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Relative decline in density of Northern Hemisphere tree species in warm and arid regions of their climate niches

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Although climate change is expected to drive tree species toward colder and wetter regions of their distribution, broadscale empirical evidence is lacking. One possibility is that past and present human activities in forests obscure or alter the effects of climate. Here, using data from more than two million monitored trees from 73 widely distributed species, we quantify changes in tree species density within their climatic niches across Northern Hemisphere forests. We observe a reduction in mean density across species, coupled with a tendency toward increasing tree size. However, the direction and magnitude of changes in density exhibit considerable variability between species, influenced by stand development that results from previous stand-level disturbances. Remarkably, when accounting for stand development, our findings show a significant change in density toward cold and wet climatic conditions for 43% of the species, compared to only 14% of species significantly changing their density toward warm and arid conditions in both early- and late-development stands. The observed changes in climate-driven density showed no clear association with species traits related to drought tolerance, recruitment and dispersal capacity, or resource use, nor with the temperature or aridity affiliation of the species, leaving the underlying mechanism uncertain. Forest conservation policies and associated management strategies might want to consider anticipated long-term species range shifts alongside the integration of contemporary within-distribution density changes.

species density | climate change | climatic sensitivity | stand development | forest dynamics

Significance

Although climate-related tree species distribution shifts have long been expected, observational evidence of the anticipated changes toward cold and wet regions has been relatively elusive. Our analysis of 73 widely distributed species in 126,422 forest inventory plots across Europe and North America reveals a reorganization of density favoring colder and wetter regions of their climatic niches. However, contrary to the anticipated change toward smaller individuals over time due to climate change, our findings reveal a tendency toward increasing tree size over recent decades. The species-specific information on the direction and magnitude of climate-driven changes in density can form an important input for conservation, management, and restoration plans in an era of unprecedented human-caused environmental change.

Forests worldwide are largely shaped by human activity (1). Humans have strongly modified forest structure, composition, and distribution for millennia through land-use changes and alteration of disturbance regimes (2, 3). In the Northern Hemisphere, the concurrent changes in land use and intensive forest harvesting have decreased stand age (4) and increased forest area and biomass (5, 6). These human-driven alterations in stand development directly determine tree demographic responses to climate by modifying functional traits related to tree age and size, density-dependent processes, and species interactions (7–10). At the same time, temperature and water availability are major constraints on tree demography (11, 12), and since temperature and water deficit are increasing due to climate change, changes in species density toward relatively colder and wetter climatic conditions are expected (13). However, studies tracking changes in tree species density have shown multiple directions in response to climate (14–18), largely because climate responses interact with changes in stand development (19). Thus, a substantial challenge lies in accurately assessing climate-driven changes in species density while accounting for the effects of stand development.

Here, we use harmonized data from national forest inventories from Europe and North America to analyze changes in species density. Changes in species density were calculated as the annual change in the number of stems per hectare for all trees larger than 12.7 cm in diameter at breast height between consecutive forest inventory censuses across the period 1985 to 2019 (mean ± SD census interval = 8 ± 3 y). For our analyses, we considered more than two million measured trees from 73 widely distributed species across 126,422 forest inventory plots (*SI Appendix*, Table S1). As our aim was to quantify changes in species density within their present range, we used plots where the species was present in the first census, excluding those where all trees were missing in the subsequent census to mitigate potential management-related impacts like clear-cutting (mean ± SD initial number of stems across species = 108 ± 72 stems per hectare). Changes in species density are closely associated with early indicators of species range shifts, particularly shifts in

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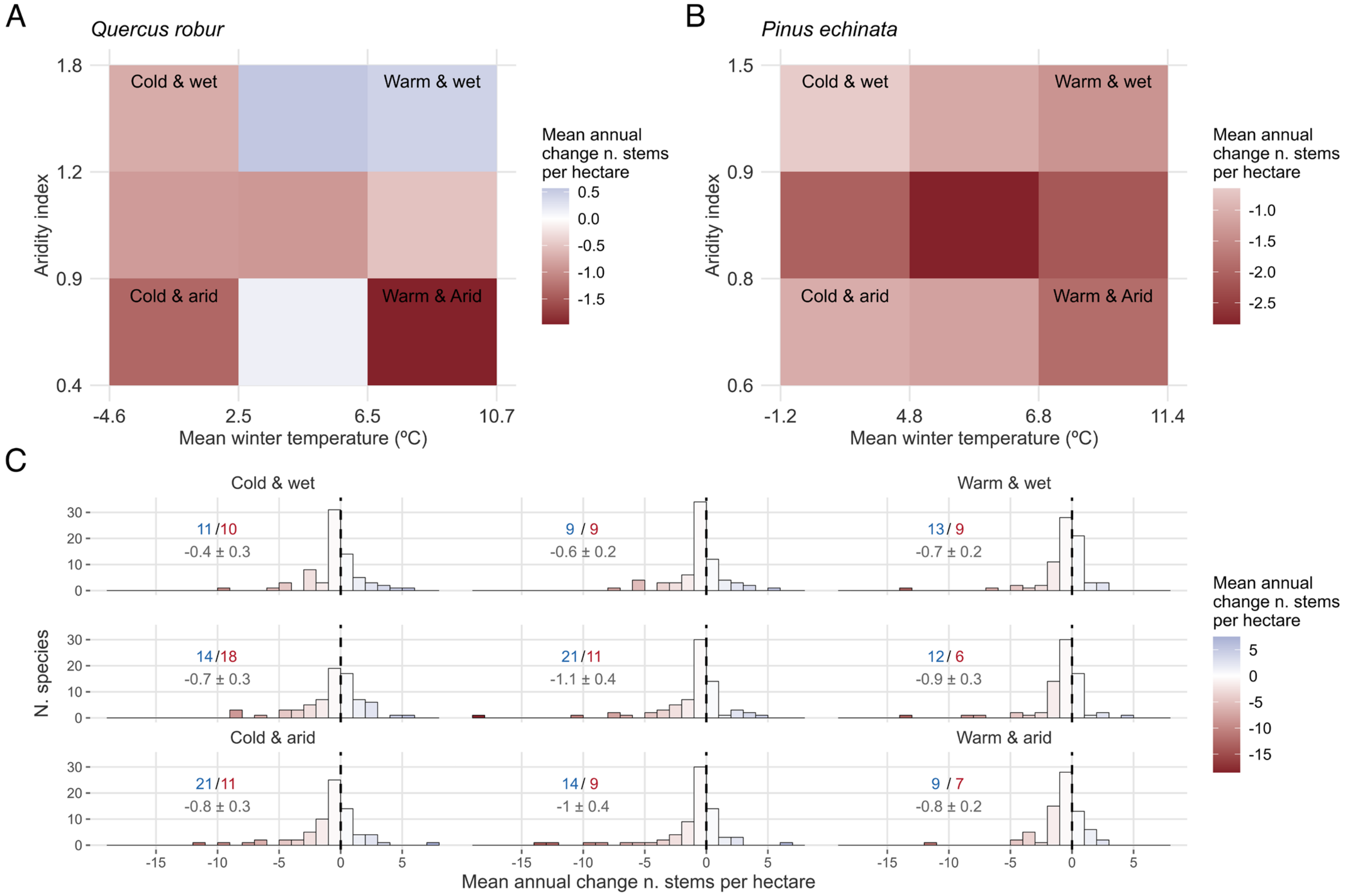

Fig. 1. Decline in mean density of the 73 species analyzed across their climatic niches, with considerable variability in the direction of changes in density between species. We partitioned the climatic niche occupied by each species into nine climatic regions defined by the terciles in mean winter temperature and aridity across the species' observed range. For each of the nine regions, we calculated mean changes in density (i.e., annual change in the number of stems per hectare for all trees larger than 12.7 cm in diameter at breast height between consecutive forest inventory censuses) considering all inventory plots sharing those climatic conditions across the period 1985 to 2019. Panels in the top row show results for two illustrative species with contrasting climatic niches (*A*) *Quercus robur* and (*B*) *Pinus echinata*. A full set of results for all species is found in *SI Appendix*, Figs. S2 and S3. (*C*) Histograms showing the mean annual change in the number of stems per hectare for all 73 species and for each of the nine climatic regions defined by temperature and aridity terciles. Numbers show the number of species with significant increases (blue) and decreases (red) in density (*SI Appendix*, Fig. S4), along with the overall mean change ± SE across species. Dashed lines indicate no change and negative values indicate a decrease in overall mean density. Note that legends in (*A* and *B*) are on different scales, and higher values of the aridity index imply less aridity.

species' optimum along their climatic ranges (20, 21). Thus, changes in density are crucial for quantifying species' climatic sensitivity and anticipating population extinctions (13, 22). We quantified changes in species density in relation to climate and stand development. Specifically, we tested whether, and in which direction, species density is changing across different regions of the species' climatic niches and whether these changes are modulated by the local stand developmental stage. We also examined the relationship between species' climatic niches, measured as the tolerance to cold temperatures and aridity, species traits such as xylem water potential at 50% loss of conductivity (P_{50}), seed dry mass, and nitrogen mass per unit leaf area, and the magnitude of climate-driven density changes.

We quantified changes in species density by partitioning the climatic niche occupied by each species based on mean winter temperature and aridity. Mean winter temperature influences species' local densities by limiting survival, growth, and reproduction due to cold stress (23–25). Moreover, winter temperature also reflects growing season constraints, encompassing both mean temperature and the length of the growing season (*SI Appendix*, Fig. S1). Similarly, aridity determines tree reproduction and survival by regulating hydraulic conductance and carbon assimilation (26, 27). For each plot where a species was found, we obtained the climatological mean winter temperature and the aridity index for the period 1970 to 2000. For characterizing mean winter temperature, we used the mean temperature of the coldest quarter of the year. The aridity index was calculated by dividing the mean annual precipitation by the mean annual reference evapotranspiration, with higher values indicating wetter conditions.

We found that local species mean density changed according to the position of the population in the species' climatic niche (see Fig. 1 *A* and *B* as an example for two species with contrasting climatic niches). Changes in mean density were often relatively modest and showed large variability between species (Fig. 1*C* and *SI Appendix*, Figs. S2–S4), aligning with previous studies observing divergent directions of species responses to climate change (14–18). However, looking across all species, the mean annual number of stems per hectare decreased on average across all climatic regions (Fig. 1*C*).

The decline in species mean density could result from self-thinning during stand development (28), particularly as the age structure of temperate forests is known to have been shifted by land-use history and harvest toward a younger distribution than would naturally occur (4, 29). For example, we observed that species mainly distributed in southern Europe have increased in mean density, which is a direct consequence of the abandonment of agricultural activities and traditional forest-use [*SI Appendix*,

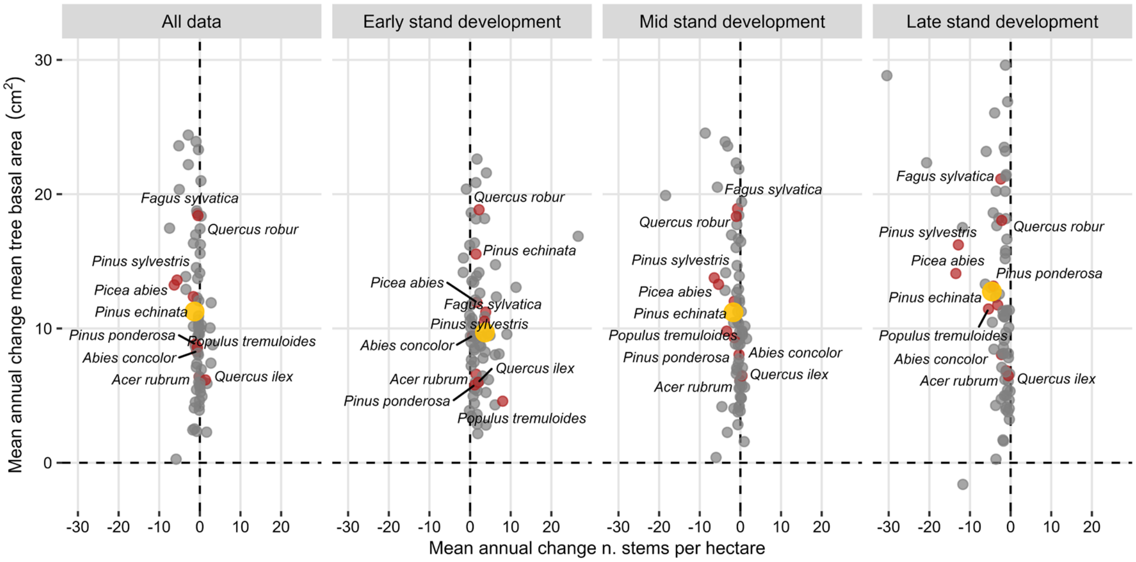

Fig. 2. Relationship between changes in density and changes in mean tree basal area between censuses. Mean tree basal area was calculated as the average basal area of living trees of each species in each plot, and changes in mean tree basal area as the annual change in mean tree basal area between censuses. Mean changes in density were calculated as the annual change in the number of stems per hectare between censuses. Both changes were quantified for all trees larger than 12.7 cm in diameter at breast height between consecutive forest inventory censuses across the period 1985 to 2019 and averaged for each species. Gray points represent mean changes in density and basal area for all analyzed species across all the plots where each species was present, while red points highlight example species covering climatic gradients in Europe and the United States. The yellow points indicate the overall mean of all species. Early, mid, and late panels include only sites that have low, mid, or high stand basal areas compared to the highest stand basal area values found in the climate space in which the stand was located (*Materials and Methods*).

Fig. S2; (30)]. However, it might also indicate that a decrease in species density in warm and arid regions of their climatic niches is not accompanied by an increase in cold and wet regions, and therefore species densities are not following climate change in European and US forests (18, 31).

To better understand the role of land-use history and forest management, we calculated an index of stand development according to whether the stand basal area was relatively low (early development) or high (late development) compared to the highest stand basal area values found in the climate space in which the stand was located. We then quantified the relationship between changes in density and changes in mean tree basal area between censuses. Strikingly, all examined species exhibited a mean increase in mean tree basal area between censuses (Fig. 2). However, mean changes in density displayed important variation depending on stand development: While early stands generally increased in the number of stems, late stands experienced a decline in the number of stems (Fig. 2). The observed increases in mean species density in early development stands suggest ongoing recruitment of saplings and smaller trees into the larger size (12.7 cm in diameter at breast height) analyzed here. In contrast, the decrease in mean species density in late development stands is likely due to competition, leading to density reductions and resulting in fewer but larger tree individuals (28), although for some commercially managed species these reductions could also be associated with commercial thinnings. These results contrast with recent studies suggesting changes toward smaller individuals over time, with a leading driver expected to be water stress (1, 32, 33). Instead, observations across the European and North American continents suggest a tendency toward increasing tree size, at least when tree losses from stand-replacing disturbances are discounted. This shift toward larger tree sizes could potentially be due to land-use change legacies coupled with the positive effects of carbon dioxide and nitrogen fertilization, effectively counterbalancing the negative impacts of climate change on tree growth in Northern Hemisphere forests over the analyzed period (6, 34).

To enhance our understanding of the respective roles of climate and stand development in driving species density changes, we used generalized additive models to model, for each species, the number of stems recorded in each plot in the second census as a function of the initial number of stems (i.e., first census), the number of years elapsed between censuses, the country, plot area, and the interaction between climate and stand development. The interaction between mean winter temperature, aridity, and stand development was modeled with tensor product smooths (35). Using predictive comparisons (36), we calculated for each species the number of stems expected per plot in the last census in cold and wet conditions (defined as the first quartile of mean winter temperature and third quartile of aridity index for that species), median (i.e., second quartiles of mean winter temperature and aridity index), and warm and arid conditions (i.e., third quartile of mean winter temperature and first quartile of aridity index; Fig. 3). In addition, to assess the effect of stand development, we replicated each of these predictions for actual, early, and late stand development stages (i.e., setting stand development at actual, first, and third quartile values, respectively, see *SI Appendix, Supplemental Methods* and Fig. S13). This approach allowed us to improve the goodness of fit and predictive power of the models and enhance the interpretation of the non-linear interactions between stand development and climatic drivers. Then, we obtained annual changes in species density per hectare as the difference between the predicted number of stems per plot in the climatic and stand development conditions explained above and the number of stems in the first census, divided by the years elapsed between censuses, and extrapolated to the hectare. Finally, we calculated the relative difference in density changes between cold-wet and warm-arid conditions within species, which we call "climatic sensitivity." Hence, the climatic sensitivity of each species was calculated as the difference in the annual change in the number of stems per hectare between cold and wet, and warm and arid climatic conditions. We calculated climatic sensitivities for each of actual, early, and late stand development.

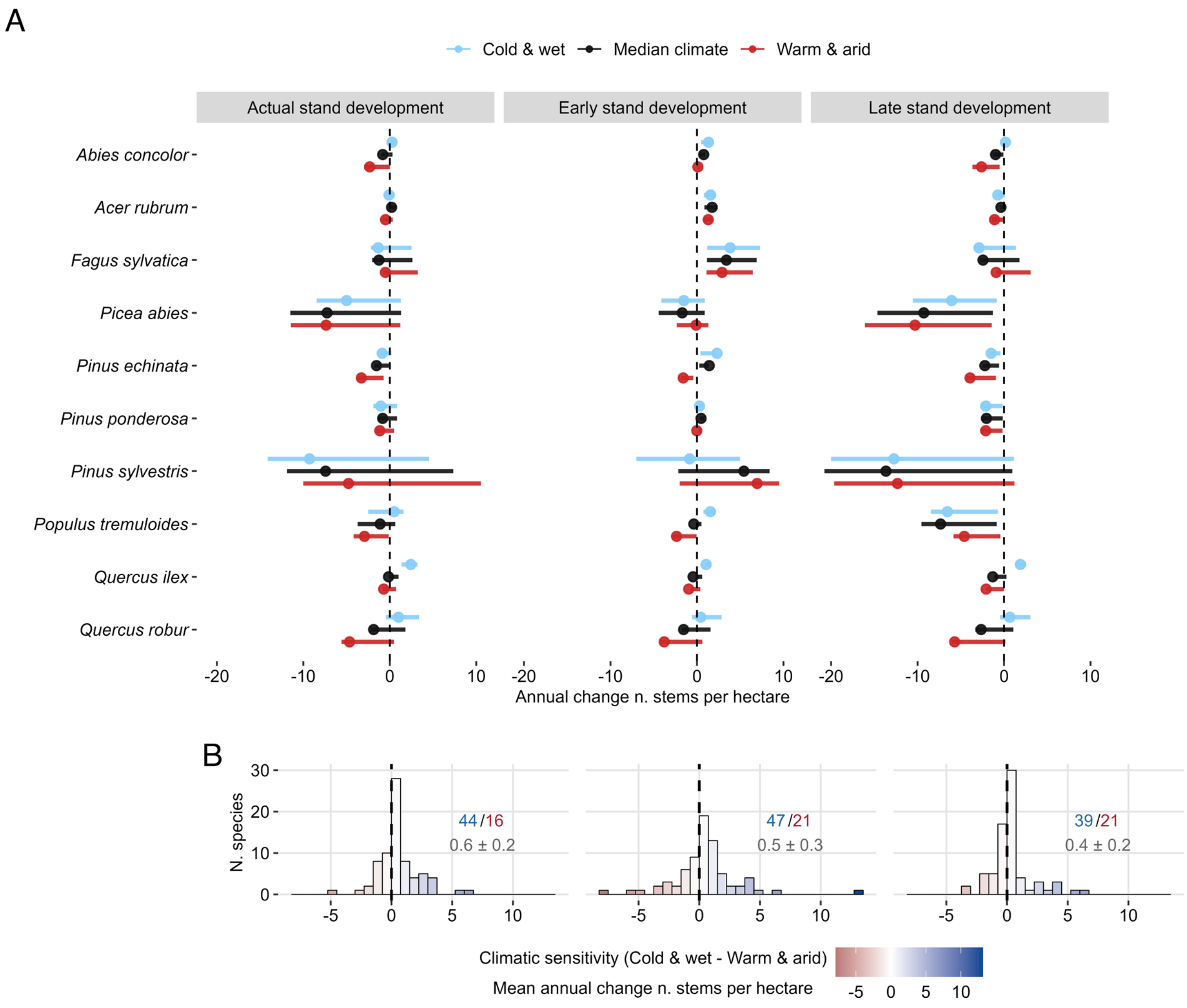

Fig. 3. Climate-driven changes in species density adjusting for stand development. (*A*) Predicted changes in species density (i.e., annual change in the number of stems per hectare for all trees larger than 12.7 cm in diameter at breast height between consecutive forest inventory censuses across the period 1985 to 2019) by species-level models when setting mean winter temperature and aridity index in cold and wet (blue), median climate (black), and warm and arid (red) conditions within each species' climatic niche, and setting stand development in actual, early, and late stand development values (*Materials and Methods*). Points indicate mean changes in species density and intervals 50% equitailed CI, with positive values indicating increases and negative values decreases in density over time. The selection of species for representation was made by covering climatic gradients of Europe and the United States. A full set of results for all species is found in *SI Appendix*, Figs. S5 and S6. (*B*) Histograms showing the mean climatic sensitivity of each species in actual, early, and late stand development conditions. Species' climatic sensitivity was calculated as the mean difference in the annual change in the number of stems per hectare expected when setting climatic conditions as cold and wet or warm and arid, according to each species' climatic niche. Positive values indicate that in cold and wet climatic conditions, species would gain more individuals, or lose fewer individuals, than in warm and arid conditions. Negative values indicate that in cold and wet conditions, species would gain fewer individuals, or lose more individuals, than in warm and arid conditions. Numbers on each histogram panel show the number of species with significant increases (blue) and decreases (red) in density (*SI Appendix*, Table S2), along with the overall mean climatic sensitivity ± SE across species. Dashed lines indicate no difference between cold and wet and warm and arid climatic conditions within species.

When adjusting for stand development, we found that species density generally showed larger increases, or smaller decreases, in cold and wet conditions compared to warm and arid conditions within species' climatic niches (Fig. 3). The overall climatic sensitivity was generally modest, and we observed large variation between species in both sign and magnitude. However, more than half of the species (64% in early-development stands and 53% in late-development stands) showed a significant increase in relative density toward cold and wet conditions (Fig. 3*B* and *SI Appendix*, Table S2). Overall, 43% of the species significantly increased toward cold and wet conditions in both early- and late-development stands. In contrast, only 14% of the species showed a significant increase in relative density toward warm and arid conditions in both early- and late-development stands. The remaining species showed no significant or divergent patterns between early- and late-development stands (*SI Appendix*, Table S2).

The observed differences in density between cold and wet and warm and arid climatic conditions were often large. For instance, in the case of *Quercus ilex*, considering an average density of 87 stems per hectare and a climatic sensitivity of 4 stems per hectare per year observed in late-development stands implies a percentage change of 4.6% per year or 46% per decade (*SI Appendix*, Table S2). The density reorganization in favor of cold and wet climatic conditions within species' climatic niches might indicate intermediate states in an ongoing range-shifting process and be an early indicator of species range shifts toward relatively colder and wetter climatic conditions (13, 22). While our study focused on quantifying changes in density for adult individuals within their climatic niches, the observed change aligns with patterns observed in tree fecundity and seedling recruitment of northern species across North America (37). Considering that we adjusted for stand development and that management effects are unlikely to act systematically with climatic drivers (38), the observed variation is likely attributable to climate change.

The diverse evolutionary histories of species have resulted in a wide range of responses to climate (39). However, identifying key species-level attributes that drive species responses to climate is crucial for predicting their vulnerability to climate change. Thus, we tested whether species' climatic sensitivity (i.e., mean difference in density changes between cold and wet and warm and arid conditions of each species' climatic niche as shown in Fig. 3*B*) was related to species' mean winter temperature or aridity niche position, xylem water potential at 50% loss of conductivity (P_{50}), seed dry mass, and nitrogen mass per unit leaf area using a linear model. Xylem water potential at 50% loss of conductivity reflects species' drought tolerance, while seed dry mass indicates species' recruitment capacity, both crucial for understanding density changes in warm and arid conditions, where species may approach their physiological limit to water availability (40, 41). Nitrogen mass per unit leaf area relates to resource use, and seed dry mass also explains dispersal capacity, both important for understanding density changes toward cold and wet conditions (41, 42).

In early-development stands, we found that aridity niche position was the only significant predictor, showing increases in mean density toward cold and wet conditions for species located in wetter conditions (*SI Appendix*, Fig. S7). However, we observed that this pattern was primarily driven by *Tsuga heterophylla*, the species with the highest aridity niche position (i.e., living in the wettest regions in our database). After excluding this species from the analyses, aridity niche position no longer remained significant, and mean winter temperature niche position emerged as the most influential variable. Although not statistically significant, more warm-tolerant species increased mean density toward cold and wet conditions. This result might suggest that for warm-tolerant species, cold stress might be increasingly less limiting in cold and wet conditions of their ranges due to climate warming (43). In late-development stands, we did not find any important relationship between species' climatic sensitivity and temperature or aridity affiliation of species, P_{50}, seed dry mass, and N mass per unit leaf area (*SI Appendix*, Fig. S8). Presumably, this suggests that the changes are either a result of a more complex strategy space than can be captured with the traits used in this study, or there is an additional biotic filtering effect of competition (44). On average, species showed larger increases in density, or lower decreases, in relatively cold and wet climatic conditions, regardless of their traits, temperature, or aridity affinities (*SI Appendix*, Figs. S7 and S8). The apparent discrepancy between our study and previous studies on tree mortality related to species traits (40, 45) can be reconciled when considering life history theory; species that are more vulnerable to mortality are also likely to be more rapidly able to respond to more favorable conditions (46). We speculate that because our results consider species density changes across their whole ranges, the net change for different life-history strategies may prove to be similar. Our results therefore suggest that temperature or aridity tolerance and species traits are not particularly helpful to anticipate these species' overall vulnerability to climate change (47).

Although species occurrence data are abundant in existing literature, the scarcity of data on changes in density over time is notable. The harmonization of forest inventories across many European countries and continental United States has revealed that many Northern Hemisphere tree species are changing their density toward cold and wet regions of their climatic niches. Our results highlight that climate-driven changes in species density are largely influenced by stand development following natural disturbance or harvesting (48). The generally positive climatic sensitivity displayed by species with different climatic niches and trait values indicates that no forest region appears clearly more resilient against climate change. However, the 14% of species that showed a significant increase in relative density toward warm and arid conditions in both early- and late-development stands (Fig. 3*B* and *SI Appendix*, Table S2) suggests that factors other than climate may be influencing the density of these species in cold and wet regions (44) or that these particular species are relatively more resilient to climate change. Plausibly, these species are able to take advantage of declines of competitor species, either through ecological or management processes. It remains unclear whether these species would continue to show increased relative densities in their warm and arid region once migration of species typically associated with warmer and more arid regions is completed and new species assemblages emerge. Therefore, one of the next critical frontiers is to account for novel competitive interactions within novel future climates to accurately predict species responses to climate change (49). By determining climate-driven species density changes, our study shows that despite a masking effect of stand development, including a tendency for individual trees to get larger, tree species densities are responding to climate change in European and US forests, shifting toward relatively colder and wetter regions. Forest conservation policies and associated management strategies might want to consider expected long-term range shifts (39, 50) concomitantly with the incorporation of contemporary within-distribution density changes.

Materials and Methods

Forest Inventory Data. We calculated changes in species density using harmonized forest inventory data from seven European countries and the continental United States, with censuses spanning between 1985 and 2019 (Mean ± SD census interval = 8 ± 3 y; *SI Appendix*, Table S1). For all countries, we analyzed the last two available consecutive forest inventory censuses with a census interval ≥4 y. For all tree species, we excluded plots where the species was missing (i.e., zero stems were recorded) in the first census, as our focus was on assessing changes in density in regions where species were already present. We also excluded plots where all trees were missing in the subsequent census to mitigate potential management-related impacts like clear-cutting. In the end, we used a total of 126,422 plots. We calculated density as the number of stems per hectare for all trees larger than 12.7 cm in diameter at breast height and changes in species density as the annual change in the number of stems per hectare between consecutive forest inventory censuses. In plots where not all trees were measured in all subplots (e.g., variable radius plots) we generated stochastic stem counts from a one-truncated Poisson distribution with λ equal to the number of stems extrapolated to the plot area using *extraDistr* R package (51). To select the most widely distributed species, we aggregated the data into 0.1° × 0.1° grid cells (i.e., ~11.1 km at equator) and we only considered native species to Europe and the United States that have a good coverage in our dataset (i.e., species with ≥ 50,000 individuals of >12.7 cm in diameter at breast height and that were present in ≥500 cells and ≥1,000 plots in our dataset). In total, we selected 73 species (*SI Appendix*, Table S2).

Species' Climatic Niches and Traits. We quantified the climatic niche of each species using the climatological mean winter temperature and the aridity index (*SI Appendix*, Fig. S1). To characterize mean winter temperature, we used the mean temperature of the coldest quarter obtained from WorldClim 2 (52). The mean temperature of the coldest quarter is calculated as the mean temperature of the coldest three months of the year. Aridity was obtained from Global Aridity Index and Potential evapo-transpiration (ET0) Climate Database v2 (53). This variable is based on the Global Aridity Index and it is calculated by dividing the mean annual precipitation by the mean annual reference evapo-transpiration. Values for the aridity index increase with wetter conditions. Both climatic variables represent the average for the period 1970 to 2000 with a 30 arc-seconds spatial resolution (~ 1 k m at equator).

We characterized species' mean winter temperature and aridity niche position using species' chorological maps for European species (54) and Little's range maps for US species (55, 56). We quantified species mean winter temperature niche position and aridity niche position using the average of the mean winter temperature and aridity index across the whole species' range, respectively. Xylem water potential at 50% loss of conductivity (P_{50}; MPa), seed dry mass (mg), and nitrogen mass per unit leaf area (mg/cm^2) for each species were obtained from the TRY Database (57) and supplemented by a literature review of 75 research publications (58). We used the median value of each trait for each species. We then calculated genus-level trait averages for species lacking trait data. Specifically, we used genus-level trait averages for 5 species for N mass per unit leaf area and 15 for P_{50}. Ultimately, we obtained mean winter temperature niche position, aridity niche position, seed dry mass, and N mass per unit leaf area data for all analyzed species and P_{50} data for all but one.

Stand Development. Basal area is commonly used as a proxy of stand development (e.g., ref. 59), as basal area increases during stand development (28). However, the maximum stand basal area (i.e., that expected to be observed in late-development stands) depends on climate and soil conditions (30, 60). Thus, to account for the primary process of secondary succession influencing species density, we calculated stand development based on the basal area of each plot with respect to the maximum basal area found in plots with similar climate and soil characteristics.

First, we created clusters of plots with similar climate and soil characteristics along Europe and the United States considering key factors driving basal area increment: annual mean temperature, annual precipitation (log-transformed), and nitrogen availability (30, 60). Climatological mean annual temperature and precipitation at 1 km^2 were obtained from WorldClim 2 (52) and nitrogen availability in 0 to 30 cm at 250 m from SoilGrids v2 (61). Since nitrogen between 0 and 30 cm was obtained from different layer thicknesses (0 to 5, 5 to 15, and 15 to 30 cm), we calculated the weighted mean of nitrogen by adjusting for the thickness.

Second, we computed the k-means clustering using *stats* R package (62) for values of *k* ranging from 10 to 100 clusters with increments of 10. For each *k*, we calculated the total within-cluster sum of squares, and using the elbow method, we identified the optimum number of clusters [*SI Appendix*, Figs. S9 and S10; (63)]. We selected 40 clusters in both Europe and the United States with a compactness (i.e., the similarity of the plots within the same cluster) of 95.5% and 96.2% in Europe and the United States, respectively. Additionally, to ensure that the selection of 40 clusters was optimal, using the same sequence from 10 to 100 with an increment of 10, we analyzed the median cluster size and the minimum cluster size (*SI Appendix*, Figs. S9 and S10). We also confirmed that the coefficient of variation of cluster precipitation, mean temperature, and nitrogen availability followed a similar pattern to that of the within-cluster sum of squares (*SI Appendix*, Figs. S9 and S10). Furthermore, we observed that the coefficient of variation of basal area remained high regardless of the number of clusters, suggesting a high variability of stand development stages within the cluster. Once the number of clusters was set to 40, we validated it using the silhouette method with an average silhouette width 0.26 and 0.29 in Europe and the United States, respectively (*SI Appendix*, Figs. S11 and S12).

Finally, for each of the forest inventory plots, we obtained a stand development value ranging from 0 to 1 by dividing the basal area of each plot to the maximum basal area of its corresponding cluster (i.e., 95th percentile of the basal area of the cluster to which this plot belonged). For plots exceeding the 95th percentile of the basal area of the cluster, we assigned a value of 1. Since maximum basal area is not specific to individual plots but rather to clusters, and therefore aggregated over numerous plots, it is less susceptible to plot idiosyncrasies, such as those related to forest management.

Analyses. First, we determined how changes in species density varied across each species' climatic niche. For this aim, we divided the climatic niche of each species into nine climatic regions. These regions were defined by the terciles in mean winter temperature and aridity across the species' observed range. Specifically, populations were categorized based on their location within the 0 to 33%, 33 to 66%, or 66 to 100% range of each species' distribution in our dataset. This approach allowed us to quantify a climatic niche that ranged from cold and wet to warm and arid regions. For each of the nine regions, we calculated the mean annual change in the number of stems per hectare, considering all inventory plots sharing those climatic conditions. Then, we averaged values from all species to obtain the overall mean change, along with the SE across species. We also calculated species-level means and SD of changes in density by fitting a linear mixed model for each climatic region using *lme4* R package (64). These models considered all plots within each region and assumed a normal distribution, with changes in density as the response variable, and plot identity and species identity included as random effects. Changes in density across species' climatic niches were visualized with *terra* and *tidyverse* R packages (65, 66), and all analyses were performed using R Statistical Software [v4.2.0; (62)].

Second, to comprehend the impact of stand development on changes in density, we assessed, for each species, the relationship between changes in density and changes in mean tree basal area between censuses. Mean tree basal area was calculated as the average basal area of living trees of each species in each plot for all trees larger than 12.7 cm in diameter at breast height, and changes in mean tree basal area as the annual change in mean tree basal area between consecutive forest inventory censuses. We quantified this relationship for early, mid, and late stand development. Early stand development was defined by sites with low stand basal area values (i.e., below or equal to the first quartile of stand development when considering all species together) in the climate space in which the stand was located. Mid stand development was defined by sites with mid stand basal area values (i.e., above the first quartile of stand development and below the third quartile of stand development when considering all species together) in the climate space in which the stand was located. Late stand development was defined by sites with high stand basal area values (i.e., above or equal to the third quartile of stand development when considering all species together) in the climate space in which the stand was located.

Then, we quantified the effect of climate and stand development on species density across each species' range by fitting generalized additive models [GAM; see *SI Appendix*, *Supplemental Methods* and Fig. S13; (35, 67)] to each species separately using *mgcv* R package [*SI Appendix*, Figs. S5 and S6; (68)]. We modeled the number of stems in the second census following a negative binomial distribution with a tensor product smooth of aridity, mean winter temperature, and stand development of each plot. The basis for the tensor product smooths was cubic regression splines. We also included the interaction of the natural logarithm of the number of stems in the first census and the census interval as fixed effects to adjust for the initial number of stems in the plot and the number of years elapsed between censuses, respectively. In addition, we included the country in which each plot was measured to adjust for different sampling methods among countries and an offset of the natural logarithm of plot area to adjust for different plot areas. We diagnosed each species' GAM fit, checking the residuals plots using *mgcv*, *gratia,* and *DHARMa* R packages (68–70). We also checked the relationship between the response and main effects with *visreg* R package (71), estimated smooths using *gratia* R package (69), the performance of the model using *performance* R package (72), and evaluating predictions on the observed data (for further details see *SI Appendix*, *Supplemental Methods* and Fig. S13 and https://doi.org/10.5281/zenodo.10882718).

We evaluated the effects of climate and stand development on species density using average predictive comparisons [*SI Appendix*, *Supplemental Methods* and Fig. S13; (36)]. To calculate the effect of climate, we predicted changes in density in different climatic conditions: first setting mean winter temperature in the first quartile and aridity index in the third quartile (i.e., cold and wet), second by setting mean winter temperature and aridity index in the second quartiles (i.e., median climate), and finally setting mean winter temperature in the third quartile and aridity index in the first quartile (i.e., warm and arid) of each species' climatic niche. Each of these three predictions was repeated three times: i) using the actual stand development values in the plot; ii) setting stand development values to the first quartile when considering all species together (i.e., early stand development); and iii) setting stand development values to the third quartile when considering all species together (i.e., late stand development). Then, we obtained annual changes in species density per hectare as the difference between the predictions of each model (i.e., number of stems in the second census) and the number of stems in the first census, extrapolated to the hectare and dividing by the years elapsed between censuses. The climatic sensitivity of each species was calculated as the mean difference in the annual change in the number of stems per hectare expected when setting climatic conditions as cold and wet or warm and arid in actual, early, and late stand development. Positive values indicate that in cold and wet climatic conditions, species would gain more individuals, or lose fewer individuals, than in warm and arid conditions. Negative values indicate that in cold and wet conditions would gain fewer individuals, or lose more individuals, than in warm and arid conditions. Then, we calculated the overall mean climatic sensitivity by averaging the climatic sensitivity values from all species, along with the associated SE across species. We visualized changes in species density along climatic and stand development gradients using *ggdist* and *tidyverse* R packages (66, 73).

Modeling the number of stems in the second census as a response and including the number of stems in the first census as an explanatory variable aligns with the recommendations of several studies [*SI Appendix*, *Supplemental Methods* and Fig. S13; (74, 75)]. First, the model fit and predictive power are greatly improved when the state variable, rather than the change, is used as response. Second, modeling changes in percentage could lead to a skewed interpretation, where a change of one stem might represent a significant percentage change for a low-density plot but remain insignificant for a plot with a higher stem count. Therefore, the interpretation of the change magnitude becomes dependent on the baseline (i.e., initial number of stems). Finally, the need to include nonlinear interactions between stand development and climatic drivers prevents the direct interpretation of effect sizes from model parameters. In this context, interpretation must rely on predictive comparisons (36). Hence, both the model fitting and the interpretation were enhanced when modeling states rather than changes.

Finally, we quantified the importance of species' mean winter temperature niche position, aridity niche position, xylem water potential at 50% loss of conductivity, log-transformed seed dry mass, and nitrogen mass per unit leaf area on species' climatic sensitivity, as calculated above. We fitted a multivariable linear model including species' mean winter temperature niche position, aridity niche position, xylem water potential at 50% loss of conductivity, log-transformed seed dry mass, and nitrogen mass per unit leaf area as fixed effects. We fitted a multivariable model because the diverse effects of these traits could either be additional or offset each other (41). We fitted the model setting stand development values to the first quartile (i.e., early-development stands) and third quartile when considering all species together (i.e., late-development stands). We diagnosed each model fit, checking the residuals plots using *DHARMa* R package (70), and predictions were visualized using *ggeffects* and *tidyverse* R packages (66, 76).

Data, Materials, and Software Availability. Processed data and code [R data format (.rds)] used for this manuscript are openly available in Zenodo at https://doi.org/10.5281/zenodo.10882718 (77).

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