



# High tree diversity exposed to unprecedented macroclimatic conditions even under minimal anthropogenic climate change

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Tree species worldwide face increasing exposure to unprecedented macroclimatic conditions due to anthropogenic climate change, which may trigger biome shifts and ecosystem disruptions. We quantified climate change exposure—shifts to species' currently unoccupied climate zones—for 32,089 tree species globally by 2100, assessing both species-level and local tree diversity risks. On average, 69% of species are predicted to experience macroclimatic shifts in at least 10% of their range, while 14% face exposure in over 50% of their range under a high-emission (4 °C warming) future scenario. This suggests that most species retain substantial climate refugia within their current range. However, local tree diversity exposure is predicted to be severe in vast regions, including Eurasia, the northwestern United States and Canada, northern Chile, and the Amazon Delta. Under a moderate (2 °C warming) scenario, high tree diversity exposure is mostly restricted to taiga regions in the Northern Hemisphere. These findings provide conservative estimates of climate-driven biodiversity risk, as our approach focuses solely on macroclimate and does not account for additional stressors such as land-use change or species interactions. Identifying tree species and areas of high macroclimatic shift exposure allows for targeted conservation strategies, including species stability monitoring, assisted migration, and the protection of climate refugia. Our results offer a foundation for prioritizing conservation actions in a rapidly changing climate, ensuring long-term ecosystem resilience.

area-based conservation | climatic refugia | future climate change | novel climate | tree diversity

Trees are crucial to maintaining Earth's biosphere functioning. They are pivotal for climate change adaptation via increasing ecosystem resilience and reducing ecosystem vulnerability (UN decade of ecosystem restoration, [www.decadeonrestoration.org](http://www.decadeonrestoration.org)). Yet, unprecedented rates of climate change and temporally co-occurring climate extremes in the Anthropocene severely affect our ecosystems (1–3). Specifically, climate change causes widespread tree mortality and large-scale forest diebacks (4, 5). In turn, these may trigger a spiral of events affecting ecosystems further via shifts in species interactions and synergistic interactions with other stressors like fire (6). As global warming continues, there is an increasing risk of tree species extinction and losing invaluable ecosystem functioning from local tree diversity (7, 8). To ensure ecosystem resilience in a rapidly changing world, we need to understand spatial variation in climate change impacts on tree diversity so that we can identify regions that may be relatively stable and those that are most at risk (9).

Long-lived organisms like trees may experience substantial short-term climatic variability throughout their lifespans driven by seasonal fluctuations, yet long-term directional climate changes tend to drive population-level responses. These may involve evolutionary adaptation, although tree taxa often exhibit climatic niche conservatism (10, 11), which can, at least in some cases, lead to local declines (12). We propose a species-specific approach that leverages climate zones as broad-scale descriptors of tree species' climate niches to provide a more comprehensive understanding of how big the impact of anthropogenic climate change is on both individual tree species and broader ecological communities. Unlike conventional species distribution models that require detailed ecological data for individual species, our approach' use of macroclimates allows for a more generalized, data-efficient assessment of climate change across thousands of tree species, including those with limited occurrence data. We defined macroclimates as the Köppen–Geiger climate zones (13), which are clusters combining multiple climate variables that regionalize the world's climate (*SI Appendix, Figs. S1–S3*). Macroclimates are considered to provide substantially different living conditions for trees as they empirically reflect biomes (14) and biomes delineate unique floristic compositions (15–18). Consequently, shifts in macroclimate automatically result in exposure to unprecedented conditions that is unlikely

## Significance

Trees play key roles in terrestrial ecosystems but are sensitive to large climatic changes. Our work quantifies end-of-century climate change exposure—shifts to species' currently unoccupied climate zones—for 32,089 tree species globally. While most species are projected to retain climate refugia within their current range, 45% of Earth's tree-covered land experiences major climatic shifts; within this, 17% faces exposure to novel climatic conditions for half the local tree diversity. These findings emphasize the need for targeted conservation strategies: stability monitoring for highly exposed species, proactive measures such as assisted migration, and protecting climate refugia from anthropogenic disturbances including industrial and extractive activities. Our results provide a foundation for climate-informed biodiversity conservation and long-term ecosystem resilience planning.

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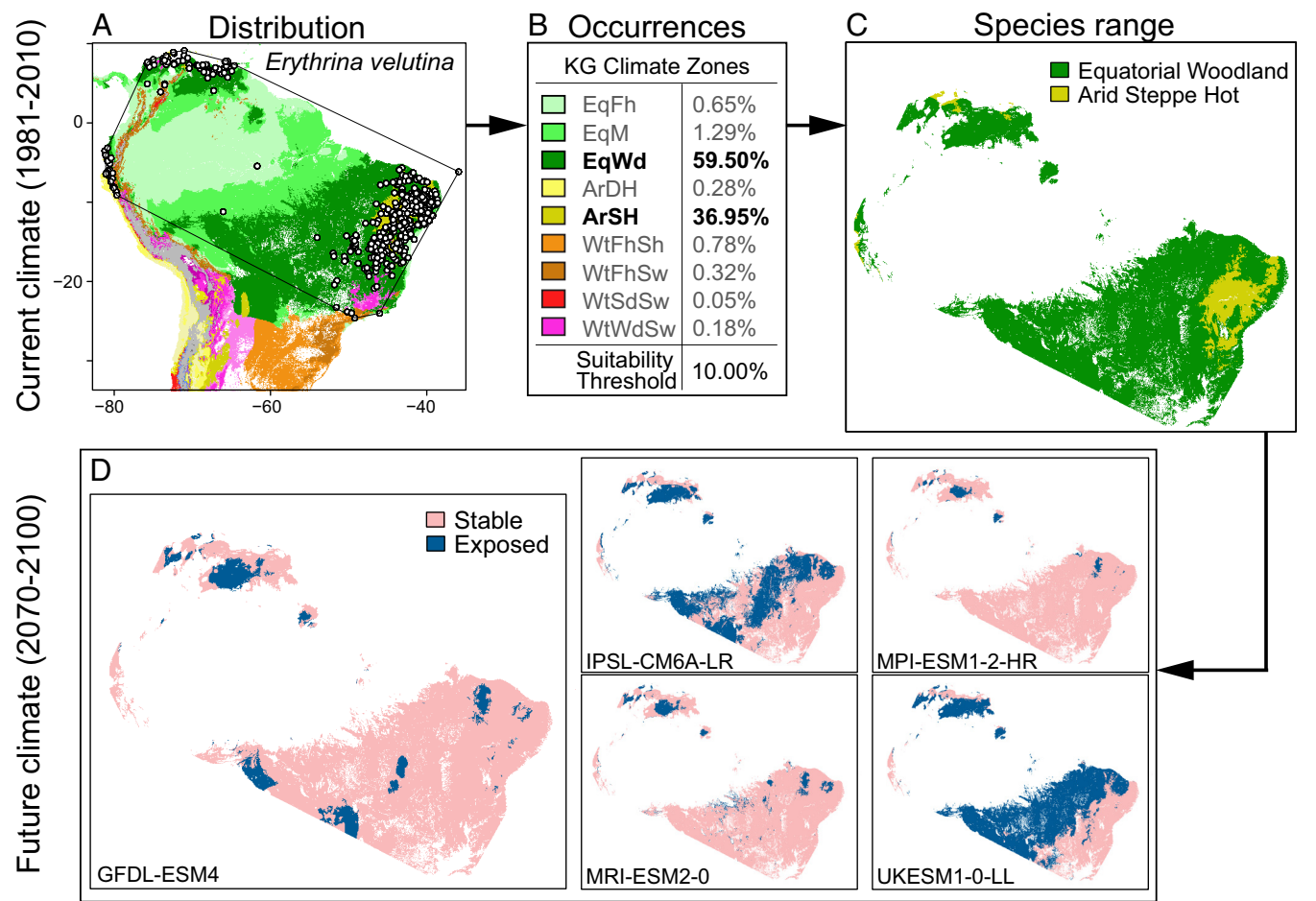
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to be overcome by acclimation or migration (19–24) and threaten local tree diversity and carbon storage (10, 25–27). Yet, even in the Anthropocene, regions exist that experience slower dynamics of anthropogenic climate change (28) where tree diversity exposure is more limited (29–31). These regions could potentially serve as refugia from climate change. Assuming tree species are not able to escape current, rapid climate change (19, 20, 22–24), locating such refugia (i.e., sites where most or all tree species are unexposed to unprecedented climate) can ultimately, potentially minimize tree diversity losses on a gradual scale via place-based monitoring and conservation (28, 32, 33). This is different from the status quo where sites with currently threatened species are conserved (34–37). Protecting these refugia against other anthropogenic threats like land use change will help maintaining tree diversity and associated ecological, climatic, and sociocultural values (33, 38, 39). In this study, we 1) quantified species' exposure to unprecedented macroclimates throughout their current geographic range and 2) localized areas where large proportions of local tree diversity are free from macroclimatic shifts, i.e., climate refugia. We operationally defined "exposure" as shifts in macroclimate at a given location (grid cell) within a species' range to a climate zone that

falls outside the species' inferred suitable macroclimatic conditions, based on the recent historical (1981–2010). Tree species' exposure to macroclimatic shifts was quantified as the relative area of species' ranges that transformed into unsuitable climate zones, where species' ranges were estimated as the extent of occurrence (EOO) excluding unsuitable area, i.e., water, cropland, urban area, and currently unoccupied climate zones (Fig. 1). Estimating exposure to end-of-century (2071–2100) macroclimatic shifts (14) was done for 32,089 tree species at approximately 1 km grid cell resolution. Three scenarios of global change were used ranging from a plausible future approximating a warming of 3.6 °C (ssp3 RCP7.0, referred to as the "high" greenhouse gas emission scenario), a sustainability future with 1.8 °C warming (SSP1 RCP2.6, referred to as "optimistic"), and a "fossil-fueled development" future with 4.4 °C warming (SSP5 RCP8.5, referred to as "extreme") compared to 1850–1900 (40) (*SI Appendix, Fig. S4*). Per scenario, we considered five General Circulation Models (hereafter referred to as climate models; GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL), where the projected future climate variables are categorized into climate zones following the same decision tree (*SI Appendix, Figs. S1 and S5*). In addition to the original 31 Köppen–Geiger climate zones



**Fig. 1.** Methodological overview to define species ranges. *Erythrina velutina* was used as an illustrative example. (A) From the distribution of occurrence records (white points), the EOO was estimated as the minimum convex polygon using 99% of species' occurrences (black line). Colors indicate Köppen–Geiger climate zones, considered in this study as macroclimates, where white represents unsuitable area for any tree species (water, urban area, cropland). (B) The table highlights the species' suitable climate, which is defined as the climate zones that are occupied by at least 10% of the occurrence records. Abbreviations can be found in *SI Appendix, Fig. S2*. (C) Species' current range was defined as the area of suitable climate within the species' EOO. The colored area is considered to be this species' range. (D) Future species' range (pink) based on end-of-century (2071–2100) climate zone projections using five General Circulation Models, each plot indicating the species' range using a different climate model. Here, the results for the most extreme greenhouse gas emission scenario (SSP5 RCP8.5) are illustrated. The areas in pink indicate climate refuge areas for this species as climate zones are projected to stay suitable under future climate change (Stable). Blue areas indicate exposure to unprecedented macroclimates as climate zones are projected to change into unsuitable climate for this species (Exposed). White indicates area outside the species' range.

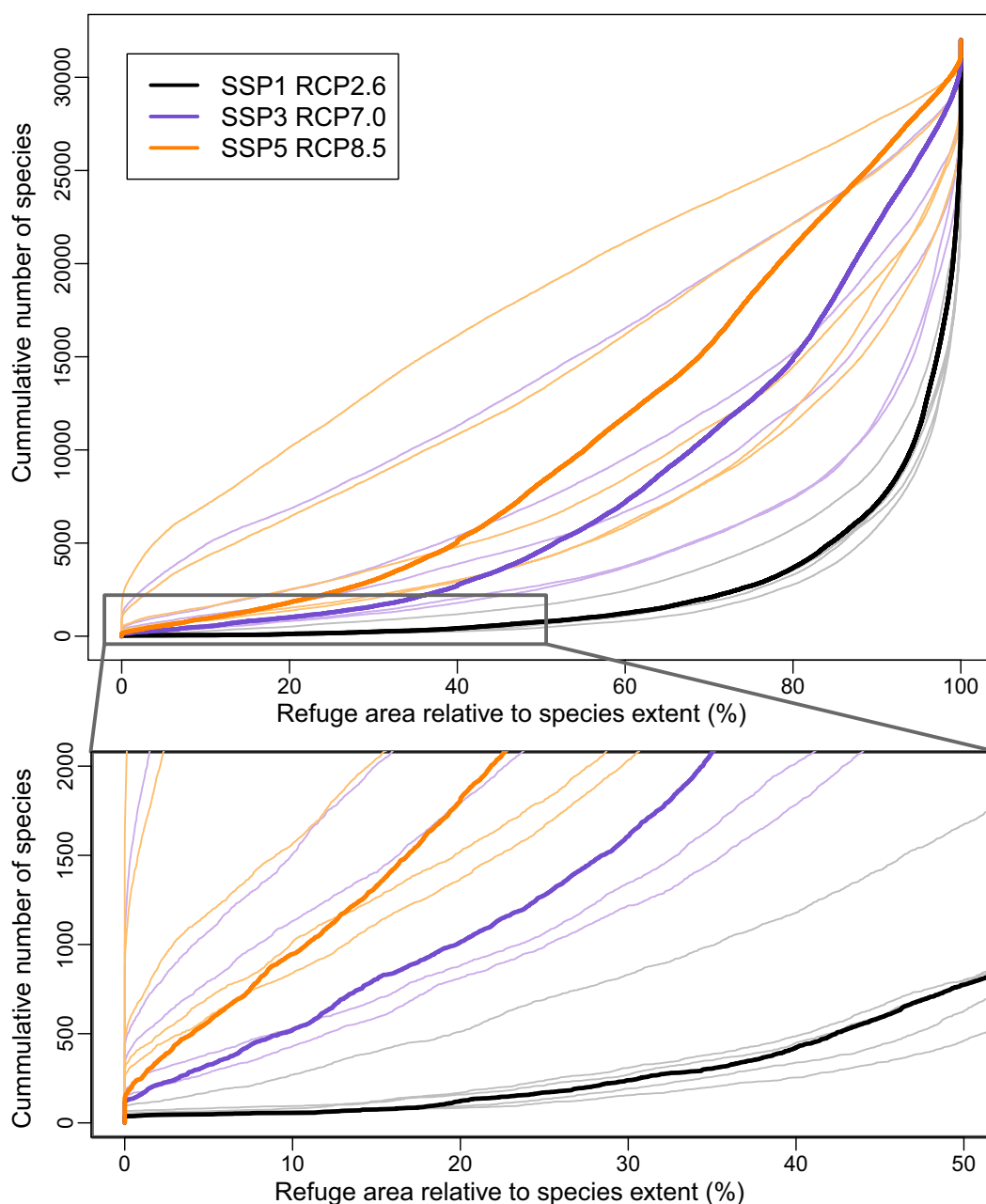
provided by Beck et al. (14), we introduced a “Non-analog Hotter” climate zone to account for the impact assessment of novel climate conditions on tropical ecosystems, which has been shown by various studies (41, 42).

We present the global impact of future macroclimatic shifts on both tree species and local tree diversity and identify areas where species-specific climate refugia may persist. These projections are conservative because they account only for macroclimatic exposure, excluding other major global change drivers that could adversely impact tree species and may further exacerbate climate-driven risks, such as land-use change and species interactions. By focusing on macroclimate, one of the most reliably projected components of future biodiversity scenarios (43–45), we provide a robust foundation for identifying spatial conservation and monitoring priorities aimed at minimizing anthropogenic impacts

(38, 46). Overall, our study highlights candidate climate refugia that are critical for safeguarding Earth’s tree diversity from the impacts of future climate change.

## Results

**Climate Change Impact on Trees at the Species Level.** Under future climate projections from the high-emission scenario, 31% (average over climate models) of all considered tree species were predicted to find refuge from macroclimatic shifts in more than 90% of their current range (Fig. 2). On the other hand, 22,084 species (69%) experience exposure to macroclimatic shifts in (more than) 10% of their current range, with exposure in more than 50% of species’ range for 4,593 species (14%) and in more than 90% species’ range for 521 species (2%). These numbers



**Fig. 2.** Cumulative plot of tree species indicating the relative refuge area compared to tree species’ extent, determined as area with stable climate under three future change scenarios: optimistic (SSP1 RCP2.6; gray), high (SSP3 RCP7.0; purple), and extreme (SSP5 RCP8.5; orange), ranging from the least amount of climate change to the most, respectively. Thicker, darker lines indicate averaged values over five climate models per emission scenario, whereas thinner, lighter lines indicate results from individual climate models per emission scenario.

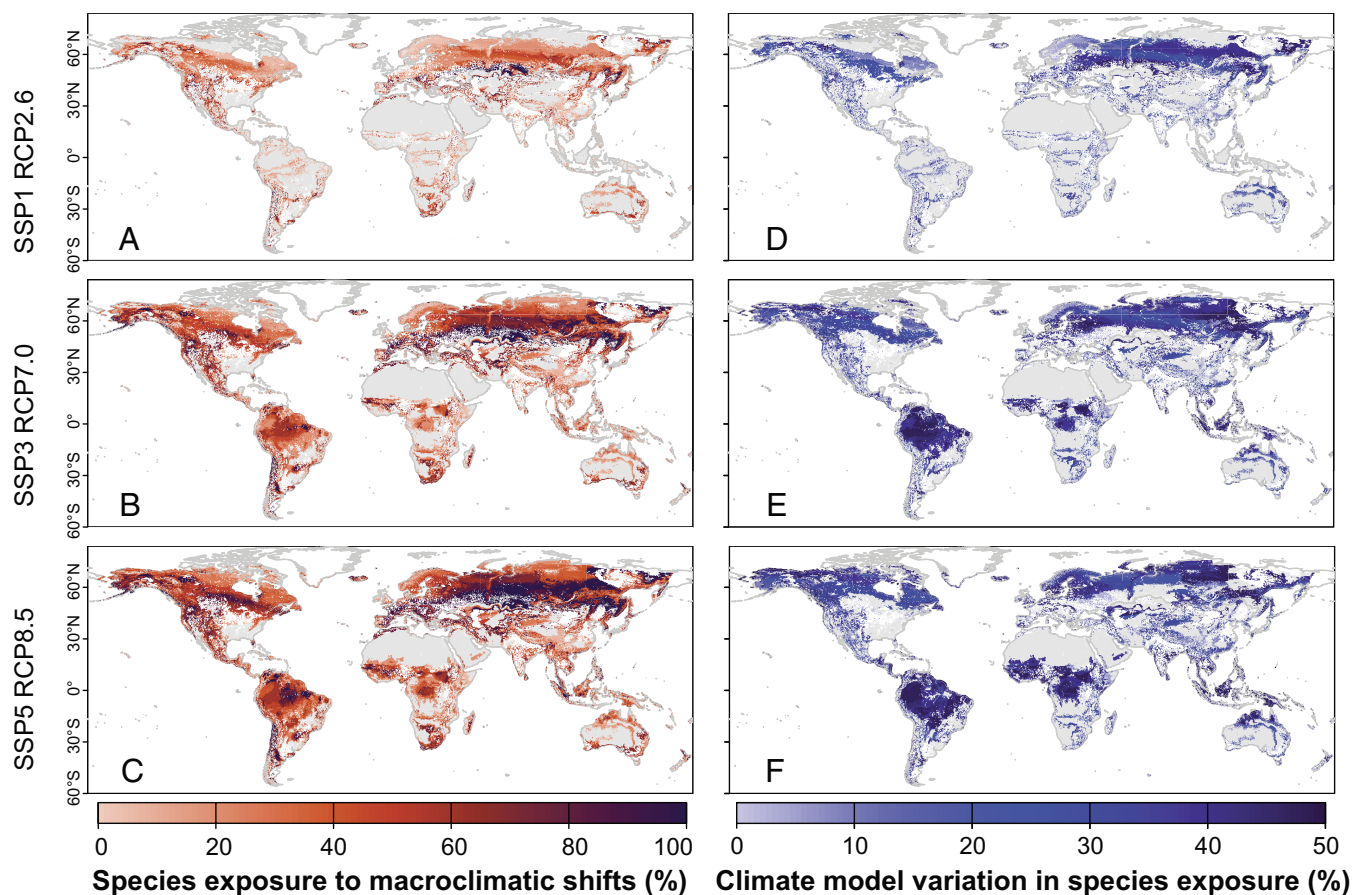
decreased under the optimistic emission scenario to 7,133 [10%], 774 [50%], and 55 [90%] species experiencing exposure (Fig. 2; note that we use square brackets to indicate exposure as percent of species ranges). Conversely, the numbers increased under the extreme emission scenario to 25,605 [10%], 8,271 [50%], and 946 [90%] species experiencing exposure (Fig. 2).

Species of various range sizes are projected to find both refuge and exposure from macroclimatic shifts across nearly their entire range (*SI Appendix, Fig. S6*). The distribution of relative refuge area over different taxonomic orders indicates a similar pattern, where most orders include species that find refuge or exposure to macroclimatic shifts across nearly their entire range (*SI Appendix, Fig. S7*). Upon visual inspection, the six orders with over 2,000 species (*Fabales*, *Malpighiales*, *Myrtales*, *Gentianales*, *Ericales*, and *Sapindales*) and five orders with more than 1,000 species (*Lamiales*, *Malvales*, *Rosales*, *Magnoliales*, and *Laurales*) did not appear to be affected differently by macroclimatic shifts compared to the smaller orders (*SI Appendix, Fig. S7*).

Uncertainty in future biodiversity predictions in response to climate change has multiple sources: an unknown magnitude of climate change, the unknown species responses to no-analog environments, and variation in future climate projections from different climate models (Fig. 2). To provide society with the possible consequences of anthropogenic climate change, we provide predictions under multiple emission scenarios, consider no-analog

warmer climates and use multiple climate models. The range of exposure estimates across climate models highlights areas where climate change predictions are most variable. These high-uncertainty zones warrant particular attention for adaptive conservation planning. Substantial levels of variation in predictions are found between climate models using the same emission scenario, with the highest variation found in predictions between climate models being 13,584 tree species under the high-emission scenario (maximum minus minimum number of species predicted to find refuge from macroclimatic shifts in more than 90% of their range). As a reference, this variation between climate models is greater than the maximum variation (11,489 species) in exposed species when considering or ignoring future no-analog climates. This means that single-climate model predictions ignoring no-analog warmer climates can predict worse biodiversity prospects than single-climate model predictions considering no-analog warmer climates (Fig. 2 and *SI Appendix, Figs. S4, S8, and S9*).

**Climate Change Impact on Local Tree Diversity.** Tree diversity exposure to macroclimatic shifts is predicted to occur everywhere across the planet. Under the high-emission scenario, vast areas are projected to face great changes in tree diversity in the Northern Hemisphere (Fig. 3), with the highest relative exposure (more than 90% of local tree species richness, i.e., number of species ranges overlapping in a specific grid cell) in northern Asia around



**Fig. 3.** Local tree diversity exposed to macroclimatic shifts. The number of tree species exposed to macroclimatic shifts relative to the number of tree species predicted in that grid cell is depicted in plot (A–C). Values are the average predictions of five different climate models, whereas results per climate model can be found in *SI Appendix, Fig. S8*. The uncertainty in the predicted number of tree species exposed to macroclimatic shifts due to variation in future climate predictions, quantified as the 95% CI, is depicted in plot (D–F). The presented values are the CI around the average from the results of each of the five climate models' predictions, and indicate that possible relative species numbers exposed to macroclimatic shifts will be between the predicted mean (A–C)  $\pm$  CI value (D–F), where CI is calculated as  $1.96 \times \text{SD}/\text{square root of sample size } (=5)$ . Three greenhouse gas emission scenarios are plotted, optimistic (SSP1 RCP2.6; A and D), high (SSP3 RCP7.0; B and E), and extreme (SSP5 RCP8.5; C and F), ranging from the least amount of climate change to the most, respectively. White areas indicate regions of water, cropland, urbanization, or areas with no tree species. In *SI Appendix, Fig. S11*, the uncertainty is depicted when no-analog warmer climates would be ignored.

a latitude of 50°N, northern and western North America, and central and eastern Europe (SI Appendix, Fig. S10). In the Southern Hemisphere, exposed tree species are mostly found at the borders of Köppen–Geiger climate zones with up to 90% of local tree diversity exposed to macroclimatic shifts in Chile and Argentina along the borders of the temperate broadleaved forest and temperate and dry steppe, and in Ethiopia and Indonesia (Fig. 3 and SI Appendix, Fig. S10). High values of local tree diversity exposure were also found along the Amazon River and especially at a larger area near the Amazon River delta (SI Appendix, Fig. S10). This is a direct result from the projected no-analog warmer climates than observed in the historical variation among all climate models (Figs. 3 and 4).

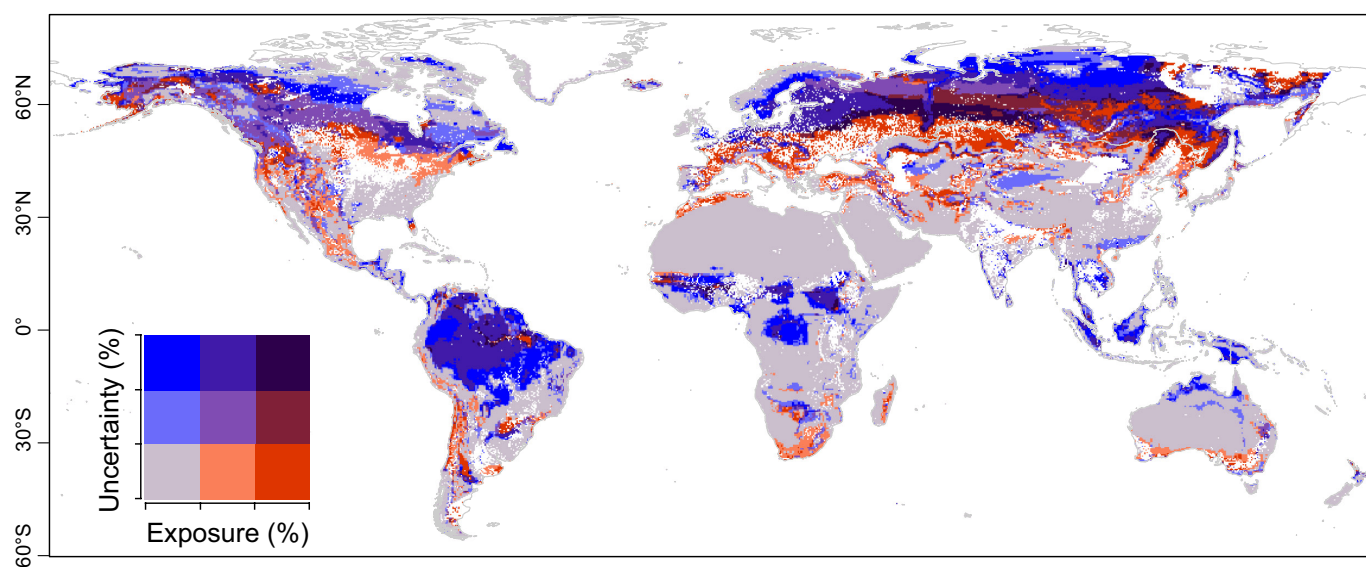
Mapping climate model variation in predicted tree diversity exposure to macroclimatic shifts illustrates that the largest uncertainties are found in the highest latitudes where taiga and tundra vegetation dominate (Fig. 3 and SI Appendix, Fig. S11). Uncertainties for areas where we projected the Non-analog Hotter climate zone were also high, indicating that climate change predictions in Equatorial regions are more uncertain than other regions, yet similar to the predicted uncertainties at high latitudes. No-analog warmer climates highlight climate projection uncertainty but it is not the cause of the great uncertainty in exposure predictions. The definition we gave to the no-analog warmer climates identifies specific locations as uncertain while other locations with greater climate model variation are not specifically highlighted as the climate models predict within the broad climate ranges of the tropical climate zones.

Under the optimistic emission scenario, we find the uncertainty is retained in the taiga and less in the tundra, whereas the uncertainty under the extreme emission scenario is mostly restricted to the tundra (Fig. 3). This indicates that climate models find consistency in the trend of climate change yet vary in how fast warmer climate zones move northward (Figs. 3 and 4). Regarding the lower latitudes, uncertainty in exposed tree diversity is high around the Amazon River for the optimistic scenario (Fig. 3). For the warmer scenarios, uncertainty increases in all regions where the no-analog warmer climates are predicted, meaning that more models predict a change compared to a single model, while the uncertainty decreases in the area around the Amazon River (Figs. 3 and 4).

The maps in Fig. 3 may appear to show a similar pattern, yet regions with most uncertain predictions do not match regions with highest exposed tree diversity ( $r = 0.22$  for absolute species numbers,  $r = 0.43$  for relative species numbers). For example, the largest areas with high relative species exposure are predicted on the border of the subarctic (fully humid cold summer) to humid continental (fully humid warm summer) regions of Russia (around a latitude of 65°N) which have a relatively low uncertainty (Fig. 3 and SI Appendix, Fig. S5.1). This contrast becomes even more apparent when exposure and uncertainty results are categorized into three equal intervals—“low,” “medium,” and “high”—by dividing the ranges evenly (0 to 100% for exposure and 0 to 48% for uncertainty) (Fig. 4). Fig. 4 highlights regions that are predicted to face high tree diversity exposure to macroclimatic shifts with little uncertainty due to climate change predictions. These are located in vast areas around the latitude of 50°N. Looking more closely, these regions span high-latitude boreal and temperate zones in North America, Europe, and Asia, including parts of the northern and central United States, Canada, and Russia. In the Southern Hemisphere, these regions include arid and tropical regions of South America, southern Africa, and Australia. Additionally, vulnerable zones are identified in parts of the Mediterranean Basin, Central Asia, as well as select island ecosystems such as Madagascar.

## Discussion

Our results demonstrate that local tree diversity is likely to be highly impacted by end-of-century macroclimatic shifts. Anthropogenic climate change is expected to impact species differently all around the world, yet shifts in climate zone, as considered in this study as a conservative estimate to climate change exposure, will impact 45% of the Earth's terrestrial area under the high-emission scenario SSP3 RCP7.0. Specifically, vast areas in North Eurasia and smaller regions in Europe, the American northwest, Chile, and Argentina will face high tree diversity exposure to macroclimatic shifts, possibly impacting up to 90% of the local tree species. As these sites mostly include temperate grasslands, temperate broadleaf and mixed forest, and boreal forests



**Fig. 4.** Certainty on tree diversity exposed to macroclimatic shifts. The high-emission scenario (SSP3 RCP7.0) is presented here, and the other scenarios are presented in SI Appendix, Fig. S16. The x-axis of the color gradient identifies the species exposure to macroclimatic shifts from 0 to 100% of the local number of species exposed. The y-axis of the color gradient identifies the climate model variation in species exposure expressing the uncertainty of our exposure predictions (CI, %, see caption Fig. 3) from 0 to 48%. White areas indicate regions of water, cropland, urbanization, or areas with no tree species.

(*SI Appendix*, Fig. S10 and Table S1), which are biomes known for concentrated climate change impact (47, 48), localized macroclimatic shifts suggest a steep vegetation transition in these areas. However, the exact projected location of macroclimatic shifts (*SI Appendix*, Fig. S3) and hence our future biodiversity predictions are greatly dependent on the climate model projections and their uncertainties (49–51) (*SI Appendix*, Fig. S5). In addition, a precise timing of ensuing vegetation transitions is uncertain, because projected macroclimatic shifts from suitable to unsuitable do not explicitly consider 1) the trees' tolerance or adaptation to new climates creating response lags (6, 10), 2) the slowing or hindrance of new species' arrival due to dispersal (dis)abilities and interspecific interactions (10), 3) changes in pests or diseases due to climate change, and 4) expedited vegetation impact following increased fire intensity or frequency due to excess dead biomass from climate change-induced forest dieback (41). Additionally, 5) we did not explicitly include biotic interactions, as these typically occur within shared macroclimates, and macroclimatic shifts impact entire ecological communities, as previously argued. Notwithstanding, evidence from paleoecological studies suggests that tree species often respond independently to past climatic changes (52), indicating that macroclimatic conditions together with dispersal limitations may be the primary determinants of future tree species distributions. Together with the focus on macroclimates—excluding other threats to species—we provide conservative exposure estimates yet identify regions where current tree diversity will be subjected to substantial climate change, without implying specific outcomes such as diversity loss, gain, or species turnover. Under a tree diversity conservation prioritization framework (53), locations, rather than species, can be protected from other anthropogenic disturbances such as industrial and extractive activities, allowing areas with relatively low tree diversity exposure to macroclimatic shifts to act as refuge areas from anthropogenic climate change.

Critically, 96% of all considered tree species will be exposed to end-of-century macroclimatic shifts under the high-emission scenario. The majority of tree species (54%,  $n = 17,199$ ) are exposed in less than 20% of their current range, and 14% of tree species ( $n = 4,593$ ) are exposed in more than 50% of their current range. While these numbers may seem optimistic, the interdependence among species that is not specifically considered in this study could instigate profound cascading ramifications due to the disappearance of even a small number of species (54, 55). There are almost 800 tree species that are predicted to be heavily exposed to macroclimatic shifts even under the optimistic emission scenario, and more importantly, they are mostly found in the same areas: Madagascar, the southeast of southern Africa, the southeast of Brazil, and the south of Australia (*SI Appendix*, Fig. S12). This may suggest risks of abrupt changes in vegetation and possibly in ecosystem functioning as a result of future climate change, following the conclusion on the impact of macroclimatic shifts on tree diversity. Although our study does not incorporate species abundance, the loss of highly dominant tree species could lead to cascading ecosystem disruptions, which is to be investigated by future studies integrating abundance-weighted exposure estimates. More strikingly may be the 40 species that are predicted to lose more than 99% of their current range, even under the optimistic emission scenario. Most of these species are endemic or restricted to Lord Howe Island and Norfolk Island in the Tasmanian Sea and may require assisted migration or translocation in order to survive future projected climate change. The Australian government, at present, has acted upon this threat by including these species in allocation programs (56). However, a species may be more or less vulnerable

to macroclimatic shifts independent of the climate change exposure. Hence, macroclimatic shift exposure in a small fraction of a species' range or climate change more subtle than macroclimatic shifts may already negatively impact the ability of a species to survive.

Climate warming is faster in arctic regions compared to the rest of the world (57), and climate conditions of generally colder regions are likely to shift into an existing equivalent, which allows for informed predictions on potential vegetation shifts. Trees at lower latitudes are already responding to heat stress (58, 59), but future climates for these warm tropical regions do not have a currently existing analog. This leads to uncertain prospects for tropical tree species, compounding many species' unknown adaptive capacity for warmer and drier climates (60). Future climate change studies working with continuous climate variables already indicate the risk on e.g., the Amazon rainforest (42), but when climate or vegetation is used categorically only an expansion of tropical biomes or climates is predicted (47). Ideally, future no-analog climates should be considered in order to adequately estimate climate change effects in the tropics, as indicated in this study. For example, without the consideration of a Non-analog Hotter climate zone, we would predict a large difference in tree diversity exposure to end-of-century macroclimatic shifts between the northwest (part of the Amazon Irregular Plains and Piedmont) and the rest of the Amazon forest, whereas the consideration of the Non-analog Hotter climate zone allowed for more spatial differentiation in tree diversity exposure predictions and identified other areas of concern (*SI Appendix*, Fig. S13). These predictions indicate unequal stress on tree diversity across Amazonia, and, maybe more importantly, the uncertainty of future climate change impact on tree diversity is unequally distributed (61).

In the end, large-scale future biodiversity predictions are highly uncertain due to the accumulation of such uncertainties; climate projections, biodiversity predictions, and this study's additional uncertainty of defining and thereby assuming a no-analog climate. While intrinsic climate model uncertainty is not considered in this study, the across-model variation reflects uncertainty in the area exposed per species and greatly increases in some regions due to the consideration of the Non-analog Hotter climate zone; the range of exposed tree species between the five included climate models went from 9 to 42%, without and with considering the Non-analog Hotter climate zone (variation in predicted number of species with a maximum of 10% range exposed to macroclimatic shifts under the high-emission scenario SSP3 RCP7.0). While the inclusion of a new climate zone will methodologically inherently lead to all species being exposed to a macroclimatic shift in all cells where the Non-analog Hotter climate zone is predicted, in reality this may be more gradual and highly dependent on species-specific climate sensitivity. In turn, this leans on our assumption that climate zones create an occupancy barrier, i.e., species are excluded from unoccupied regions due to climatic unsuitability. Nonetheless, tree species exposure to macroclimatic shifts can still be underestimations, as no-analog climates are only defined by temperature and do not include any changes in seasonality, precipitation, or periodic extremes as drought spells and heat waves on tree stress (62). Future work should explore how shifts in precipitation regimes, seasonality, and extreme events contribute to novel macroclimatic conditions that may further challenge species persistence. Considering this, our approach provides global-scale estimates of climate change risk for thousands of tree species and overall tree species diversity, despite limited ecological knowledge for many species by focusing on their potential climatic niche.

Trees play fundamental roles in terrestrial ecosystems, and greater tree diversity enhances ecosystem resilience to future climate change (63, 64). Our study provides a global-scale, dual assessment of species-level and local tree diversity exposure to macroclimatic shifts, offering critical insights for conservation planning. Globally, severe tree diversity exposure to macroclimatic shifts is predicted in specific regions even limited anthropogenic climate change. While severe tree diversity exposure is predicted, more extreme emission scenarios highlighting regions with no-analog warmer climates, dramatically expand the number of exposed tree species and affected areas. However, our findings also highlight that many species retain substantial climate refugia within their current ranges. This underscores the need for a place-based conservation approach that prioritizes regions with high climate refuge potential, ensuring that these areas remain protected from additional anthropogenic pressures such as land-use change, deforestation, and industrial activities (28, 32, 33, 53, 65–68). Together, proactive conservation strategies, including assisted migration and habitat protection, will be essential to mitigate the ecological disruptions associated with climate-driven shifts in tree diversity. Our findings provide a foundation for identifying and safeguarding future climate refugia, reinforcing the importance of integrating climate resilience into long-term biodiversity conservation efforts (28, 32, 33, 53, 65–68).

## Materials and Methods

**Tree Data.** All species that are “a woody plant with usually a single stem growing to a height of at least two meters, or if multitemmed, then at least one vertical stem five centimeters in diameter at breast height” (69) are considered to be trees in this study. Species names were extracted and standardized using the world tree species checklist GlobalTreeSearch v.1.6 on the 10th of May 2022 (69) and the online Taxonomic Name Resolution Service (70), respectively.

Tree species’ occurrence records were obtained from open-access, publicly available data from five aggregators: the Global Biodiversity Information Facility (71), the public domain of the Botanical Information and Ecological Network v.3 (72), Latin American Seasonally Dry Tropical Forest Floristic Network (73), RAINBIO database (74), and the Atlas of Living Australia ([www.ala.org.au](http://www.ala.org.au)). We cleaned the data using the TREECHANGE workflow (75), only including occurrence records with the high-quality labels AAA to C, suggesting high security in geographic coordinates and no duplicates or botanical garden records. This resulted in a dataset with 41,835 tree species and 8,408,454 occurrence records covering a time range of 1820–2021. Finally, we only retained species that had five or more observations, as required for the next steps of our analysis. Our final dataset includes 32,089 species and 8,387,454 occurrence records (see *SI Appendix, Fig. S14* for a taxonomic overview).

Tree species’ ranges were iteratively estimated, where we started with the species’ EOO and removed areas we considered unsuitable for the species. The EOO was determined as the minimum convex polygon using 99 percent of the species’ occurrences created by the “mcp” function in the adehabitatHR R package (76). Unsuitable area that was removed from species’ EOO was defined as unsuitable climate (defined below), water bodies for the year 2015 (77), cropland for the year 2019 (78, 79), and urban area for the year 2020 (78) (Fig. 1). Species range sizes (km<sup>2</sup>) were then quantified in Julia Programming Language (80) by summing the area of each grid cell where the species’ range polygon covered the grid cell center. All raster processing and analyses in this study were done at the 0.0083-degree resolution (~1 km<sup>2</sup> grid cells at the Equator) using the ArchGDAL.jl package (<https://yeesian.com/ArchGDAL.jl/latest/>) and the Rasters.jl package (<https://rafaqz.github.io/Rasters.jl/dev/>). This approach of defining species ranges offers the advantage of generality across tree species. By using climate zones as broad-scale descriptors of species’ climate niche, we eliminate the need for detailed, species-specific ecological information and climate change sensitivity data required by conventional species distribution models. Additionally, our approach allows for the consideration of species with small sample sizes, which constitute a major proportion of tree species globally (81), whereas these cannot be considered with more conventional species distribution models. While climate

exposure predictions may be more uncertain for species with small compared to larger sample sizes, the use of climate zones helps reduce this uncertainty. This is because climate zones aggregate predictions from multiple climate variables into a single category, mitigating the potential inaccuracy of future climate model predictions of a single climate variable at the level of individual grid cells.

**Defining Species’ Climate Suitability.** Climate was described by the Köppen-Geiger climate classification after Peel et al. (13, 82), where grid cells are classified as a climate zone based on combinations of local climatic variables. The recent climate zone map (1981–2010) was downloaded from Chelsa 2.1 (83).

Species-specific suitable climate zones were determined as the current macroclimates that cover more than 10% of all grid cells within 1 km radius buffer zones around each species’ occurrence record. This threshold was selected to remove occurrences in specific microenvironmental sites, e.g., riverbanks and pole facing mountain slopes, and to remove remnant effects of old aged trees that occurred in a different climate zone during a climatically critical life stage (e.g., seedling stage) than it currently lives in.

**Future Climate Refugia.** Our analysis was based on identifying areas within species’ ranges that were transformed into climate zones outside species’ inferred suitable climate by the end of the century (averaged climate projections between 2071 and 2100), thereby exposing a species to macroclimatic shifts at a particular location. Specifically, per species, the unique climate zones comprising its suitable climate were compared to the unique climate zones projected for the future within the current species’ range (Fig. 1). Each grid cell within a species range that was predicted to have a future climate zone that is not defined as the species’ suitable climate, was marked as “exposed” for that species (Fig. 1). Thus, species ranges could only decrease in the future as portions of their present range become climatically unsuitable. All other grid cells were identified as stable for that species, even when climate zones were projected to change in the future from one suitable climate zone to another. Hence, a species range may remain constant through time despite turnover in climate within that range, so long as the new climates are suitable. The refuge area from macroclimatic shifts per species (km<sup>2</sup>) was then quantified as the sum of the grid cell area of the grid cells marked as stable. Additionally, we generated a species richness raster in which each grid cell represents the sum of the overlapping species ranges (*SI Appendix, Fig. S15*), and a raster where, for each grid cell, the number of species are summed that are exposed to unsuitable climate at that given location due to future climate change.

**The Non-Analog Hotter Framework.** Future projected temperature increases will generally lead to changes in climate zones. However, the Köppen-Geiger climate zones include open upper temperature ranges for the warmest climate zones, hence, under the typical construction of climate zones, a projected future increase in temperature would not lead to a change in climate zone. Nonetheless, this may result in no-analog conditions that are beyond the niche limits of the species that occupy the warmest climate zones (84). To address this limitation, we designate a novel Non-analog Hotter climate zone to grid cells that 1) are currently labeled as Equatorial, Hot Desert, or Hot Steppe and 2) are projected to experience future mean annual temperatures that exceed the current maximum temperature of the specific climate zone plus 10% of the current maximum temperature range of the specific climate zone to be conservative in defining a Non-analog Hotter climate zone and to consider species’ potential ability to withstand limited climate variety assuming species are not living at their critical thermal maximum (*SI Appendix, Fig. S1*). Here, mean annual temperature is defined as the daily mean air temperatures averaged over 1 y. Maximum temperature is defined as the maximum value of mean annual temperature averaged between 1981 and 2010 within the specific climate zone, following Trisos et al. (8), where species niche limits are defined as the maximum temperature across species’ entire ranges. And maximum temperature range is defined as maximum minus minimum value of mean annual temperature averaged between 1981 and 2010 within the specific climate zone.

The current and future temperature predictions that were used to define the Non-analog Hotter climate zone were downloaded from CHLSA 2.1 (14, 83) for each of the 15 emission scenario-climate model combinations described in the introduction. For each emission scenario-model combination, locations identified with the Non-analog Hotter climate zone were projected onto the corresponding future climate zone map, resulting in 15

updated future climate zone maps (5 GCMs  $\times$  3 SSP-RCP combinations, [SI Appendix, Fig. S5](#)). In the main text, the 15 updated maps that include the Non-analog Hotter climate zone are used to produce results. In the Supporting Information, the results of the same analyses are presented yet using the original 15 maps that ignore no-analog warmer climates, downloaded from CHELSA-BIOCLIM+ (14, 85).

**Spatial Visualization.** Per species, we tested future climate zone suitability within species' range per emission scenario, per climate model, and per climate zone framework. All figures in the main text present the average value over the climate models for each emission scenario, unless otherwise indicated. All maps were created in R (86) using the terra package (87).

**Data, Materials, and Software Availability.** Spatial analyses were carried out in Julia, for which we provide all code on [GITHUB\\_REPOSITORY\\_SelwynHoeks](#). Data selection and result visualization were carried out in R heavily utilizing the terra R package, for which we provide all code on [GitHub \(https://github.com/SHoeks/MacroClimaticShifts\)](#) (88). Tree occurrence data are openly available on GBIF, BIEN v.3, dryflor, RAINBIO, and ALA. The TREECHANGE workflow was used for data quality assessment and control. We provide species' ranges as shape files and all produced maps as .tif raster files on [figshare \(https://doi.org/10.6084/m9.figshare.25639356\)](#) (89). Climate refuge data and an overview of species' suitable climate zones are available on [GitHub: https://github.com/ColineBoonman/MacroClimaticShifts](#) (90).

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