_{k,z}$; Equation S4a). Zeros at SWNA reflects the Central Valley and arid lands east of the Sierra Nevada, where tree cover is sparse.

[d]Median value across species and grid cells for terrain analysis region ($v_{k,z}$; Equation S4b).

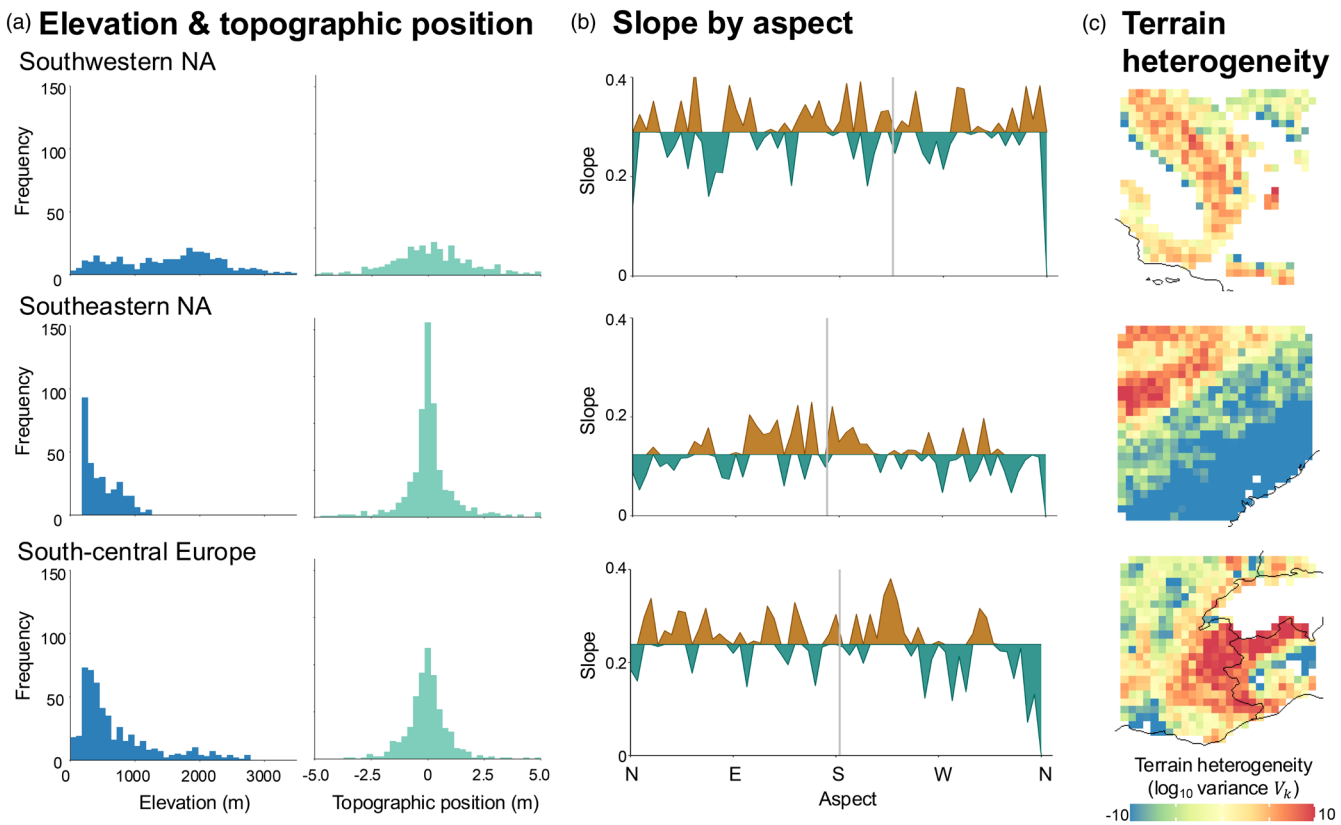

FIGURE 3 Terrain attributes for the three terrain analysis regions in Figure 2. (a) Distribution of elevation and topographic position (TPI). (b) Mean slope by aspect; brown/teal shading shows departures from regional mean slope. (c) Three regions from inset maps in Figure 2 showing terrain heterogeneity ($\log_{10}$ variance V_k; Equation S4a) calculated from topographic covariance of the six nearest inventory plots and lattice points for each 0.2°×0.2° grid cell. Values range from low heterogeneity (blue) to high heterogeneity (red). Forest inventory data are lacking for Switzerland and non-forest regions of Southwestern North America (SWNA).

predictive distributions. Step 3 includes terrain analysis to quantify associations between E×R and species diversity across three example regions in North America and Europe (Figure 2).

3.1 | Data

Fecundity analysis is restricted to data that reference seed produced by a tree each year. Two complementary data types come from the Masting Inference and Forecasting (MASTIF) network: seed traps (ST) and crop counts (CC). We exclude studies based on ordinal summaries (e.g. 'low', 'medium', 'high') or seed counts per unit time, the latter bearing a non-linear relationship with actual seed production (the higher the production, the smaller the fraction counted). We also do not convert raw seed-trap counts directly into estimates of seed production per area (seed count per trap divided by trap area), as these are dominated by contributions from a few nearby trees and therefore do not represent stand-level production. Instead, ST data used in

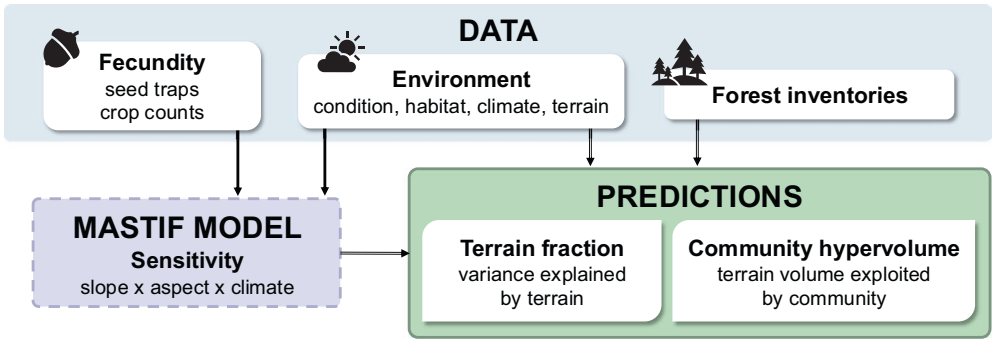

FIGURE 4 Workflow begins with three data streams (top, blue) through model fitting (left, purple), which quantifies sensitivity, and informs predictive distributions and community hypervolume (right, green). Sensitivity coefficients (left, purple) are combined with forest inventories to obtain fecundity predictions for each tree (right, green). Terrain fraction integrates sensitivity with landscape variability to determine the terrain contribution to fecundity. Community hypervolume quantifies niche volume occupied by the community.

MASTIF come from mapped inventory plots where seed production is modelled from tree condition, environment, tree-to-trap distance and identification errors (Clark et al., 2004, 2019; Moran & Clark, 2011; Muller-Landau et al., 2008). CC observations are both longitudinal and opportunistic, including through the iNaturalist project MASTIF. A CC observation consists of fruit counts recorded with an estimate of the fraction of the entire crop observed, or crop fraction (CF). The data model for a CC observation is beta-binomial for the probability of a seed count given the true seed production. The model accommodates censored data for both ST and CC counts (Bourg et al., 2013).

Predictors include individual condition, climate and terrain (Table 2). Individual condition variables include species, tree diameter and shade class determined by crowding from neighbours. Climate variables include temperature, moisture deficit and late-freeze degree days (LFDD). To isolate the associations with site and interannual variation, all three climate variables are represented in the model as both location norms and annual anomalies (Clark et al., 2014; Table 2). Moisture deficit is calculated as the cumulative monthly difference between potential evapotranspiration and precipitation from the previous year through current-year fruit development. LFDD captures the non-linear effects of late spring freeze on flower and fruit development (Clark et al., 2026a, 2026b; Supporting Information). These climate variables do not capture fine-scale topographic effects, which are instead modelled directly through terrain variables.

Terrain variables capture topographic effects through slope, aspect and their interactions with moisture deficit. Terrain data come from the NASA Shuttle Radar Topography Mission (SRTM) 30-meter digital elevation model (DEM) (Farr et al., 2007), supplemented with the USGS National Elevation Dataset for areas beyond SRTM coverage (Gesch, 2002). Landscapes vary in slope s (m/m), aspect a (radians in polar coordinates) and topographic position p (elevation relative to the mean for the surrounding 600 m radius). Because aspect can influence fecundity through insolation, heat load and wind exposure, its effects may deviate from a simple north–south (or NE–SW) gradient. We therefore fit aspect effects directly to

TABLE 2 Predictors used to fit the Masting Inference and Forecasting (MASTIF) model and their data sources. Subscripts denote tree i, site j and year t. Norms are calculated for the 15-year period from 2010 to 2024. Annual anomalies are indicated by superscript a. Variable selection results in a species-specific subset of these predictors. Late freeze (L) is detailed in Clark et al. (2026a, 2026b).

Predictor	Units	Data source
Tree diameter ($G_{ij,t}$, $G^2_{ij,t}$)	cm, cm^2	MASTIF[a]
Shade class ($B_{ij,t}$)	Class 1–5	
Moisture deficit norm (d_j)	mm	terraClimate,[b] CHELSA[c]
Deficit anomaly ($d^a_{j,t}$)		
Temperature norm (T_j, T^2_j)	°C	
Temperature anomaly ($T^a_{j,t}$)		
Late freeze norm (L_j)	DD	Daymet,[d] ECAD[e]
Late freeze anomaly ($L^a_{j,t}$)		
pH$_j$ (0–30 cm)	Log concentration	soilgrid250m[f]
Slope (s_i)	m/m	DEM[g]
Slope × Aspect[h]	m/m	
Slope × Aspect × Deficit[i]	m/m × mm	
Topographic position (p_i)	m	
Ecoregion (for year effects)	Categorical	World Wildlife Fund[j]

[a]Clark et al. (2021).
[b]Abatzoglou et al. (2018).
[c]Karger et al. (2017).
[d]Thornton et al. (2022).
[e]Cornes et al. (2018).
[f]Poggio et al. (2021).
[g]Gesch (2002).
[h]Two terms: $(\sin a_i, \cos a_i)s_i$, see Supporting Information.
[i]Two more terms: $(\sin a_i, \cos a_i)s_i d_j$.
[j]Olson et al. (2001), ecoregions reference year effects (Equation 1).

data (Clark, 1990) rather than assuming a fixed orientation (see Supporting Information).

3.2 | Model fitting

The MASTIF hierarchical Bayesian state-space model used to obtain estimates is detailed in previous publications (Clark et al., 2019, 2021). The analysis includes 2,874,955 tree-years from 292 species in North America and Europe (Table S2). For each species, predictors were initially filtered for coverage and then for Variance Inflation Factors less than 10. Slope-weighted aspect distributions were inspected for inclusion in terrain analysis (Table S1), as the contribution of an aspect observation increases with its slope. Variable selection was by lowest DIC.

The MASTIF model accounts for three sources of zeros from fecundity data: (1) a tree is immature, (2) a tree is male (dioecious species) or (3) conditional fecundity for a mature individual does not exceed the threshold represented by one fruiting structure. These 'failed' seed crops are common across many species. Maturation status is modelled as a function of diameter (Clark et al., 2019).

Conditional on mature status, fecundity of a mature individual i depends on tree condition, climate and terrain as follows:

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

Here, $f_{ij,t}$ is fecundity conditional on maturation for tree i at location j in year t, $\mathbf{x}_{ij,t}$ is a vector of predictors with corresponding coefficients $\boldsymbol{\beta}$, $\alpha_{i,j}$is a random individual effect, $\gamma_{j[r],t}$ is a year effect for trees within ecoregion r, and $\epsilon_{ij,t}$ is Gaussian error. The row vector $\mathbf{x}'$ is the transpose of $\mathbf{x}$. The year effect captures shared variation among trees not attributed to other predictors, including climate, which is particularly important for masting species where synchronous reproduction across individuals can otherwise inflate apparent climate signals (Clark et al., 2019; Qiu et al., 2023).

Terrain effects are modelled explicitly through topographic position, slope, slope × aspect and slope × aspect × moisture deficit. The *terrain function* ($U(s_i, a_i)$) is:

$$\mathbf{x}_{ij,t} = \ldots + U(s_i, a_i)$$

$$U(s_i, a_i) = s_i\left[\beta_s + \beta_{a_1}\sin(a_i) + \beta_{a_2}\cos(a_i)\right] \quad (2)$$

for slope s (m/m) and aspect a, where the ellipsis represents the intercept and other model predictors (Clark, 1990). Each term of the terrain function has the log fecundity scale (Equation 1). Aspect $a \in (0, 2\pi)$ is taken on standard polar coordinates, counterclockwise from east. Importantly, aspect cannot have a main effect because flat terrain (zero slope) has no aspect; aspect only exists as an interaction with slope. A slope effect ($\beta_s \neq 0$) can be positive (high fecundity on steep slopes) or negative (on flat terrain). Together, $(\beta_{a_1}, \beta_{a_2})$ determine the orientation of high seed production. There can only be an aspect effect, $\beta_{a_1} \neq 0$ and/or $\beta_{a_2} \neq 0$, if there is an effect of slope (again, $\beta_s \neq 0$).

Terrain effects depend on both the estimated coefficients and the specific slope-aspect characteristics of a given landscape (Figure 3). For example, in mountainous regions with predominantly north–south ridges (e.g. parts of the Sierra Nevada) will show different terrain effects than those with east–west orientations (e.g. parts of the Pyrenees and Balkan peninsula). Terrain effects can further depend on climate through the interaction between moisture deficit, slope and aspect, allowing slope × aspect effects to shift across the moisture gradient (Supporting Information). A species with a small U relative to other terms in Equation (2) shows little fecundity variation with terrain, while a species with a large relative U varies widely in fecundity across the landscape.

The fitted model includes a joint posterior distribution over all sensitivity coefficients, errors and latent variables, including maturation status, fecundity status and individual and year effects. This joint distribution absorbs the dependence between uncertain fecundity estimates, parameters and random effects, which is necessary for valid credible intervals. Variable selection, model evaluation and diagnostics are detailed in Clark et al. (2019).

3.3 | Predictive distributions for inventory plots

The fitted fecundity model was used to construct predictive distributions of fecundity for 10.6 million trees across inventory plots, allowing terrain analyses at the landscape scale (Figure 2). North American inventory plots include USDA's Forest Inventory and Analysis (FIA) programme and the National Ecological Observatory Network (NEON). European inventory plots come from national inventories, supplemented with additional plots from MASTIF monitoring. Plots vary in the minimal diameter used to include trees. We exclude trees below 12 cm in diameter to make plots comparable across inventories. Few trees below this size threshold are reproductive, so the effect on results is minimal. Species-level parameter estimates are available for more than 87% of trees on inventory plots, with the remainder summarized by genus-level estimates. Because exact plot locations are not available for many inventory plots, we rely on the large sample size to average out spatial uncertainty in terrain effects.

The spatial resolution of terrain analysis was motivated by data attributes and the scale of hydrologic influence. For model fitting, tree locations are precisely known. However, precise locations are unavailable for prediction on inventory plots. For this reason, terrain attributes cannot be evaluated at arbitrarily fine resolution (approximately 1 km, e.g. FIA uses 1 mile; Riley et al., 2021). We therefore adopted a 600 m radius to evaluate slope, aspect and topographic position, a scale that accommodates location uncertainty while remaining ecologically meaningful (Supporting Information). This is the spatial resolution used for model fitting, but the methods can be applied at other scales where data allow.

Predictive distributions combine environmental heterogeneity and species sensitivity to characterize landscape-level fecundity patterns (Supporting Information). Predictor variables (Table 2) were extracted for all trees on inventory plots and individual tree predictions were aggregated to the plot scale. The *terrain fraction* $T_{k,z}$ quantifies the fraction of model variance for species z at location k that is attributable to terrain variables, including the slope × aspect × moisture deficit interaction and topographic position (Equation S4b). Terrain fraction can be averaged over locations and species for a landscape metric of terrain importance.

The *community hypervolume* H_E quantifies the terrain environment space occupied by fecundity responses across the community (Clark, 2016). H_E is large when predictors vary widely, they are weakly correlated with one another (Figure 5c,d) and species differ in how they respond to combinations of these predictors (Figure 5b,d). For example, insolation and moisture might be weakly correlated, and the community includes species that respond differently to combinations of light and moisture. Conversely, hypervolume is small when predictors are correlated (Figure 5a,b), and species respond to those predictors in similar ways (Figure 5a,c): niche space is narrow and it is not partitioned between species. For example, fertility might be correlated with moisture (rich soils in moist, alluvial sites), and all species benefit from moisture and fertility. Finally, if the environmental variance is small (small diagonal values in matrix **V**), then species cannot respond and thus contribute to the niche hypervolume (Supporting Information).

Phylogenetic signal in species' topographic responses was quantified using Pagel's λ, estimated using the phylosig function in R (Revell, 2024). Statistical significance was assessed using a likelihood ratio test.

4 | RESULTS

We estimated fecundity responses to terrain and other predictors for 198 species in North America and 94 species in Europe, representing 90% of trees on inventory plots in North America and 89% in Europe (Table S1). For the remaining species, we used genus-level estimates to generate predictive distributions.

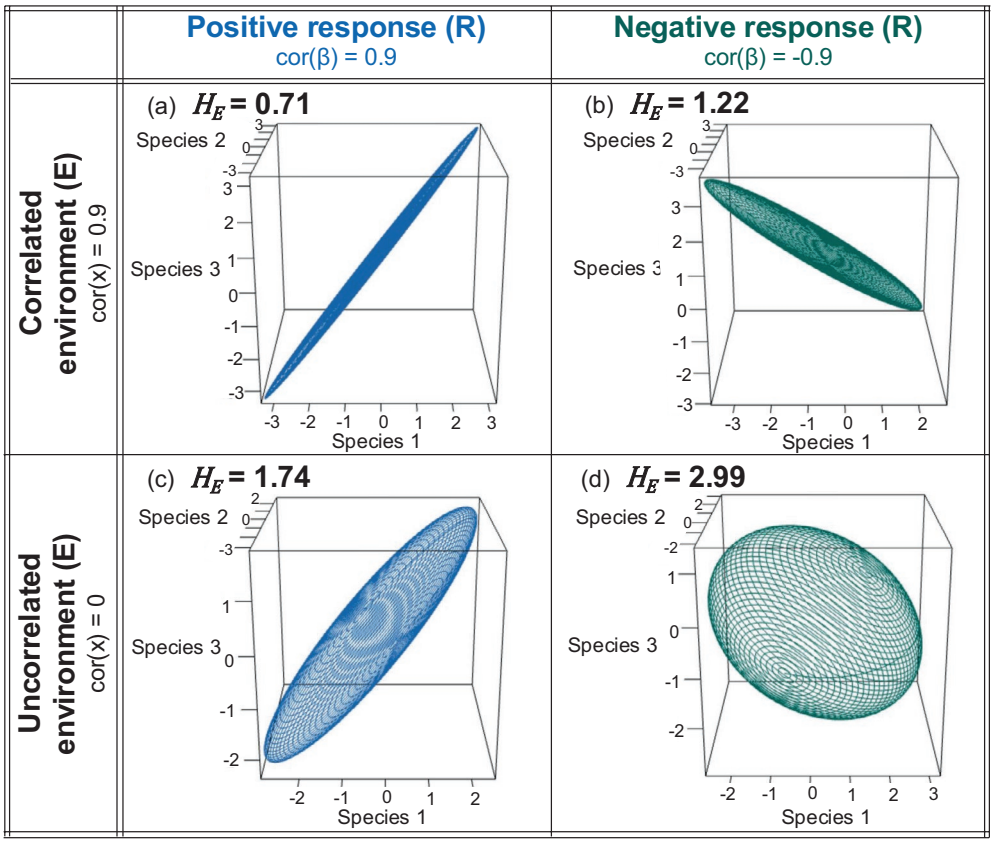

FIGURE 5 Community hypervolume H_E is highest when environmental variables are uncorrelated and species responses differ (d). Each panel shows the **E** matrix volume for three species, where axes are in units of covariance (Supporting Information). In (a) and (c), species respond similarly to environmental variation (positive response correlation; no niche partitioning), while (b) and (d) show species responding differently to environmental variation (negative response correlation; niche partitioning). Comparing rows, panels (c) and (d) show species with uncorrelated environmental variables, resulting in higher H_E than in panels (a) and (b), where correlated environmental variables provide limited opportunity for niche partitioning.

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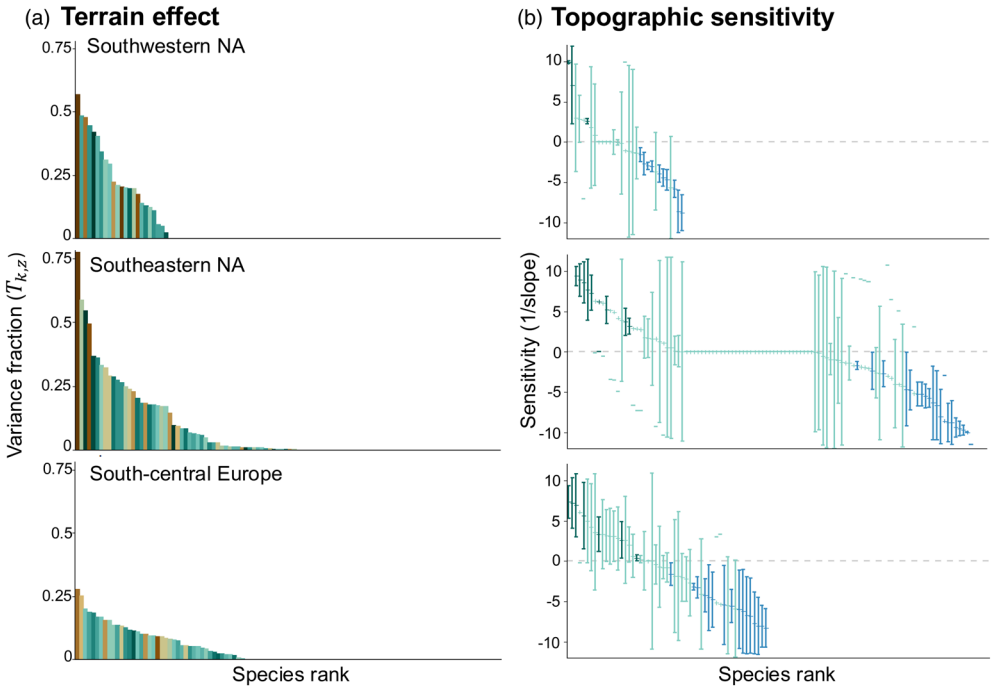

FIGURE 6 Species-level terrain variance fraction and sensitivity across three terrain analysis regions. (a) Fraction of fecundity variance explained by terrain ranked by species (T_z; Equation S4b averaged over locations k). Effects are highest in southwestern North America (SWNA) (13/31 = 41.9% of species with fractions >0.2) and southeastern North America (SENA) (16/107 = 15.0%). Only two (of 53 total) species reach this threshold in south-central Europe (SCEU). Variance fractions are not closely aligned with genus (bar colours). Species shown in Figure S3. (b) Slope sensitivity coefficients ranked for the same species. Boxes span 68% (1 SE), whiskers span 95% of the posterior distribution and centre lines indicate medians. Species centred at zero did not include slope in the final model. Dark lines indicate species where 95% of the posterior distribution excludes zero.

4.1 | Species-specific terrain sensitivity varies among regions

Across all species, terrain-mediated fecundity responses show wide variation and regional contrasts (Figure 6a). The fraction of fecundity variance explained by terrain ($T_{k,z}$; Equation S4b) is high for many species in SENA and SWNA. Taking a variance fraction of 0.2 as reference, 13 of 31 species (41.9%) in SWNA and 16 of 107 species (15.0%) in SENA exceed 0.2, while SCEU shows the weakest terrain effects, with only 2 of 52 species (3.8%) exceeding this threshold (Figure 6a). Species range in response to slope from positive (high fecundity on steep terrain) to negative (high fecundity on flats), though most species (86.8% in SCEU, 89.7% in SENA and 90.3% in SWNA) show negative or no response to slope (Figure 7b). Many species in SENA (30%) did not include slope in the best fitting model but still responded to topographic position. SENA exhibits the greatest diversity of slope responses, both negative and positive. SCEU shows a similar mix of directions. SWNA shows predominantly negative sensitivities.

As expected for species that can be differentially limited by light, moisture and heat stress (Hypothesis 1), individual species vary widely in the direction and magnitude of topographic response (Figure 7a). For example, *Quercus alba* and *Fagus sylvatica* show high fecundity on northeast aspects, indicating that seed production benefits from cool, moist microhabitats, while *Pinus ponderosa* shows high fecundity on warm, dry south aspects. The full species-level summary is provided in Supporting Information.

4.2 | Climate modulates terrain effects on fecundity

For many species fecundity responses to terrain differed in wet versus dry climates (Figure 7b). For example, *Q. alba* shows high fecundity on northeast aspects in dry parts of its range but shifts to southwest aspects in wet parts. *Fagus sylvatica* shows the opposite pattern, with high fecundity on south aspects in dry ranges and northeast aspects in wet ranges. *Pinus ponderosa* shows a positive fecundity effect on south aspects in its wet range and a negative effect on east aspects in dry conditions (Figure 7b).

To aggregate aspect-related fecundity responses across regional climate gradients, for each species we subtracted the terrain function at the 10% quantile for moisture deficit ('wet') from the 90% quantile ('dry'). We then averaged these differences over species. For example, a species that experiences high fecundity on north aspects in dry climates and south aspects in moist climates would show the pattern illustrated for SENA and SCEU species in Figure 8. Averaged across species, SENA and SCEU taxa show higher fecundity on northeast-facing aspects in cooler, moist microhabitats, particularly in the drier portions of their ranges. In contrast, the

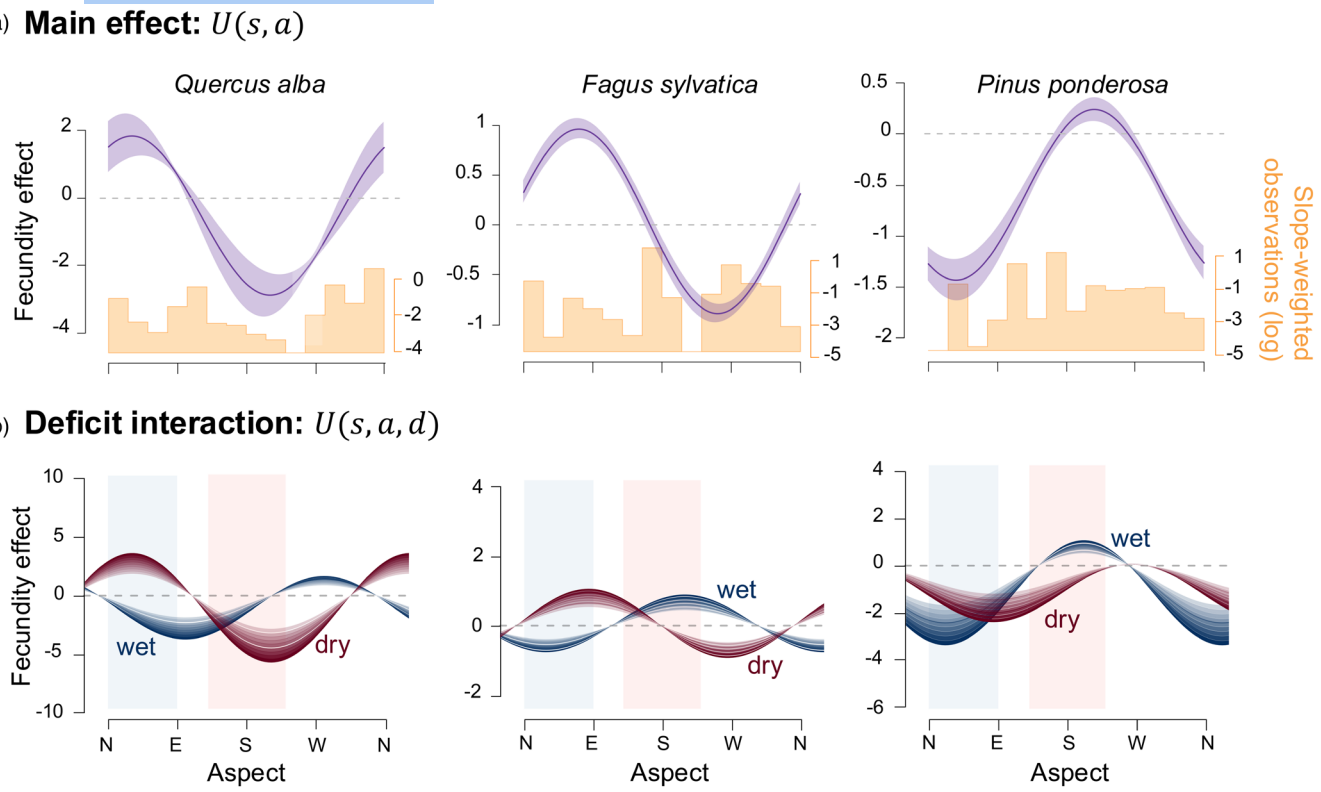

FIGURE 7 Fecundity responses of three example species. (a) The terrain function (Equation S3) quantifies effects of slope on fecundity depend on aspect (shading shows 95% credible intervals). Vertical axis is the magnitude of the terrain function in units of log fecundity. Background histograms show the distribution of slope-weighted aspect observations (zero slope contributes zero aspect information). (b) The terrain-moisture deficit interaction shown for contrasting moisture deficit values. Shaded envelopes show fecundity response on slopes ranging from 0.1 m/m (pale) to 0.2 m/m (dark). Two curves contrast dry versus wet portions of the range, defined by quantiles of 10% (blue) and 90% (red) moisture deficit. For the three species, respectively, moisture deficit values are −31, −53, −10 cm (wet) and 0, −19, 16 cm (dry). Background shading indicates moist NE aspects (blue) and high insolation S aspects (red), as in Figure 1.

opposite is true in SWNA, where fecundity shifts to south-facing aspects in dry parts of the species range (Figure 8).

4.3 | Regional differences in community hypervolume

Broad overlap in average terrain features belies contrasts in how species exploit terrain in the three regions. The tendency for heterogeneity to increase with elevation in all regions (e.g. Figure 3c) averages out when evaluated as regional median values. The median terrain contribution to fecundity variance (Equation S4b), taken over species z and location k, ranges from 0.057 in SWNA to 0.043 in SCEU, with SENA intermediate, and these differences are modest relative to wide 90% intervals (Table 1).

Landscape-climate interactions create microclimatic heterogeneity that becomes meaningful only when species exploit it in different ways. SENA combines moderate habitat variability with diverse species sensitivity to generate high community hypervolume (Figure 9a). Despite moderate relief and grid-averaged slopes reaching only 0.2 m/m (Figure 3), SENA spans the extremes in fecundity variation from the low-relief Coastal Plain to the Appalachian highlands (Figure 9b). Per-species hypervolume (Equation S5) still exceeds other regions (Figure 9a). SENA supports the most tree species, so this high per-species hypervolume results from the diversity of species responses rather than species richness alone.

By contrast with SENA, the rugged terrain of SWNA and SCEU shows only scattered locations of high fecundity variance (Figure 9b). Despite the diverse terrain evident in Figure 3, with grid-averaged slopes reaching as high as 0.4 m/m, SWNA exhibits moderate community hypervolume (Figure 9b) owing to a low diversity of fecundity responses across species and locations. SCEU has the lowest hypervolumes overall, again reflecting muted responses to topographic gradients, which is the opposite of niche partitioning. In both regions, complexity is not exploited to the extent seen in the lower-elevation Appalachians.

4.4 | Topographic responses lack phylogenetic signal

Topographic responses show no evidence of phylogenetic signal (Pagel's $\lambda \approx 0$, $p = 1.0$), meaning closely related species do not tend to

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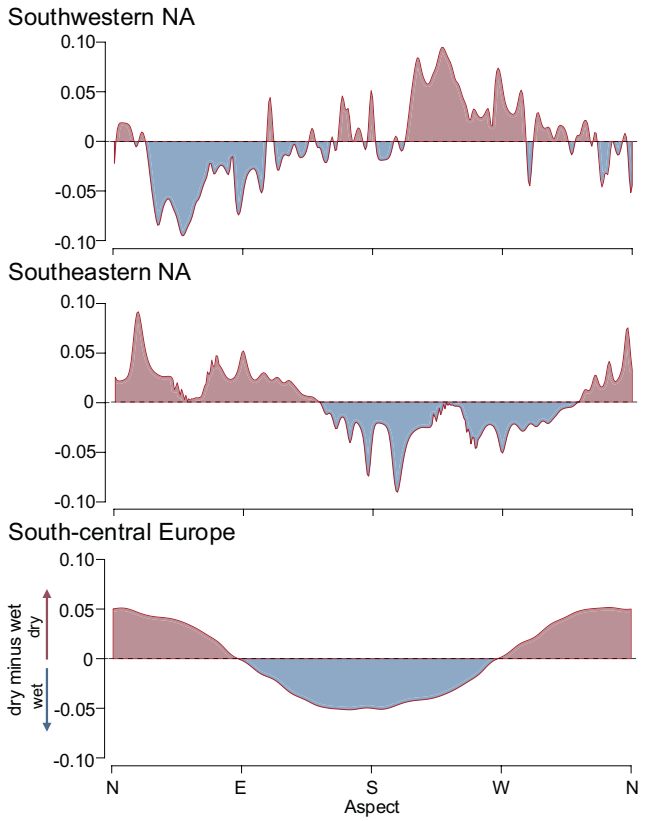

FIGURE 8 There are regional differences in climate modulation of terrain effects, averaged over all species. The vertical axis is the average difference in terrain functions (Equation S3), in units of log fecundity, in dry versus wet climates. In dry portions of their ranges, species in southeastern North America (SENA) (middle) and south-central Europe (SCEU) (bottom) have high fecundity on northeast-facing aspects in cool and moist microhabitats. The opposite is true in southwestern North America (SWNA) (top), where fecundity shifts to south-facing aspects in dry parts of the species' range. The North American sites show much higher variation across aspect, but it is unclear why the variation is high in these regions.

be similar in their responses to terrain. This is consistent with divergent terrain associations within genera such as *Quercus* (Cavender-Bares, 2019) and suggests that topographic responses represent species-specific adaptations rather than evolutionarily conserved traits, with local environmental heterogeneity overriding broader phylogenetic constraints in shaping reproductive responses to terrain.

5 | DISCUSSION

Although terrain effects on vegetation patterns and tree growth are the subject of many studies (Bałazy et al., 2019; Tukiainen et al., 2017; Verbyla & Fisher, 1989; Whittaker, 1956), our results show that fecundity also responds to terrain and regions differ in how environmental space is exploited. Fecundity responds to slope and aspect (Figures 6 and 7), and this response depends on climate (Figure 8). As climate change alters these terrain-climate relationships, the spatial patterns that support reproductive success will also shift.

Traditional assumptions that slope exposure follows a N–S (or NE–SW) dichotomy are at odds with the knowledge that limitations from low light, moisture and heat stress can occur at the same place at different times (Hypothesis 1). Consistent with this, results show that most species responses are intermediate, rather than aligning strictly N–S or NE–SW (Figures 6 and 7). This range of responses to exposure is consistent with previous studies showing the diversity of fecundity responses to light availability and its interaction with moisture (Clark et al., 2014), as well as with evidence that limitations on fecundity may shift seasonally, for example, temperature cues in winter and spring versus moisture stress in summer (Bogdziewicz et al., 2020; Charrier et al., 2015, 2021; Clark et al., 2026a, 2026b; Stephenson, 1981). Although our terrain variables (slope, aspect, topographic position and interactions with moisture deficit) capture key gradients, they do not account for all relevant effects of terrain. Seasonal temperature inversions, snowpack and wind fields may also influence fecundity. However, at biogeographic scales, model predictors are constrained to variables that are consistently available at large spatial extents. Despite the limited terrain information that can be gleaned at local to regional scales, responses to terrain clearly differ among regions and species.

The fact that terrain effects on vegetation patterns can vary with climate (Ackerly et al., 2020; Dobrowski, 2011; Whittaker, 1956) is shown here to extend to the demographic level. Consistent with Hypothesis 2, reproduction is influenced by interactions between topography and microclimate. In SENA, species that do not respond to slope (zero values in Figure 6b) can still respond to topographic position, likely due to variation in moisture. In contrast, the tendency for SWNA species to benefit from flatter terrain (negative slope coefficients) suggests that drainage plays a key role in shaping fecundity in these water-stressed habitats.

Fecundity responses to aspect show striking regional contrasts. In dry parts of their range, SENA and SCEU species shift reproduction towards cool, moist northeast-facing slopes. SWNA species show the opposite pattern, benefiting from south-facing slopes under dry conditions (Figure 8). Several mechanisms may explain this regional contrast. First, western species under stress may prioritize growth over reproduction (Bilir et al., 2021; Grossiord, 2020; Wang et al., 2020), favouring sun-exposed slopes that maximize photosynthesis despite water costs. Under water limitation, this strategy may reflect a trade-off between energy capture on sun-exposed slopes during favourable conditions and the benefits of conserving moisture. Additionally, interactions between terrain and fire regimes may likewise contribute to this interaction (Bilir et al., 2021; Westerling, 2016). However, these unexplained moisture shifts in SWNA should be a subject of additional study.

We find that the region with the highest species diversity, SENA (Table 1), had the highest environment×response (E×R) hypervolume (H_E, regions in red in Figure 9). The southern Appalachians have been long recognized as a biodiversity hotspot, perhaps due

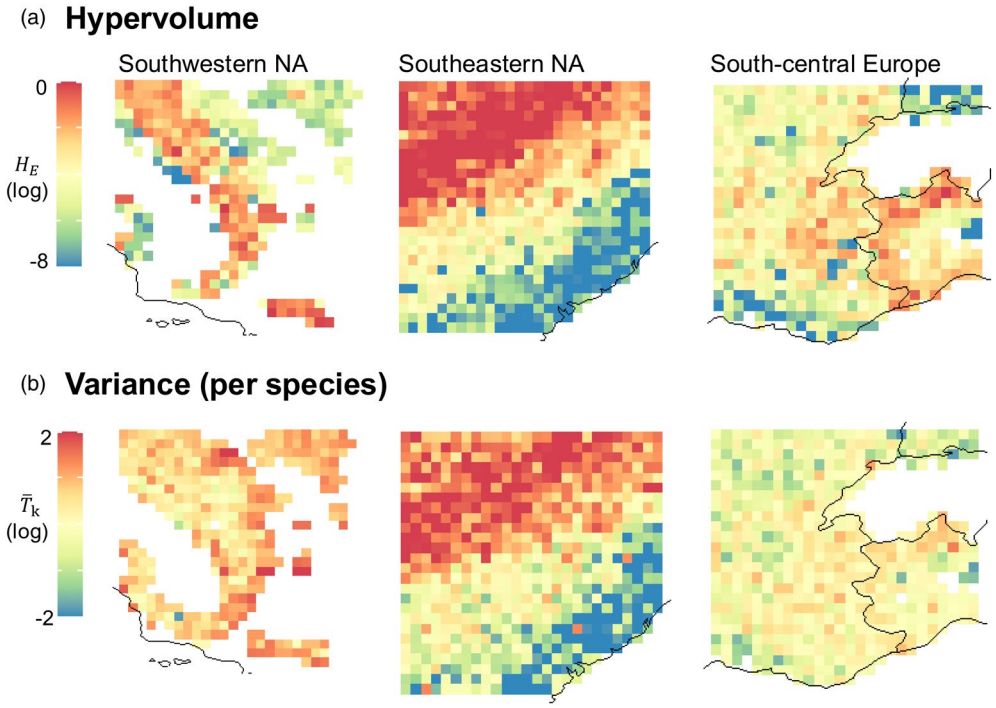

FIGURE 9 Terrain effects on fecundity vary in magnitude and spatial extent across regions in Figure 2. (a) Community hypervolume H_E (log scale), calculated from the covariance of species-specific terrain sensitivities and habitat heterogeneity at each grid cell (Equation S5). Large hypervolumes (red) indicate communities where species show diverse responses to terrain, collectively occupying a wide range of environmental niche space. Small hypervolumes (blue) indicate communities with limited responses. (b) Fecundity variance ($\bar{T}_k$, log scale) averaged across all species present in each grid cell (Equation S4b). High values (red) indicate wide variation in fecundity, reflecting strong terrain sensitivity and environmental interactions. Blue indicates low per-species variance, where fecundity predictions are more spatially uniform within grid cells. Estimates are shown only for locations with forest inventory plots (see Figure 2).

to a combination of a temperate climate with topographic variation and limited barriers to migration during glacial cycles (Currie & Paquin, 1987; Jenkins et al., 2015; Qian & Ricklefs, 2000; Ricketts & Imhoff, 2003). A foundational study on forest composition from this region demonstrated strong species-specific responses to interacting terrain features, including slope, aspect, drainage, elevation and climate (Whittaker, 1956). This diversity of environmental conditions and species responses to that environmental variability results in the high H_E seen in Figure 9.

No study of modern niche variation can by itself explain regional patterns of diversity shaped by Cenozoic speciation and extinction (Kremer et al., 2025; Manos & Stanford, 2001), and our analysis does not establish cause and effect. Broad niche exploitation, defined by the breadth of E×R or H_E, can result from two mechanisms: (i) high environmental diversity or (ii) high biodiversity, providing more species to fully exploit available environmental variation. Both effects could contribute to high niche exploitation observed in the southern Appalachians (Figure 9). If Quaternary climate refuges and migration corridors promoted high diversity in SENA, then the large H_E we observe would be an expected consequence of that diversity. However, if high diversity were driven primarily by transient responses to climate or disturbance rather than niche differentiation, there is no reason to expect an association between species diversity and response hypervolume. The expansive hypervolume for fecundity in this region is consistent with species that partition reproductive niche space across terrain heterogeneity to a greater degree than in the other montane regions we analysed. The absence of phylogenetic signal in fecundity responses, both here and in response to weather extremes (Clark et al., 2026a, 2026b), further suggests a role for local adaptation, which can occur rapidly in trees (Alberto et al., 2013; Cavender-Bares, 2019; Hanlon et al., 2019; Hord et al., 2025).

Terrain-climate interactions are often missing from biodiversity and climate models (Ashcroft et al., 2009; Daly et al., 2009), while those that include terrain typically assume specific orientation effects rather than fitting aspect effects together with slope and moisture interactions. Our approach generates estimates, with full uncertainty, that can be directly incorporated into models of demography (e.g. Equation 1) and its contributions to niche exploitation. Regional differences include the fine-scale terrain variation in SENA that creates diverse reproductive niches and the weaker role in SCEU, where human impacts may have degraded the climate-biodiversity links.

Terrain-mediated fecundity effects will determine forest resilience under climate change (Kremer et al., 2025). In this study, areas with topographic diversity and strong responses to terrain (e.g. SENA) may require spread to nearby favourable slopes or aspects (Ackerly et al., 2020; Dobrowski, 2011). In contrast, regions with low topographic diversity or weak terrain responses may require migration over larger distances to track suitable climate (Aitken et al., 2008; Sharma et al., 2022). Finally, weak terrain-climate interactions may

identify species with limited sensitivity to climate change. The additional effects of terrain on seedling establishment remains an important topic for research (Crone et al., 2013; Luu et al., 2024).

The fact that the SENA community exploits a broad range of environmental variation is no guarantee of high resilience for individual species. Whether or not each species in this biodiverse landscape can adjust through movement or local adaptation is not informed by studies of current environmental exploitation. By showing that the community exploits a broad environmental space, this analysis suggests capacity to maintain diversity in the future. However, it offers limited insight for individual responses. For example, lack of terrain response can indicate broad environmental tolerance that can minimize the risks of climate change. Alternatively, terrain sensitivity may indicate species that can shift their distributions as habitats change.

Effective stewardship practices require estimates of species' capacities to persist or migrate with climate change. Conservation planning for climate change can exploit insights on the terrain-climate interactions, prioritizing protection of topographically diverse landscapes where fine-scale redistribution may buffer populations against regional climate shifts (Bower et al., 2024; Potter et al., 2013). Our results demonstrate that reproduction varies with terrain in different ways for each species. While terrain diversity offers potential for species diversity, it represents only half of the story: response diversity is the other half. Conservation and management strategies that preserve topographic variability while maintaining connectivity across environmental gradients will be essential for allowing forests to adapt to a changing climate.

AUTHOR CONTRIBUTIONS

James S. Clark, Inés Ibáñez, Lauren Jenkins, Roland Kays, Georges Kunstler, Emily V. Moran, Miranda D. Redmond, and Tong Qiu conceived the study. Lauren Jenkins and James S. Clark developed models and analysis and wrote the manuscript. All authors contributed data and revised the manuscript. All authors approve the final manuscript for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70369.

DATA AVAILABILITY STATEMENT

Data supporting this study are openly available in the Duke Digital Repository at https://doi.org/10.7924/r42v2t66k (Clark et al., 2026b). Code is available via the R MASTIF package on CRAN (https://cran.r-project.org/web/packages/mastif/index.html).

ORCID

Lauren Jenkins https://orcid.org/0000-0001-6537-575X
Inés Ibáñez https://orcid.org/0000-0002-1054-0727
Roland Kays https://orcid.org/0000-0002-2947-6665
Georges Kunstler https://orcid.org/0000-0002-2544-1940
Sierra McMurry https://orcid.org/0009-0000-0268-8062
Tong Qiu https://orcid.org/0000-0003-4499-437X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Number of species (292 total) with each predictor included in the model and those that are different from zero (see Section 3).

Figure S1. Analysis on the 0.2° longitude/latitude lattice (grey) obtains terrain variances (slope aspect, topographic position) from the six closest locations on the regular 0.1° lattice (blue).

Figure S2. The **E** matrix obtained when species respond similarly to environmental variables (a) contrasted with the case where they respond differently (b). Hypervolume H_E is highest where species respond differently to environmental variation (b).

Figure S3. Species-level terrain variance across three terrain analysis regions, with species labelled. Fraction of fecundity variance explained by terrain ranked by species (T_z; Equation S4b averaged over locations k), ranked by species. Colours reference genus. This figure is identical to Figure 7a in the main text but includes species names for each bar here.

Table S2. Species included in analysis. Full list of tree species and their study regions used in terrain-fecundity analysis.

Table S3. Sheet fitlog. Rows are organized by genus and region and then by lowest DICweighted.

Table S4. Sheets parEst and parSE. Posterior mean estimates and standard errors. Non-significant or excluded variables (Table S1) are zeros.

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