Forest Ecology and Management 586 (2025) 122718

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Assessing tree migration potential: Growth deviations and range dynamics in eastern U.S. forests

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ARTICLE INFO

Keywords:
Tree migration
Climate change
Growth residuals
Importance value
Range shifts
Eastern U.S. forests

ABSTRACT

Understanding how tree species respond to climate change is essential for predicting future forest composition and ecosystem dynamics. This study evaluates the migration potential of tree species in the eastern United States by integrating growth residuals, absolute growth rate, and Importance Value (IV) as complementary indicators of species' responses to environmental change. Growth residuals, which measure deviations from expected growth after accounting for tree size and environmental factors, provide insight into species' recent responses to climate variability. Absolute growth rate reflects species productivity trends across latitudinal gradients, while IV serves as a historical baseline of species abundance and demographic stability. Using Random Forest modeling, we identified basal area, mean temperature, and mean precipitation as the most influential predictors of tree growth. We then applied Huisman-Olff-Fresco (HOF) models to assess latitudinal patterns in growth residuals, absolute growth rate, and IV. Our results revealed three major patterns: (1) species exhibiting northward growth residual peaks, suggesting poleward expansion potential; (2) species with southward growth residual peaks, indicating possible range contraction or climate limitations at northern edges; and (3) species with stable growth residuals, implying demographic inertia or localized climatic stability. Additionally, frequent mismatches between growth residuals and IV suggest that many species remain abundant in historical ranges despite shifting climatic suitability. While regeneration strategy is a key factor influencing species distributions, our findings suggest that it primarily affects IV rather than short-term growth responses. Wind-dispersed species, such as red maple and sugar maple, exhibited strong northward trends across all three metrics, whereas heavy-seeded species like sweetbay and slash pine had IV peaks farther south than their growth residuals, suggesting that past recruitment dynamics may lag behind recent growth patterns. These results highlight the need to consider both historical abundance and recent growth responses when evaluating migration potential. Our study provides empirical evidence that climate-driven range shifts in eastern U.S. tree species are highly species-specific, shaped by growth performance, demographic history, and recruitment dynamics. These findings underscore the complexity of tree migration and emphasize the importance of integrating multiple metrics to better assess species' responses to climate change.

1. Introduction

Climate change is expected to cause systematic changes in vegetation distribution via phenology (Fu et al., 2022; Piao et al., 2019), growth and demographic patterns (Wilmking et al., 2020; Purves, 2009; Iverson et al., 2004), dispersal and migration processes (Corlett and Westcott, 2013), or biotic interactions (Fricke et al., 2022; Bardgett and Wardle, 2010). Changes in vegetation distribution, in turn, exert some degree of influence on climate through vegetation-climate feedback (Bonan, 2008). Thus, predicting the climate-driven redistribution of tree species is essential for anticipating climate shifts, and implementing forest management strategies to lessen its impacts.

The geographic extents of North American tree species have changed periodically in response to changes in past climates (e.g., glacial-interglacial cycles), as evidenced by many palaeoecological studies (Copenhaver-Parry et al., 2017; Williams et al., 2004). However, anthropogenic warming trends are occurring at unprecedented rates when compared with historical records (Jones and Mann, 2004). Indeed, climate change has already caused substantial tree distribution shifts to higher elevations (Beckage et al., 2008; Bell et al., 2014; Kelly and

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https://doi.org/10.1016/j.foreco.2025.122718
Received 11 March 2025; Received in revised form 4 April 2025; Accepted 7 April 2025

Goulden, 2008) and poleward (Parmesan and Yohe, 2003; Chen et al., 2011). Many local empirical studies have documented upslope tree line shifts, often driven by minimum winter temperature (Dullinger et al., 2004), which is a primary control on tree species' survival in mountainous areas (Beckage et al., 2008). These local studies suggest that temperature-driven changes may underpin larger-scale tree species redistributions; however, direct empirical evidence of widespread latitudinal range shifts remains limited. Predicting latitudinal distribution shifts is particularly challenging because latitude represents multiple factors—such as temperature, water availability, or glacial history—that can mask the effects of expected warming trends. Moreover, tree species have long generation times, causing time lags in their responses; therefore, their ability to genetically adapt to the environment may not match the pace of contemporary climate change (Jump and Peñuelas, 2005; Lindner et al., 2010).

Iverson and Prasad (2002) pioneered the use of Forest Inventory and Analysis (FIA) data combined with climate-envelope models (CEMs) to project tree species redistribution by modeling current Importance Values (IV) and predicting future suitable habitats for eastern U.S. tree species under various climate scenarios. Their work predicted that many species would migrate northward under climate change scenarios, depending on habitat connectivity and species-specific dispersal capabilities. However, more recent studies have reported inconsistencies in redistribution patterns. For example, Zhu et al. (2012) analyzed 92 tree species in relation to 20th-century temperature and precipitation changes, finding that over half exhibited range contractions rather than expansions. Similarly, Bell et al. (2014) observed that seedling distributions for many species contracted despite warming trends. These results underscore the complexity of predicting latitudinal range shifts and highlight the need for further empirical evidence to determine whether tree species can reliably track contemporary warming trends.

CEMs predict viable habitats by correlating bioclimatic factors with species occurrences (Pearson and Dawson, 2003; Araújo and Peterson, 2012). While useful for projecting potential distributions under climate change (e.g., Huntley et al., 2008; Lawler et al., 2009), CEMs rely on the assumption of climate equilibrium that species occupy their entire range of suitable climate conditions, known as their fundamental niche. This assumption often limits their predictive accuracy, as it neglects demographic constraints, dispersal limitations, and differences between fundamental and realized niches. To complement modeling approaches, empirical studies have explored observed patterns of tree species abundance and their range shifts. Empirical studies have primarily used static variables - such as seedling or sapling abundance (counts per unit area or IV), relative to adult trees - to infer colonization rates and demographic shifts (e.g., Zhu et al., 2012; Murphy et al., 2010). For instance, Woodall et al. (2009) observed a potential northward shift in 11 of 15 northern species, with seedlings exhibiting a significantly higher mean latitude than adult trees. Conversely, Murphy et al. (2010) found that Pinus taeda (loblolly pine) was unlikely to migrate northward due to lower abundance at its northern boundary compared to its southern boundary. However, Canham and Murphy (2016) reported a decline in the growth rate of Pinus taeda at its southern range limit, suggesting environmental stress or suboptimal conditions. These findings reveal a critical limitation of abundance-based metrics: while they effectively quantify tree density and distribution, they may fail to capture growth dynamics and environmental sensitivities. Growth rate, which is directly influenced by factors such as temperature, moisture availability, and resource competition, provides a dynamic measure that can signal migration potential before demographic shifts, such as changes in abundance or regeneration, become evident (Fritts and Swetnam, 1989; Wason et al., 2017). Detecting systematic changes in growth rates across a species' range offers a means to identify early indicators of range shifts, avoid demographic delays (Wason et al., 2017), and better understand future species compositions, range dynamics, and migration capabilities in response to climate change.

This study evaluates 56 eastern U.S. tree species to assess their potential for climate-driven range shifts by integrating multiple complementary metrics: growth residuals, absolute growth rate, and Importance Value (IV). Growth residuals, serving as the primary indicator, reveal species' near-term responses to environmental variability, capturing deviations from expected growth that may indicate emerging migration patterns. Absolute growth rate provides insight into species productivity across their range, distinguishing between those maintaining robust growth and those experiencing climatic stress. IV, a historical measure of species relative abundance, reflects long-term demographic patterns, offering a baseline for assessing whether species distributions are actively adapting or lagging behind changing climatic conditions. By examining these three metrics in tandem, this study aims to identify species actively tracking warming trends, those maintaining stability, and species experiencing demographic inertia. This multimetric approach offers a nuanced understanding of tree migration potential and range dynamics, with implications for forecasting future forest composition and guiding conservation and management strategies under climate change.

2. Materials

2.1. Study area

The study area encompasses the 31 eastern-most states of the United States, providing a sub-continental scale for analyzing forest dynamics. These forests span approximately 140 million hectares, accounting for 50 % of the total forested area in the United States (Gray et al., 2012). This region exhibits high environmental and climatic diversity, containing three of the six major global Köppen climate classes (Mild Mid-Latitude, Tropical Humid, and Dry) and three of the eight global biomes (temperate broadleaf deciduous forest, temperate grassland, and boreal forest).

2.2. Forest inventory and analysis (FIA)

The Forest Inventory and Analysis (FIA) program is the primary source of information on the extent, condition, status, and trends of U.S. forest resources (Smith et al., 2002). Using a nationally consistent sampling protocol and a quasi-systematic design, the FIA program ensures comprehensive representation of diverse landscapes and ownership types. The sampling intensity corresponds to one plot per 2428 ha of forest land (Bechtold and Patterson, 2005). Forested land is defined as areas with at least 10 % canopy cover by tree species, spanning at least 0.4 ha and 36.6 m in width. Each FIA plot consists of four fixed-radius subplots (7.2 m in radius), arranged in a triangular pattern with one subplot at the center (Bechtold and Patterson, 2005). Trees with a diameter at breast height (d.b.h.) of at least 12.7 cm, including live and standing dead trees, are inventoried in these subplots. To protect landowner privacy, the FIA program applies location masking techniques to plot coordinates before releasing the data. These techniques include fuzzing, where plot coordinates are randomly relocated within a 0.5-mile radius, and swapping, where plot coordinates are exchanged between two plots within the same county that share similar stand characteristics (Bechtold and Patterson, 2005). To mitigate the uncertainties introduced by these methods and ensure spatial reliability, this study aggregated the FIA data into 20 km × 20 km grid cells, providing a balance between geographic precision and privacy protection.

Tree-level basal area (BA) was incorporated as a predictor variable for growth rate modeling. Plot-level stand origin (STDORGCD) data was used to screen and retain only FIA plots representing natural stands, excluding those with evidence of artificial regeneration. For this study, FIA data were extracted from the two most recent inventory cycles to calculate individual tree growth over time, spanning 2011–2015 and 2016–2022, which together encompass 69,022 inventory plots across 31 eastern U.S. states (FIADB version 9.0, as of April 01, 2023; http://fia.fs.

fed.us/). These data include a total of 285 tree species found in the forests of the eastern United States.

2.3. Predictor variables

The selection of predictor variables was initially guided by Kwon et al. (2018) (Supplementary Data, S1), which categorized 18 environmental variables into seven key ecological groups: Areal factors, Climatic seasonality, Energy availability, Energy-water dynamics, Habitat heterogeneity, Limiting climatic factors, and Water availability. While these variables were originally developed to model tree species richness, they represent fundamental ecological constraints on tree growth, making them a suitable starting point for this analysis. To refine the selection of predictor variables for species-specific growth modeling, we conducted Random Forest (RF) models (Breiman, 2001) separately for each species, evaluating the relative importance of each variable in explaining annual growth rates. While species exhibited varying sensitivities to different environmental factors (Supplementary Data, S2), two predictor categories—Energy availability and Water availability—consistently emerged as the most influential across species. Consequently, we selected Mean Temperature and Mean Precipitation - 30-year average climatology (1970–2000) from the WorldClim v2.1 dataset (Fick and Hijmans, 2017) - as the most representative variables. Mean Temperature plays a critical role in regulating physiological activity, growing season length, and metabolic processes, while Mean Precipitation serves as a primary determinant of water availability, influencing drought stress, productivity, and species viability. In addition to climate variables, basal area (BA) was incorporated as a predictor variable in this study to account for tree size and competitive effects on growth. As expected, BA turned out to be the most important predictor across all species, reinforcing its fundamental role in determining tree growth. BA, calculated from FIA tree diameter measurements, reflects individual tree size and stand-level competition, which are critical determinants of growth potential. Larger trees typically exhibit reduced relative growth rates due to resource limitations, whereas smaller trees may have higher potential for growth if resources are available. Because BA strongly influences growth independent of climatic drivers, it was included in all models to improve predictive accuracy and isolate climate-driven growth variation.

While additional factors, such as water balance metrics (e.g., Actual Evapotranspiration) and limiting factors (e.g., Coldest quarter temperature, Aridity Index), played significant roles for some species, their effects were highly species-specific and did not consistently rank among the top predictors across taxa. To maintain a robust, generalizable approach, we prioritized BA, temperature, and precipitation as the three most consistently influential variables. By focusing on these variables, we ensured that growth residuals primarily reflect climate-driven deviations rather than differences in predictor selection. This approach provides a foundation for assessing migration potential at a broad spatial scale, while recognizing that additional environmental drivers may influence growth at finer scales.

2.4. Response variables: growth, growth residuals, and abundance

Growth: The primary response variables in this study were the annual growth rate (hereafter, growth rate) and Importance Value (IV). Growth rate was quantified using the FIA variable GROWCFAL, which represents the net annual sound cubic-foot stem wood growth of live trees on forest land. It was calculated as:

$$GROWTH(GROWCFAL_{FOREST}) = \frac{V2 - V1}{T2 - T1} \tag{1}$$

where V1 and V2 denote past and current tree volume measurements, and T1 and T2 are the corresponding measurement dates. The remeasurement period (PLOT.REMPER) defined the time interval between measurements. Negative growth values indicate tree mortality ($V2 = 0$) or net volume loss due to damage, rot, broken tops, or other factors. Growth values were standardized to a per-acre estimate using SUBP_TPAGROW_UNADJ_FOREST variable from the FIA dataset.

Growth Residual: For each species, growth residuals were computed as the difference between observed and predicted growth:

$$\text{Residual} = \text{Observed Growth} - \text{Predicted Growth} \tag{2}$$

Predicted growth was obtained using species-specific Random Forest (RF) models incorporating basal area, mean annual temperature, and mean annual precipitation. Residuals were calculated at the individual species level and aggregated to 20 × 20 km grid cells. For visualization and HOF modeling (see *Analytic Methods* section), residuals were further smoothed using a 0.5° latitudinal moving average. These residuals capture deviations from expected growth, providing insight into near-term climate-related responses that may not be explained by size or long-term climatic means alone.

Abundance: Importance Value (IV) was used as a static measure to assess tree species relative abundance across latitudes, serving as a baseline reference. IV integrates relative basal area and relative stem density to quantify a species' dominance on a plot, calculated as:

$$IV(x) = \frac{100BA(x)}{BA(all\ species)} + \frac{100NS(x)}{NS(all\ species)} \tag{3}$$

where BA represents basal area and NS represents stem count. IV values were aggregated at the 20 km × 20 km grid level for each species, enabling latitudinal comparisons of species abundance and distribution.

2.5. Study species

The selection of tree species for this study was based on a comprehensive literature review of studies utilizing Forest Inventory and Analysis (FIA) data to examine tree distribution and migration patterns in eastern U.S. forests. The species list was compiled from three key sources: Zhu et al. (2014), Woodall et al. (2010), and Woodall et al. (2013), each of which applied rigorous selection criteria to ensure ecological significance and broad geographic representation.

Zhu et al. (2014) identified 65 species with substantial sample sizes in the FIA dataset, explicitly excluding genus-level taxa and riparian/hydric species to focus on upland tree species with well-defined climatic distributions. Woodall et al. (2010) prioritized species abundance by compiling two lists of 50 species each, based on biomass and tree count. Woodall et al. (2013) refined species selection further, emphasizing species with high seedling abundance and those projected to undergo substantial range shifts under climate change scenarios. From this combined list, we further refined the selection by excluding species with core distributions primarily centered in Canada—retaining only those for which more than half of their range falls within the United States. This step ensures that the FIA dataset adequately captures latitudinal growth and distributional patterns for each species. The final list of 56 species reflects a balance of ecological importance, geographic coverage, and demographic representativeness. Additionally, we incorporated species-level classifications of geographic range orientation (northern, southern, or generalist) based on Woodall et al. (2009) and regeneration mechanisms from Woodall et al. (2010), which categorize species into ecological guilds based on dispersal mode, growth strategy, and masting attributes. These classifications provide further insight into potential migration constraints and species-specific responses to climate change.

3. Analytic methods

3.1. Growth rate modeling by basal area and abiotic factors

Growth rate was modeled using the Random Forest algorithm

(Breiman, 2001) to account for its dependence on tree size (proxied by basal area) and abiotic factors, specifically the 30-year (1970–2000) annual mean temperature and annual mean precipitation, within each species' range. This modeling approach isolates deviations from expected growth patterns by examining growth residuals, which highlight trends not explained by the predictors. To comprehensively assess species migration potential, we primarily examined growth residuals and compared their patterns with absolute growth rate and Importance Value (IV) as complementary metrics. Growth residuals represent deviations from expected growth, independent of tree size and abiotic constraints, making them a more immediate and climate-sensitive indicator of potential range shifts. Absolute growth rate, on the other hand, reflects overall species productivity but is shaped by both demographic factors, such as tree size—where younger trees typically grow faster than older individuals—and environmental conditions—like longer growing seasons at lower latitudes. These underlying influences can lead to higher absolute growth in certain regions, even if they do not necessarily indicate a species' climatic preference or migration potential. IV provides a complementary perspective by serving as a static measure of species abundance, capturing historical distribution patterns that may lag behind more immediate climatic responses.

The RF models were implemented using the randomForest package in R, with the number of trees set to 500 (ntree = 500), minimum node size fixed at 5 (nodesize = 5), and the number of variables tried at each split (mtry) optimized per species using cross-validation to maximize model performance. The performance of the RF models was evaluated using the coefficient of determination (R^2), which measures the proportion of variance explained by the model. Species with R^2 values above 0.4 were included in the analysis, while those below this threshold were excluded, as low R^2 values suggest highly variable or unreliable model fits. Growth residuals were calculated as the difference between observed and predicted growth rates, allowing us to examine species-specific responses to climate variability, independent of demographic inertia captured by IV. By integrating these three metrics, this study provides a more comprehensive perspective on tree migration potential—growth residuals highlight recent responses, absolute growth rate quantifies overall productivity, and IV reflects historical distributions.

3.2. HOF model latitudinal analysis

To examine latitudinal patterns of growth residuals, absolute growth rate, and IV, we applied the Huisman-Olff-Fresco (HOF) hierarchical modeling approach (Huisman et al., 1993). This method characterizes species' ecological responses along environmental gradients, such as latitude in this study, by fitting one of five hierarchical models of increasing complexity: Flat (I), indicating no discernible trend; Monotonic (II), representing an increasing or decreasing trend; Plateau (III), where responses increase or decrease but remain bounded below a maximum value; Symmetric (IV), reflecting a bell-shaped distribution with a mid-latitudinal optimum; and Skewed (V), indicating an asymmetric response favoring either leading or trailing latitudinal edges. Prior to modeling, each metric was smoothed using a 0.5° latitudinal moving average, and the best-fitting model for each species was determined using Akaike Information Criterion (AIC). Importantly, our use of latitude in this context is not intended as a direct surrogate for temperature, but rather as an ecological gradient to examine directional trends in residual growth not explained by modeled drivers. Growth residuals that consistently peak north or south of a species' mid-range latitude may indicate spatial shifts in climatic suitability or adaptation lag—providing insights into potential range dynamics under ongoing climate change.

4. Results

4.1. Random forest growth models

We applied RF models to analyze growth rate patterns for 56 tree species in the eastern United States using the selected predictor variables: Basal Area (BA), Mean Temperature (MAT), and Mean Precipitation (MAP). These variables consistently explained the most variation in growth rates across species, aligning with their biological significance—tree growth is primarily influenced by energy (temperature), water availability, and tree size (Prechzsch, 2009). Model performance varied widely across species, with R^2 values ranging from 0.78 to below 0. Among the 56 species analyzed, we selected 20 species with R^2 values of 0.4 or higher to focus on those with more reliable model fits (Table 1). While this threshold does not represent an absolute distinction between strong and weak models, it provides a balance between including a sufficient number of species while prioritizing those with a clearer relationship between growth and the selected environmental variables. Notably, loblolly pine ($R^2 = 0.77$), shortleaf pine ($R^2 = 0.71$), and red spruce ($R^2 = 0.70$) exhibited the highest model performance, reflecting strong growth responses to temperature, precipitation, and basal area. Conversely, species with lower R^2 values, such as flowering dogwood ($R^2 = 0.03$) and sassafras ($R^2 = 0.02$), exhibited weaker model fits (Supplementary Data, S3), suggesting that additional unmeasured factors, such as competition, disturbance regimes, or microsite conditions, may play a larger role in their growth patterns.

4.2. Latitudinal patterns of growth residuals, absolute growth rate, and importance value (IV)

To assess species-specific migration potential, we examined latitudinal patterns of growth residuals, absolute growth rate, and IV using HOF models. Growth residuals provide a measure of species' responses to contemporary climatic conditions by capturing deviations from expected growth patterns after accounting for tree size and environmental factors. Absolute growth rate reflects overall productivity trends along the latitudinal gradient, while IV represents historical abundance patterns, offering insight into long-term demographic stability or shifts. The results (Table 1) revealed three major patterns: species with northward growth residual peaks (HOF Model II or III, where the peak latitude is north of the species' mid-range latitude), species with southward growth residual peaks (HOF Model II or III, where the peak latitude is south of the species' mid-range latitude), and species exhibiting no discernible trend in growth residuals (HOF Model I, where there is no significant variation). Within each category, species were further classified based on whether IV and absolute growth rate aligned with or diverged from growth residual trends. A comparative visualization (Fig. 1) integrates all three metrics, illustrating the relative positioning of their peak latitudes in relation to species' mid-range latitudes. Additionally, individual HOF model results are presented separately for each metric: growth residuals (Fig. 2), absolute growth rate (Fig. 3), and IV (Fig. 4).

For brevity, we use the abbreviations IV (Importance Value peak latitude), G (Absolute Growth Rate peak latitude), and GR (Growth Residual peak latitude) to report latitudinal trends across the three metrics. Several species exhibited increasing northward trends in growth residuals, suggesting enhanced suitability or adaptability at higher latitudes. Among these, yellow-poplar (IV: 38.1°N; G: 36.9°N; GR: 43.0°N), red maple (IV: 43.7°N; G: 45.4°N; GR: 48.5°N), and eastern hemlock (IV: 43.4°N; G: 45.3°N; GR: 47.0°N) showed consistent northward shifts across all three metrics, indicating broad latitudinal expansion. Conversely, some species exhibited southward growth residual peaks, indicating reduced adaptability at northern latitudes and potential constraints on poleward expansion. Loblolly pine (IV: 32.9°N; G: 33.2°N; GR: 28.0°N) showed a consistent southward trend across all three metrics, suggesting that its distribution remains restricted to the southeastern U.S. Similarly, shortleaf pine (IV: 35.4°N; G: 35.2°N; GR:

Table 1

HOF model results for Importance Value (IV), absolute growth, and growth residual for 20 study species, including geographic range classification (Woodall et al., 2009) and regeneration mechanism rankings (Woodall et al., 2010). R^2 values represent the performance of the Random Forest model used for growth predictions.

SPCD	Species name	Growth Residual model	Growth Residual peak	IV model	IV peak latitude	Growth model	Growth peak	geographic range orientation	Regeneration	Mid-range latitude	R^2
131	loblolly pine	II	28.0	V	32.9	V	33.2	S	3	35	0.77
110	shortleaf pine	II	30.0	V	35.4	V	35.2	S	4	35	0.71
97	red spruce	II	35.0	II	47.0	II	35.0	N	5	41	0.70
121	longleaf pine	I	31.3	III	34.2	V	30.9	S	4	31.25	0.70
621	yellow-poplar	II	43.0	V	38.1	V	36.9	S	8	36.25	0.66
318	sugar maple	I	40.8	V	45.4	V	46.3	N	5	40.75	0.57
111	slash pine	III	35.5	II	24.5	V	30.3	S	8	30	0.57
129	eastern white pine	I	41.3	V	43.3	II	34.0	G	9	41.25	0.55
711	sourwood	I	34.8	IV	36.2	I	34.8	S	5	34.75	0.55
591	american holly	I	35.3	V	40.3	I	35.3	S	5	35.25	0.54
316	red maple	II	48.5	V	43.7	V	45.4	G	1	37	0.52
832	chestnut oak	V	34.2	V	38.7	V	35.5	G	6	37.75	0.51
372	sweet birch	I	39.3	V	41.2	III	44.5	N	9	39.25	0.50
802	white oak	II	30.0	IV	38.7	V	35.0	G	6	39.25	0.49
261	eastern hemlock	II	47.0	V	43.4	V	45.3	N	5	40.25	0.48
611	sweetgum	I	34.0	V	34.0	V	34.1	S	8	34	0.44
833	northern red oak	I	39.8	V	43.2	V	45.4	N	6	39.75	0.42
653	sweetbay	I	32.8	V	27.2	IV	30.5	S	13	32.75	0.42
743	bigtooth aspen	I	42.0	IV	44.1	V	46.9	N	2	42	0.40
221	baldcypress	III	39.5	V	27.0	II	25.5	S	9	32.5	0.40

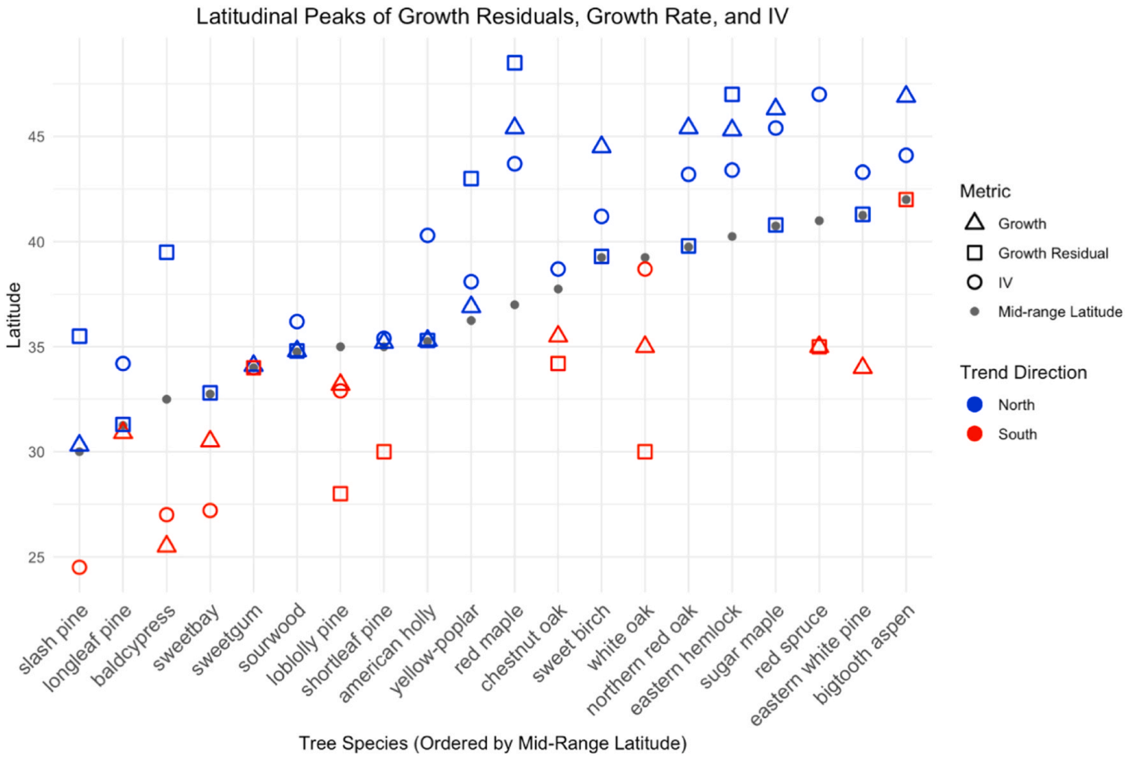

Fig. 1. Latitudinal peaks of growth residual, absolute growth and IV for 25 selected study species.

30.0°N) and chestnut oak (IV: 38.7°N; G: 35.5°N; GR: 34.2°N) maintained stable IV and absolute growth rate across their ranges, but declining northern growth residuals indicate potential range contractions. White oak (IV: 38.7°N; G: 35.0°N; GR: 30.0°N) showed a particularly strong divergence, with stable IV but both growth residuals and absolute growth rate peaking farther south, suggesting it may not be effectively tracking warming trends.

Several species exhibited no discernible trend in growth residuals (HOF Model I), indicating stable growth across latitudes. Within this group, longleaf pine (IV: 34.2°N; G: 30.9°N; GR: 31.3°N), sugar maple (IV: 45.4°N; G: 46.3°N; GR: 40.8°N), American holly (IV: 40.3°N; G: 35.3°N; GR: 35.3°N), and northern red oak (IV: 43.2°N; G: 45.4°N; GR: 39.8°N) had IV peaks positioned farther north than their growth residual peaks. This suggests that while these species historically maintained greater abundance in northern latitudes, their current growth responses to climate conditions are concentrated farther south.

The misalignment between IV and growth residuals may indicate a demographic lag, where past distributions do not yet reflect shifting

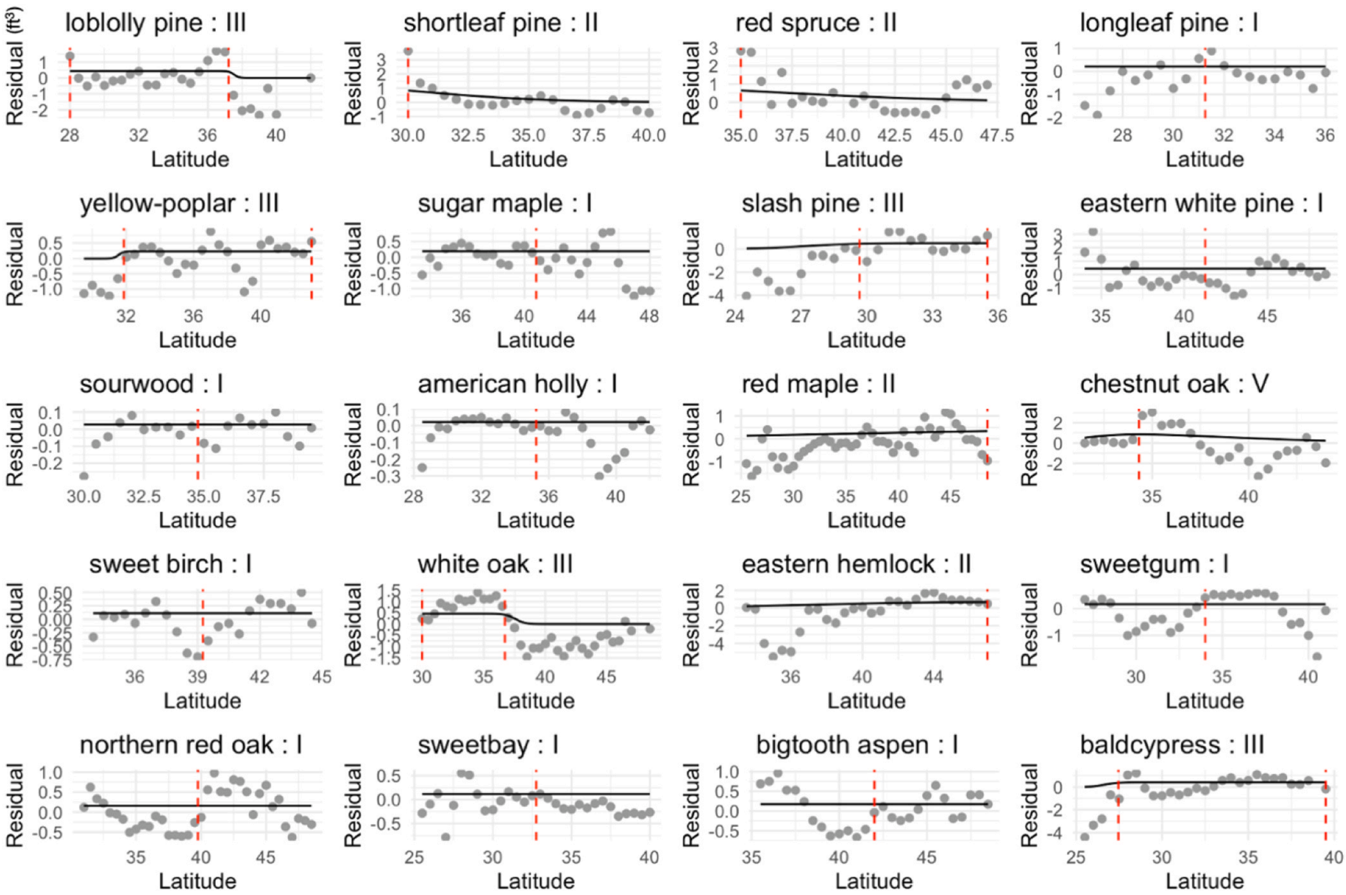

Fig. 2. Latitudinal response of growth residual predicted by HOF model. The red vertical line indicates the peak latitude, grey dots represent observed values (smoothed with 0.5° moving average), and the solid curve represents the HOF model prediction.

growth dynamics. Red spruce (IV: 47.0°N; G: 35.0°N; GR: 35.0°N) and American holly, for example, had IV peaks substantially farther north than their growth residual and absolute growth rate peaks, suggesting that while northern populations remain abundant, they are experiencing lower-than-expected growth. In contrast, for species like sugar maple, where the difference is less pronounced, northern populations remain dominant, but growth rates are stabilizing rather than shifting poleward.

Some species exhibited growth residual trends that contrasted with both IV and absolute growth rate patterns, suggesting early signals of range shifts despite historical stability. Baldcypress (IV: 27.0°N; G: 25.5°N; GR: 39.5°N) and slash pine (IV: 24.5°N; G: 30.3°N; GR: 35.5°N) had northward growth residual peaks, despite historical IV and absolute growth rate being centered at more southern latitudes. This pattern suggests that while these species have historically been abundant in the southern U.S., their recent growth rates are increasing at northern range edges, potentially signaling an early-stage migration response. Conversely, chestnut oak and red spruce exhibited a northward IV peak but declining growth residuals, suggesting that while the species has historically been distributed farther north, its current productivity is weakening in those regions, potentially indicating range contraction.

5. Discussion

This study examined latitudinal patterns of tree migration potential in eastern U.S. forests by analyzing growth residuals, absolute growth rate, and IV using HOF models. Our results demonstrate that a single metric alone may not fully capture migration dynamics. Growth residuals provide the most direct signal of climate sensitivity and adaptation potential, while absolute growth rate reflects general species productivity across latitudes. IV, as a static measure of relative abundance, highlights demographic lag and historical range stability. The integration of these complementary metrics allows for a more nuanced interpretation of species migration potential, distinguishing between active range expansion, population stability, and species facing range contraction.

5.1. *Comparison with previous studies*

Many of our findings align with prior studies documenting northward migration trends. Species such as red maple, yellow-poplar, and eastern hemlock showed strong evidence of northward expansion across all three metrics, consistent with previous findings that these species exhibit increasing seedling densities at higher latitudes (Woodall et al., 2009; Zhu et al., 2012). These results reinforce the view that certain fast-growing, generalist, or disturbance-adapted species are more likely to track climate change effectively. In contrast, some species exhibited unexpected or divergent patterns. Loblolly pine, often considered climate-resilient due to its widespread plantation use and plasticity, displayed consistent southward trends across growth residuals, suggesting limited capacity to expand northward beyond its current southeastern distribution. Similarly, chestnut oak and white oak showed southward-trending growth residuals despite maintaining stable Importance Values (IV), indicating that while these species remain abundant, their current growth is concentrated in more southern portions of their range. This may signal early-stage range contraction or a lag in adapting to warming conditions, contrasting with prior assumptions about the ecological breadth and resilience of oak species (Woodall et al., 2009). Overall, our findings highlight that even among widely distributed or abundant species, responses to climate change are highly variable, and historical abundance does not always predict future

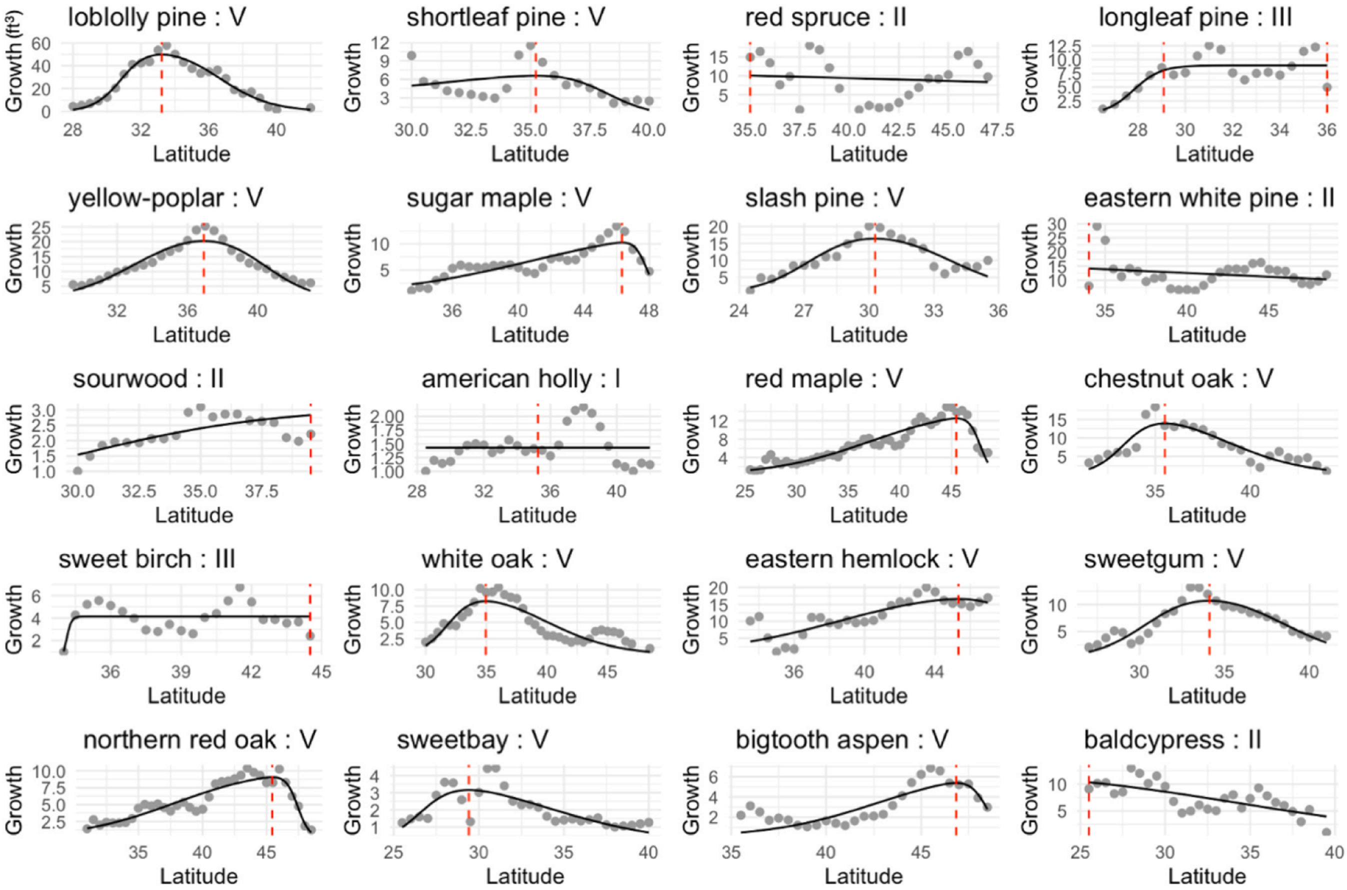

Fig. 3. Latitudinal response of absolute growth predicted by HOF model. The red vertical line indicates the peak latitude, grey dots represent observed values (smoothed with 0.5° moving average), and the solid curve represents the HOF model prediction.

growth or migration potential.

5.2. Discrepancies between growth residuals, growth rate, and IV

A key observation was the frequent mismatch between growth residuals and IV, highlighting a potential demographic lag in migration. Species such as sugar maple and American holly exhibited IV peaks significantly farther north than their growth residual peaks, suggesting that while these species historically occupied northern regions, their present-day growth rates have stabilized at lower latitudes. This may indicate a delayed response to climate change, where species remain abundant in historical ranges but have yet to fully shift their growth potential northward. Conversely, baldcypress and slash pine exhibited the opposite trend, with northward-skewed growth residuals despite their IV and absolute growth rate peaking in southern latitudes. This pattern suggests that while historical abundance remains concentrated in the south, recent growth trends indicate increasing suitability at northern range edges. These species may be at the early stages of migration, potentially expanding poleward if dispersal mechanisms allow.

5.3. Influence of geographic range and migration potential

We further examined whether migration trends correlated with species' general geographic range classification (northern, southern, or generalist), as defined by Woodall et al. (2009) (Table 1). Overall, no strong trend emerged between geographic range classification and migration potential. However, certain patterns were notable. For species classified as northern, such as eastern white pine and bigtooth aspen, our results indicate that their highest IV remains at northern latitudes within the U.S., but we cannot determine whether their growth potential extends further northward into Canada. These species showed growth residual peaks south of their IV peaks, which may indicate regional climatic constraints within the U.S., but cannot be interpreted as definitive evidence of northern range limitation without data from beyond the U.S. border. Generalist species showed variable patterns. Red maple and yellow-poplar, both widely distributed across the eastern U.S., exhibited strong northward migration signals, suggesting that broad ecological tolerance may facilitate range expansion. In contrast, species such as white oak and chestnut oak, also considered generalists, exhibited southward-trending growth residuals despite stable IV, suggesting that historical abundance does not always predict future range stability. For species classified as southern, patterns were similarly mixed. Loblolly pine and shortleaf pine, both dominant in the southeastern U.S., exhibited southward-trending growth residuals, suggesting limited poleward expansion and potential climatic constraints at their northern range edges. Conversely, bald cypress and slash pine exhibited northward-skewed growth residuals, despite their IV and absolute growth rates being centered at lower latitudes, suggesting that some southern species may be experiencing increased productivity at their northern range margins, potentially signaling early-stage expansion. These results highlight the species-specific nature of migration potential and suggest that even within broad geographic classifications, responses to climate change are highly variable.

5.4. Regeneration mechanisms and migration potential

Regeneration strategy is an important factor influencing species migration potential, as seed dispersal mode and reproductive strategy affect a species' ability to track climate change. Species with small,

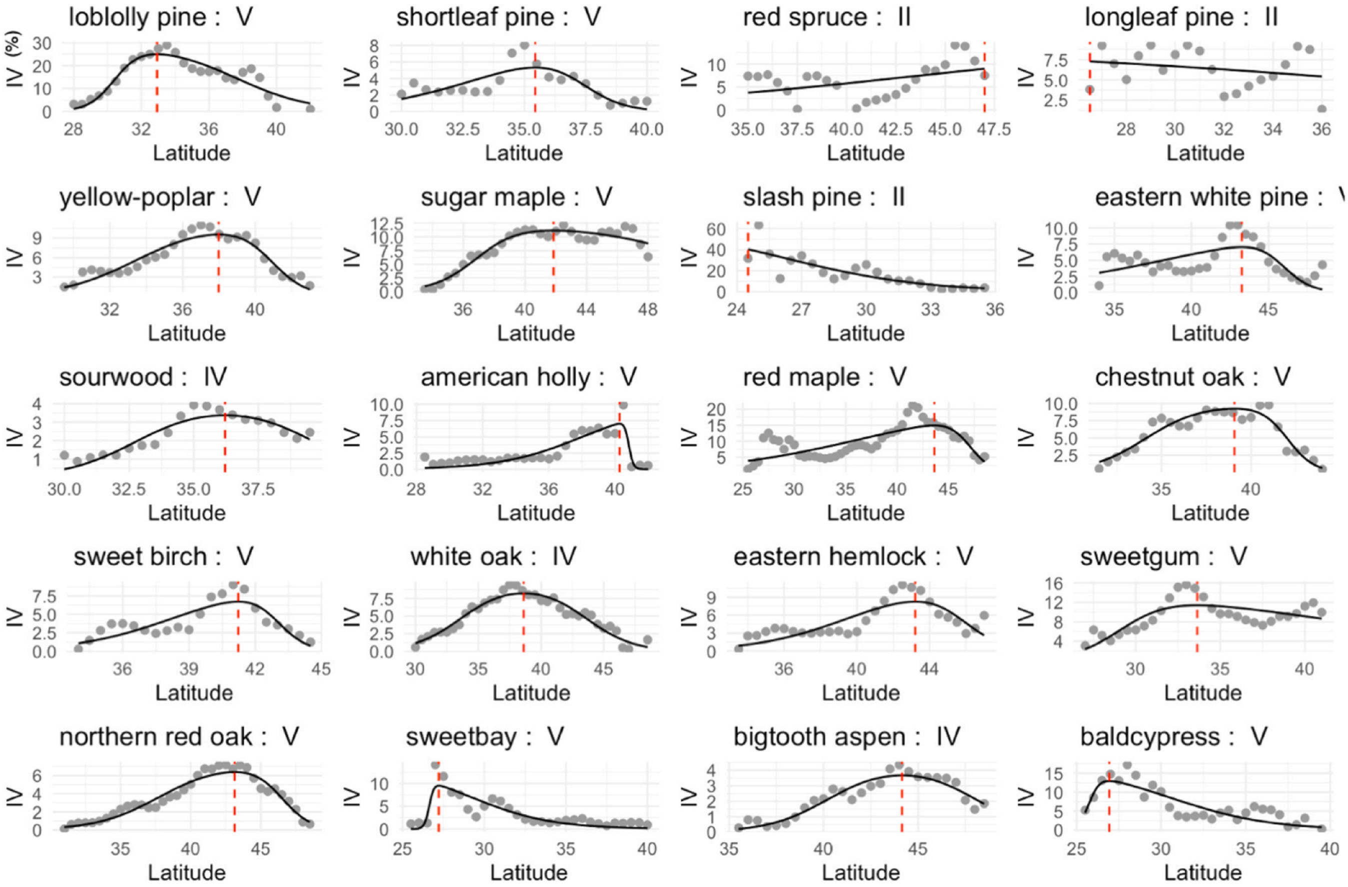
loblolly pine : V
shortleaf pine : V
red spruce : II
longleaf pine : II
yellow-poplar : V
sugar maple : V
slash pine : II
eastern white pine :
sourwood : IV
american holly : V
red maple : V
chestnut oak : V
sweet birch : V
white oak : IV
eastern hemlock : V
sweetgum : V
northern red oak : V
sweetbay : V
bigtooth aspen : IV
baldcypress : V

Fig. 4. Latitudinal response of Importance value (IV) predicted by HOF model. The red vertical line indicates the peak latitude, grey dots represent observed values (smoothed with 0.5° moving average), and the solid curve represents the HOF model prediction.

wind-dispersed seeds generally exhibit higher migration capacity, while those with heavier, animal-dispersed seeds may experience greater lag times in range shifts (Croteau, 2010). To contextualize our findings, we referenced the regeneration mechanism rankings provided by Woodall et al. (2010), which classify species into ecological guilds based on seed dispersal mode, growth strategy, and masting attributes. These rankings range from 1 (lightly seeded pioneer species) to over 10 (heavy-seeded), providing a framework for interpreting species' relative dispersal potential and migration constraints (Table 1).

Our results suggest that regeneration strategy had a stronger influence on IV than on growth residuals or growth rate. This is expected, as IV represents species abundance, reflecting long-term demographic processes such as seed dispersal, establishment success, and competitive interactions. Since IV is shaped by past regeneration and recruitment dynamics, species with higher dispersal capacities—such as wind-dispersed species—tend to show greater latitudinal shifts in IV, whereas species with limited dispersal ability often maintain a more stable distribution. In contrast, growth residuals, which capture short-term deviations in growth performance, are more directly influenced by climate variability and physiological responses, making them less dependent on dispersal mechanisms. Species ranked in higher regeneration guilds (i.e., heavy-seeded species with limited dispersal potential) tended to have IV peaks farther south than their growth residual peaks, indicating that historical abundance may lag behind recent growth trends. For example, sweetbay (guild rank = 13) and slash pine (guild rank = 8) exhibited IV peaks well south of their growth residual peaks, reinforcing the idea that species with limited dispersal ability may retain high abundance in historically favorable regions despite shifting climatic suitability. This trend contrasts with wind-dispersed species such as red maple and sugar maple (ranked in lower regeneration guilds), which exhibited strong northward trends across all three metrics, suggesting rapid dispersal and establishment at higher latitudes. Despite the general alignment between regeneration traits and IV patterns, regeneration strategy alone does not fully explain species-specific migration dynamics, as many species deviate from expected trends. This variability suggests that additional factors—such as competition, habitat availability, and site-specific climate constraints—may play a critical role in determining species' realized migration potential.

5.5. *Implications for forest composition and biodiversity*

The divergent migration responses among growth residual, absolute growth, and IV observed in this study suggest that climate change may lead to novel species assemblages, as some species expand their range while others experience growth declines. Fast-growing, disturbance-adapted species such as red maple and yellow-poplar may gain competitive advantages in newly suitable habitats, potentially reshaping forest composition by outcompeting slower-migrating species such as oaks and conifers. This shift may have cascading effects on ecosystem functions, including carbon storage, nutrient cycling, and habitat availability for dependent wildlife. Moreover, the asynchronous migration of canopy dominants and understory species could create transient ecological mismatches. For instance, if species like sugar maple maintain high abundance in northern latitudes but experience declining growth, their recruitment potential may be reduced, allowing more rapidly migrating competitors to establish dominance. Similarly, if southern species such as loblolly pine and shortleaf pine fail to expand northward, they may experience increased mortality at their trailing edges without corresponding colonization of new habitats.

While this study provides strong evidence of species-specific migration potential, further research is needed to identify the mechanisms driving range shifts. Long-term monitoring of seedling establishment, recruitment success, and adult tree mortality across latitudinal gradients will be critical for validating these findings. Additionally, although soil properties are well-recognized as important drivers of tree growth, spatially complete and consistent soil data were not available at the continental scale. For example, the gNATSGO database—among the most comprehensive U.S. soil datasets—exhibited substantial data gaps in parts of the Southeast and Midwest. As a result, soil effects could not be systematically incorporated into our models and may contribute to unexplained variation in growth residuals beyond temperature, precipitation, and basal area. Future work incorporating experimental studies, dispersal modeling, and genetic analyses will be important for distinguishing climate-driven migration from demographic inertia or environmental constraints. These efforts will help refine projections of forest responses to climate change and inform adaptive management strategies.

6. Conclusion

This study demonstrates the value of integrating growth residuals, absolute growth rate, and IV to assess tree migration potential under climate change. Growth residuals captured near-term climatic responses, absolute growth rate reflected species productivity, and IV provided a historical baseline for distribution trends. Our findings reveal species-specific and variable migration dynamics, with some species actively tracking warming trends while others exhibit demographic lags or potential range contractions. The frequent mismatch between growth residuals and IV underscores the importance of considering both historical abundance and recent growth trends when evaluating migration potential. These results highlight the need for climate-adaptive forest management strategies that account for species-specific growth responses and demographic constraints.

CRediT authorship contribution statement

Choi Junwon: Writing – review & editing, Methodology, Investigation, Data curation. **Patton Michelle:** Data curation, Conceptualization. **Kwon Youngsang:** Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

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

Acknowledgements

This work was supported in part by a grant from The University of Memphis College of Arts and Sciences Research Grant Fund. This support does not necessarily imply endorsement by the University of research conclusions.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122718.

Data availability

Data will be made available on request.

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