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Hotter Temperatures Reduce the Diversity and Alter the Composition of Woody Plants in an Amazonian Forest

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ABSTRACT

Rapid warming and high temperatures are an immediate threat to global ecosystems, but the threat may be especially pronounced in the tropics. Although low-latitude tree species are widely predicted to be vulnerable to warming, information about how tropical tree diversity and community composition respond to elevated temperatures remains sparse. Here, we study long-term responses of tree diversity and composition to increased soil and air temperatures at the Boiling River—an exceptional and unique "natural warming experiment" in the central Peruvian Amazon. Along the Boiling River's course, geothermally heated water joins the river, gradually increasing water temperature and subsequently warming the surrounding forest. In the riparian forests along the Boiling River, mean annual and maximum air temperatures span gradients of 4°C and 11°C, respectively, over extremely short distances (< 1 km), with the hottest temperatures matching those predicted for much of the Amazon under future global warming scenarios. Using a new network of 70 woody plant inventory plots situated along the Boiling River's thermal gradient, we observed a *ca.* 11% decline in tree α-diversity per 1°C increase in mean annual temperature. We also found that the tree communities growing under elevated temperatures were generally more thermophilic (i.e., included greater relative abundances of species from hotter parts of the Amazon) than the communities in cooler parts of the gradient. Based on patterns at the Boiling River, we hypothesize that global warming will lead to dramatic shifts in tree diversity and composition in the lowland Amazon, including local extinctions and biotic attrition.

1 | Introduction

Rapid global warming is an immediate threat to natural ecosystems. This threat is believed to be especially pronounced in the tropics, where species are hypothesized to be more sensitive to changes in temperature due to narrow thermal niches (Janzen 1967; Perez, Stroud, and Feeley 2016; Wright, Muller-Landau, and Schipper 2009). Indeed, many tropical forests may already be near a high thermal threshold (Araújo et al. 2021; Doughty and Goulden 2008; Mau et al. 2018; Tiwari et al. 2021).

Rising temperatures and increasing vapor pressure deficits have already led to decreasing carbon sequestration rates in the tropics (Hubau et al. 2020; Sullivan et al. 2020) and could potentially lead to mass extinctions of both plants and animals (Bennett et al. 2023; Colwell et al. 2008; Doughty et al. 2023; Thomas et al. 2004), as well as ecosystem collapse (Malhi et al. 2009).

In the Amazon, temperatures have increased by ~0.25°C per decade since the mid-1970s (Malhi et al. 2008; Malhi and Wright 2004) and are expected to rise by 3°C–6°C before the

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end of this century (Zelazowski et al. 2011). This drastic increase in temperatures will push much of the Amazon into an unprecedented climatic envelope with no near-historic analog (likely unprecedented even within the last million years) (Trew et al. 2024; Williams et al. 2007), forcing many species to adapt or acclimate to hotter temperatures and/or migrate to cooler areas in order to maintain fitness and avoid extinction (Feeley et al. 2023). Unfortunately, many plants in the Amazon may not be able to keep up with rapid warming (Doughty et al. 2023) and other concomitant changes in climate, such as shifting precipitation regimes and increasing drought. In fact, there have already been detectable directional changes in lowland Amazon tree species composition in recent years (Esquivel-Muelbert et al. 2019; Laurance et al. 2004). Although these changes are largely attributed to decreasing precipitation and intensifying drought, anthropogenic warming may also play an important role. Indeed, increasing temperatures in the Amazon may significantly reduce plant diversity (Colwell et al. 2008; Colwell and Feeley 2024; Thomas et al. 2004) or accelerate compositional changes already underway (Feeley et al. 2012; Feeley and Silman 2010). Unfortunately, we still have an incomplete understanding of how elevated temperatures affect tropical plant diversity and composition, thereby limiting our ability to predict the fate of a hotter Amazon.

Numerous studies have explored the effects of elevated temperatures on plants, but these studies have severe limitations when assessing long-term community-level responses, especially in lowland tropical forests. For example, some studies have used large-scale natural temperature gradients (e.g., across latitude or elevation), which serve as "space-for-time" proxies that resemble future climate scenarios (Feeley et al. 2011; Tito, Vasconcelos, and Feeley 2020). However, these gradients are extensive (spanning dozens to hundreds of kilometers) and cannot control for confounding variables such as precipitation, seasonality, soil properties, or species' biogeographic histories, meaning that any observed intraspecific differences may reflect local adaptation to variables other than temperature. In addition, changes in species composition across natural temperature gradients can complicate the interpretation of other plant responses. Furthermore, in the tropics, the latitudinal temperature gradient is shallow or absent (Colwell et al. 2008; Colwell and Feeley 2024; Terborgh 1973), and there is no current analog of the lowland Amazon's predicted future climate since there are no hotter rainforests (Feeley and Silman 2010).

As an alternative to using natural gradients, some studies use experimental warming to decouple temperature from other environmental variables (Carter et al. 2021; Kimball et al. 2018; Slot et al. 2014). However, these experiments invariably include only a small subset of species, are unable to warm entire large adult trees, impose instantaneous or unrealistic warming rates, and do not cover the timeframe necessary to capture the full lifespans of many plants. Other studies have built experimental mesocosms that replicate natural systems (Smith et al. 2020), but mesocosm communities are often static and usually cannot be used to evaluate tree community responses to warming, especially on ecosystem-level scales, that may result from interspecific changes in recruitment or mortality. These limitations beg for an alternative solution to investigate the effects of elevated

temperatures on lowland tropical forests, especially when studying community diversity, composition, or dynamics.

Here, we take advantage of a unique and extreme natural thermal gradient associated with a geothermal river in the central Peruvian Amazon—the "Boiling River." Along the Boiling River's course, superheated waters escape faults in the Earth's crust and enter the river, causing the river's water temperature to quickly reach > 95°C and remain heated until gradually decreasing in temperature before joining the Pachitea River (Figure 1). The heat from the river subsequently warms the surrounding riparian forest, enabling us to study the effects of increased temperatures on a lowland tropical forest and its constituent species (Kullberg et al. 2023). Geothermal features like the Boiling River are recognized as being valuable systems to study long-term responses to warming (Hošek et al. 2024; O'Gorman et al. 2015). While several previous studies have evaluated plant responses to geothermal warming (Burns 1997; Kullberg et al. 2023; Kullberg and Feeley 2024; Valdés, Marteinsdóttir, and Ehrlén 2019), until now no such study focused on community-level responses has existed in the tropics.

We investigated the effects of the increased air temperatures around the Boiling River on woody plant diversity and composition, sampling all stems ≥ 2 cm DBH. In accord with the hypothesis that increasing temperatures will lead to species extinctions and biotic attrition in the already-hot lowland tropics (Colwell et al. 2008; Rosenblad, Baer, and Ackerly 2023; Thomas et al. 2004), we predicted that woody plant α- and β-diversity would decrease with temperature. We also expected that community composition would be strongly influenced by temperature, with the woody plant communities in cooler forests being compositionally distinct from those in hotter forests. We also predicted that this compositional change from cool to hot forests would be directional. Specifically, based on findings from large-scale elevational gradients showing that hotter lowland forests support greater relative abundances of thermophilic (i.e., heat-loving) plant species than colder highland plots and that many tropical forests are increasing in their relative abundances of thermophilic species through time (a process referred to as "thermophilization") (Duque, Stevenson, and Feeley 2015; Fadrique et al. 2018; Feeley et al. 2013; Tanner et al. 2022), we predicted that the communities in hotter areas should have greater relative abundances of thermophilic species than the communities in cooler areas along the Boiling River.

2 | Materials and Methods

2.1 | Characterization of the Boiling River's Thermal Gradient

The Boiling River is located in the central Peruvian Amazon between 150 and 270 m asl (8°48′46.4′′ S, 74°43′37.4′′ W, Figure 1). Regional mean annual temperature is 26°C and mean annual precipitation is 2860 mm with a weak 4-month dry season. Dry season precipitation is ~110 mm per month, on average, while wet season precipitation is > 250 mm per month, on average. We characterized spatial and temporal air and soil temperature gradients along and around the Boiling River using a combination of remotely sensed imagery and in situ temperature logging.
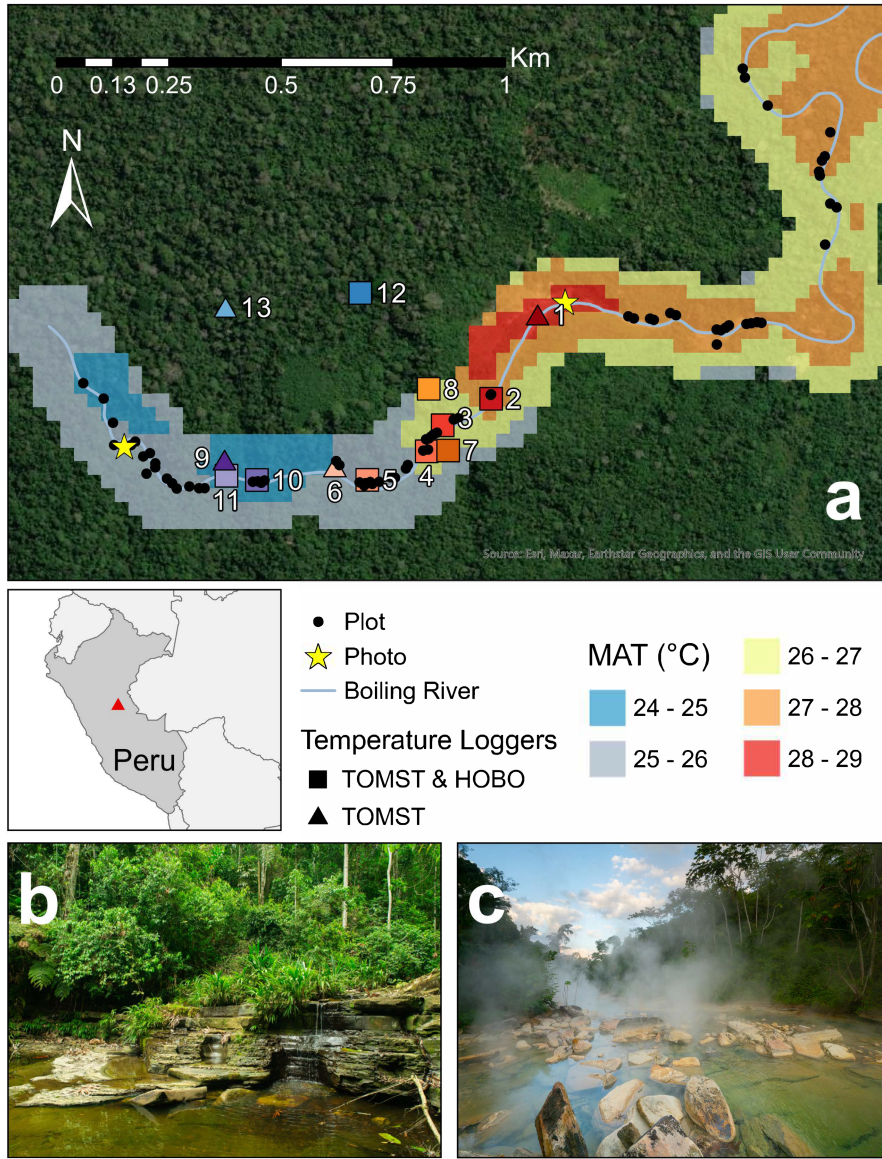
FIGURE 1 | (a) Map of the Boiling River, which flows southwest to northeast, denoting the locations of temperature loggers, 70 woody plant inventory plots, and photos over a basemap of mean annual temperature (MAT). Temperature logger colors coincide with the colors in Figure 2. (b) A photo of the river and riparian forest upstream (as indicated by the yellow star on the left of the map) of hot water inputs. (c) A photo of the river and forest downstream (the yellow star on the right) of hot water inputs. Photos by Riley P. Fortier. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

In October 2021, we deployed a network of in situ data loggers in shaded locations along the Boiling River to regularly record air temperature, relative humidity, and soil temperature over the course of 1 year. Specifically, we deployed 10 Onset HOBO MX2301 Data Loggers at ~1 m aboveground, which were used to record relative humidity every 20 min. We also deployed 13 TOMST TMS-4 dataloggers, which record air temperature at 15 cm aboveground and soil temperature 6 cm belowground every 15 min (Figure 1). Eleven of the TOMST and nine of the HOBO loggers were deployed along the river, and two of the TOMST and one HOBO logger were deployed in adjacent forests outside of the riparian zone in order to serve as reference points (see below).

Using 1 year of data (October 2021 to October 2022), we calculated the mean and maximum monthly temperatures for the TOMST sensors above- and below-ground for both the full 24-h day

and just the nighttime (18:00:00–06:00:00). We also calculated mean monthly relative humidity (RH) and vapor pressure deficit (VPD), minimum monthly RH, and maximum monthly VPD for each HOBO sensor (one HOBO logger malfunctioned early on, so we present data only from the remaining 9). 2021 and 2022 were typical years in terms of mean air temperature and precipitation in the region (https://berkeleyearth.org/).

To summarize air temperature data across the full year, we calculated the mean annual temperature (MAT) and the maximum temperature of the warmest month (hereafter referred to as "maximum temperature") of each TOMST logger at 15 cm aboveground. MAT was calculated as the mean of all recorded temperatures for each sensor, and the maximum temperature was calculated as the highest temperature recorded during the hottest month. We also characterized the daily temperature
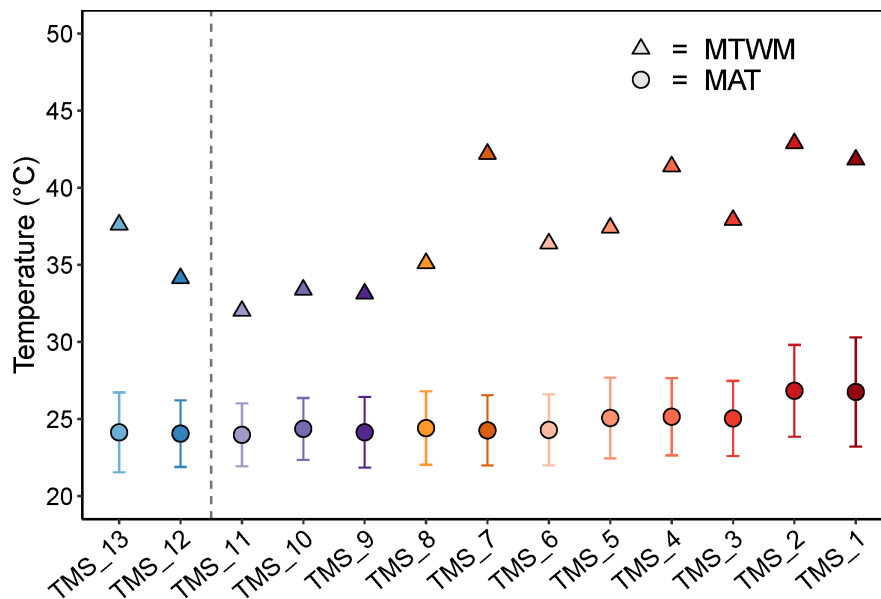
FIGURE 2 | Mean annual temperature (MAT—circles) and maximum temperature of the warmest month (MTWM—triangles) for each microclimate TOMST TMS-4 logger at 15 cm aboveground for 1 year (October 2021 to October 2022), colored by their location at the study site (see Figure 1). Loggers left of the dashed vertical line (the two blue sites) are located in a reference forest away from the river. Error bars are ±1 standard deviation of all recorded daytime temperatures at each location.

fluctuations for each logger as the difference between maximum and minimum daily air temperature (T_{diff}).

Since in situ thermometers do not provide spatially continuous temperature data and since plot locations (see Section 2: Tree plots) were not all immediately proximate to a logger, we used remotely sensed Landsat 9 imagery to calculate land surface temperature (LST) and then used LST to interpolate the in situ below-canopy air temperatures continuously across the study area. We selected a Landsat 9, Level 1, Collection 2, Tier 1 image collected on June 26, 2022, at 15:03, during the field campaign. The selected image is cloud-free in our area of interest. We calculated LST at 30-m resolution following USGS protocol (Jeevalakshmi, Reddy, and Manikiam 2017; Kullberg and Feeley 2022) by calculating brightness temperature with the thermal band (100-m resolution) and correcting for surface emissivity based on NDVI (30-m resolution).

Next, we estimated MAT and maximum temperature continuously across the study area through linear least squares and multiple regression models. We trained the models using MAT, or maximum temperature of each TOMST logger, as the response variable, and we used either LST alone or LST and distance to the river as the predictor variable(s) (variable inflation factors were all <5, the advisable threshold to exclude highly correlated predictors (Sheather 2009)). We excluded loggers 12 and 13 (see Figure 1) from temperature models since they are located outside of the riparian forest ($n = 11$). We evaluated each model with leave-one-out cross-validation by rerunning each model 11 times, leaving out one temperature logger each time to calculate R^2 and root-mean-square error (RMSE). The models with LST as the sole predictor performed better than those including distance to the river based on the lowest RMSE (Chai and Draxler 2014), and the model predicting MAT with LST performed better than the model predicting maximum temperature (Table S1). We did not find evidence of spatial autocorrelation in the residuals of these two better-performing models when we plotted Moran's correlograms (Figure S1). We projected the predicted values of MAT and maximum temperature across the study area (Figure 1) and extracted the estimated MAT and maximum temperature for each plot location. Due to its higher performance, we used the MAT model for subsequent data analyses. The strong association between remotely sensed canopy temperatures (LST) and in situ understory temperatures ($R^2 = 0.71$) indicates a consistent thermal gradient across the vertical profile of the forest along the Boiling River, although the strength of the thermal gradient and therefore the potential effects may be reduced at increased heights aboveground. Cross-validation and analysis of spatial autocorrelation were conducted with the packages "caret" and "ncf," respectively (Bjornstad 2022; Kuhn 2008) in R statistical software (R Core Team 2021).

2.2 | Tree Plots

To characterize woody plant community composition along the thermal gradient, we set up 70 circular forest inventory plots, each with a 3-m radius (28.3 m² area). Plot size was constrained by the irregular topography along the river; however, it should be noted that 28.3 m² is still larger than any warming experiment plot currently being used to assess the effects of temperature on tropical forests. Plots were spaced systematically along the river's thermal gradient to span the widest possible range of air temperatures, including the hottest and coolest areas, while avoiding any large tree falls and treeless areas covered by lianas. Plots were also kept as close to the river as possible to avoid comparing riparian communities with forest interior communities. In each plot, we measured diameter at breast height (DBH) and identified each self-supporting woody stem ≥2 cm DBH.

For cryptic, uncommon, and rare species that were challenging to identify in the field, we collected vouchers and preserved them in 75% ethanol for subsequent drying, identification, and storage in the Regional Herbarium of Ucayali (HRUIP) in Pucallpa, Peru. To confirm and/or refine species identifications, we compared vouchers to physical material stored in HRUIP and to digital material on the online databases of the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), and the Royal Botanic Gardens Kew (K). To characterize the abiotic environment at each plot, we recorded GPS locations and measured the slope and aspect of each plot. To make the aspect more ecologically relevant, it was converted to northness and eastness, which are on a scale of −1 to 1, where −1 is directly opposite north (or east) and 1 is directly north (or east).

2.3 | Soil Sampling

To account for potentially confounding effects of soil variables, we collected and analyzed soil samples along the gradient. Roughly 600 g of soil were collected at 15 locations throughout the study area in or directly adjacent to one or two of the forest inventory plots (Figure S2). Each soil sample was then homogenized and analyzed at SGS Laboratory Peru (Lima, Peru). Soil pH was measured in water. Total nitrogen was determined by the Walkley and Black method. Available potassium, calcium, and magnesium were determined using the ammonium acetate method. Available phosphorus was extracted from a sodium bicarbonate solution. Copper, iron, manganese, and zinc were extracted using a modified Olsen method. All soil analysis methods are described in more detail in Miller, Gavlak, and Horneck (2013), and summary statistics of the 15 soil samples are reported in Table S2. We then assigned soil variables directly to the 25 plots where soil was collected and used this subset of plots for all subsequent analyses dealing with soil nutrient concentrations.

2.4 | Data Analysis

We calculated three metrics of α-diversity for each forest inventory plot, including Shannon, Simpson, and inverse Simpson indices. To test for spatial autocorrelation between diversity and plot locations, we modeled semivariograms for species richness and each diversity index. That is, we used semivariograms to test if plots close to each other have similar diversity than plots far from each other. The semivariograms showed no increase in semivariance beyond ~0.00025 decimal degrees (roughly equal to 25 m, Figure S3). In other words, beyond 25 m, there is no correlation between diversity and the distance between plots. We therefore ignored plot locations from subsequent models testing for air temperature effects on α-diversity. We also tested for potential nutrient effects on diversity by running linear least-squares regressions on all diversity metrics while excluding air temperature for the 25 plots with soil data. We included total iron, total zinc, and available calcium, phosphorus, and potassium. These linear models revealed no significant relationships between soil nutrients and α-diversity (Table S3), corroborating previous studies that also found no relationships between soil nutrient concentrations and α-diversity (Clinebell II et al. 1995; Gentry 1988). As such, soil nutrients were excluded in the subsequent diversity analyses.

To determine whether air temperature influences species richness and each diversity index, we used linear least-squares regression using MAT and maximum temperature as main effects (Table S4). To further explore changes in α-diversity, we calculated rarefaction curves for pooled data of the 25 coolest and the 25 hottest plots (Figure S4). To control for potential effects of ontogeny and biases caused by poor representation of large stems in small plots, we repeated all α-diversity analyses for trees < 10 cm DBH (Figures S5 and S6; Table S4).

We determined multisite total β-diversity by calculating Sørensen dissimilarity (β_{SOR}), which can be broken down into two components: β-diversity resulting from turnover (β_{SIM}) and β-diversity resulting from nestedness (β_{NES}). All β-diversity metrics were calculated using the R package "betapart" (Baselga et al. 2023). To determine if β-diversity is higher when temperature differences are greater, we calculated β_{SOR} and the difference in MAT (ΔMAT) for each pairwise plot combination. We then performed simple Mantel tests to determine correlations between β_{SOR} and ΔMAT, geographic distance, and topography. To control for spatial autocorrelation and other potential confounding factors, we also ran a partial Mantel test between β_{SOR} and ΔMAT while controlling for geographic distance and topography. We repeated both simple and partial Mantel tests for the 25 plots with soil nutrient data. Soil nutrients were total iron, total zinc, and available calcium, phosphorus, and potassium. These nutrients were chosen due to their importance in shaping species occurrences and community composition (Condit et al. 2013; John et al. 2007) while avoiding certain nutrients that are highly correlated with each other (pH and available magnesium were highly correlated with available calcium, Table S2). All Mantel statistics and p-values are reported in Table S5.

To further explore compositional changes along the thermal gradient, we performed an ordination using non-metric multidimensional scaling (NMDS) based on Bray-Curtis community dissimilarity. To determine an optimal number of dimensions, we ran 1000 trials using 1–10 dimensions to yield different stress values. We chose three dimensions, which was the lowest number of dimensions that yielded a stress value ≤ 0.1 (Figures S7 and S8) since a stress value ≤ 0.1 should signify that the chosen number of dimensions adequately reflects the ecological processes shaping community composition. After plotting the NMDS, we fitted vectors of abiotic variables onto ordination space to visualize how they correspond to the two main ordination axes for all plots and also for 24 plots with soil nutrient data (Figure 4; Figure S9).

To characterize compositional changes of plots along the thermal gradient, we calculated community temperature scores for each plot following established protocols (Duque, Stevenson, and Feeley 2015; Fadrique et al. 2018; Feeley et al. 2013). We first characterized the thermal maximum for each species (excluding morphospecies) by gathering occurrence data from the Botanical Information and Ecology Network (BIEN) and the Global Biodiversity Information Facility (GBIF). Only records from herbarium and museum databases were included to ensure high-quality records with reliable species identifications. We removed duplicate occurrences and occurrences having coordinate issues, such as those obviously outside of a species' native range. We also discarded one species

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(*Browneopsis excelsa*) with < 10 records. We then extracted the maximum temperature for each occurrence record using climate data from WorldClim (Fick and Hijmans 2017) at 30-arc-s resolution. To calculate the thermal maximum for a species, we took the 95% quantile of maximum temperatures at all of its occurrence locations in the Neotropics (using the 95% quantile rather than absolute maximum minimizes influences of any misidentifications or georeferencing errors). For morphospecies and species with fewer than 10 occurrences, the thermal maximum was set as the average thermal maximum of all fully identified species from the plots (Table S6). Then, for each of the 70 inventory plots, we calculated the community temperature score as the average thermal maximum of all species occurring in the plot weighted by their relative number of individuals. Finally, we used a linear regression to compare community temperature scores and plot MATs. We repeated this same analysis using different characterizations of thermal maxima—e.g., the median of all maximum temperatures and the absolute maximum temperature—for each species. Then, with these new thermal maxima, we calculated community temperature scores and ran linear models as described above. Results of linear models were consistent across all three characterizations of thermal maxima, although the model using the median of all maximum temperatures was only marginally significant (Table S7).

3 | Results

3.1 | The Boiling River's Natural Temperature Gradient

The interpolated temperature map indicates a steep thermal gradient along the Boiling River, with differences in MAT and maximum temperature of ~4°C and ~11°C, respectively, across a distance of < 1 km (Figures 1 and 2). The loggers in the nearby reference forest (TMS_12 and TMS_13) recorded a similar MAT to the three loggers along the Boiling River upstream of hot water inputs (TMS_9, TMS_10, and TMS_11), although the maximum temperature was slightly higher at the reference forest sites, likely because proximity to the river provides a cooling or buffering effect. In situ and remotely sensed temperatures were highly correlated (Table S1), indicating that the thermal gradient is persistent throughout the vertical profile of the forest from the soil to the canopy, although its magnitude may decrease with increasing height aboveground.

Mean and maximum monthly 24-h and nighttime air temperatures maintained similar relative patterns throughout the year (Figure S10), as did those of soil temperatures (but as expected, the soil temperatures were more stable than air temperatures; Figure S11). Daily temperature fluctuations (T_{diff}, or the difference between the daily maximum and minimum temperature) were greater (based on ANOVA and Tukey's HSD) and had a larger positive skew at warmer sites and with increasing distance from the river, again suggesting a riparian buffering effect (Figure S12). Across all sites, T_{diff} was greater during the dry season when there was greater solar radiation and less frequent precipitation, and this was especially true at hotter sites (Figure S13). This tendency was possibly due to a lower stem density and thinner canopy at hotter sites, supported by the

greater difference in daytime (Figure S14) than nighttime temperature distributions (Figure S15) across sites. Alternatively, the larger seasonal difference in T_{diff} at hotter sites could be due to a greater relative abundance of deciduous or semi-deciduous trees, which is supported by the larger difference in daytime versus nighttime temperatures between hot and cold sites during the dry season (Figure S10).

Relative air humidity is relatively constant across the study site. Relative humidity is generally high (> 90%) but declines during the dry season (Figure S16a). Mean monthly relative humidity is generally similar but slightly lower at the end of the dry season between the reference forest (HOBO_12) and the sites near the river upstream of hot water inputs (HOBO_10, HOBO_11). Minimum monthly relative humidity is highly variable throughout the year but follows similar patterns across sites and typically differs by a maximum of ~10% between sites in any month, and hotter sites do not necessarily have lower relative humidity (Figure S16B). Consequently, mean and maximum vapor pressure deficit (VPD) were high (3–4 kPa and 3.5–6.5 kPa, respectively) but typically did not differ by more than 1.5 kPa in any month across sites (Figure S16c,d). VPD was similar throughout the year between reference forest sites and sites near the river upstream of hot water inputs.

3.2 | Woody Plant Diversity and Composition Are Influenced by Temperature

We established 70 woody plant inventory plots (each 28.3 m^2) along the Boiling River's thermal gradient. Plot centers were an average of 8 m from the river edge (maximum 25 m). Estimated plot temperatures ranged from 24.0°C to 26.3°C for MAT and 34.1°C–42.5°C for maximum temperature. In other words, there is a 2.3°C difference in MAT and an 8.4°C difference in maximum temperature among plots along the thermal gradient. Across all plots, there were a total of 648 individual woody plants, representing 197 species (Table S6). Stem densities ranged from 5 to 17 individuals with a mean of 9.3 individuals per plot (Table S8), and stem diameters ranged from 2 cm (the minimum cutoff) to 89 cm DBH with a mean of 8.5 cm (Figure S17). The five most common species were *Himatanthus articulatus* (Apocynaceae, $n = 30$ individuals in 16 plots), *Hevea brasiliensis* (Euphorbiaceae, $n = 21$ in 13 plots), *Chrysophyllum argenteum* (Sapotaceae, $n = 19$ in 9 plots), *Lonchocarpus spiciflorus* (Fabaceae, $n = 19$ in 8 plots), and *Cordia alliodora* (Boraginaceae, $n = 17$ in 10 plots).

We found significant negative relationships between MAT and α-diversity. Hotter air temperatures corresponded to a reduction in Shannon diversity and species richness along the thermal gradient ($R^2 = 0.16$, $p < 0.001$, Figure 3). There were also significant reductions in Simpson's and inverse Simpson's indices with increasing air temperature, and all patterns held whether the main effect was MAT or maximum temperature (Table S4). Meanwhile, MAT had a weak but significant negative effect on stem density and no effect on species evenness (Figure 3). To further explore changes in α-diversity, we pooled data from the 25 coolest and the 25 hottest plots and calculated rarefaction curves for species diversity vs. stem number. The rarefaction curves showed a steeper increase in species diversity in the cool plots than in the hot plots (Figure S4). This indicates
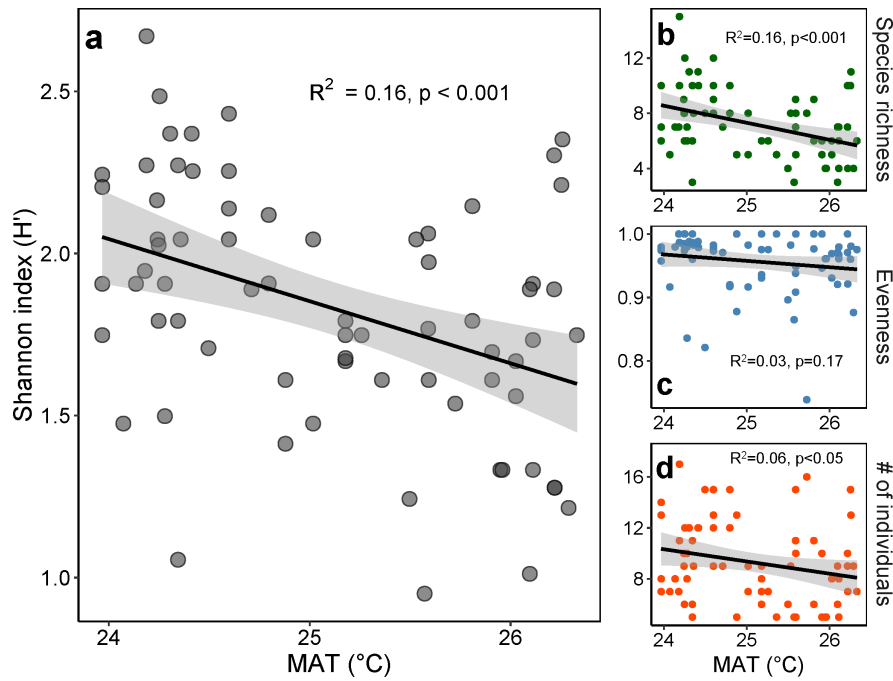
FIGURE 3 | Scatterplots showing the relationships between mean annual temperature (MAT) and (a) Shannon diversity index, (b) species richness, (c) species evenness, and (d) number of individuals in woody plant inventory plots along the Boiling River's thermal gradient. Each point is a plot. Lines indicate the linear relationship between MAT and each response variable; shaded areas represent 95% confidence intervals.
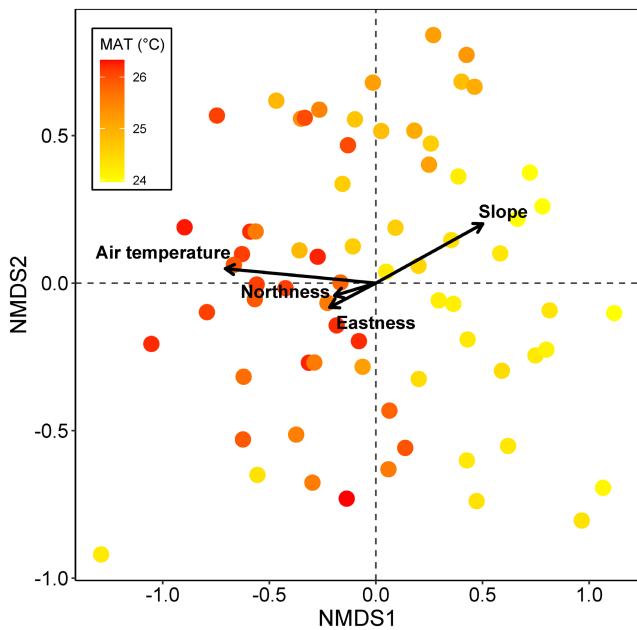

FIGURE 4 | Species abundances in each plot were used to compute the NMDS ordination in three dimensions. Each point is a woody plant inventory plot and is color-coded by its mean annual temperature (MAT). The orientation of arrows indicates the direction in ordination space in which four environmental variables (air temperature, northness, eastness, and slope) change most rapidly and in which they have maximum correlation, whereas the length of the arrows indicates the rate of change.

that diversity increases more rapidly with additional sampling in the coolest plots compared to the hottest ones, and that rare species may be more prevalent in cool plots than in hot plots. We

repeated all diversity analyses using only stems $< 10\,cm$ DBH and found similar negative relationships between diversity and air temperature (Figures S5 and S6; Table S4).

In general, there was high β-diversity between plots ($\beta_{SOR} = 0.9817$) that was attributable to high turnover rather than nestedness or species filtering ($\beta_{SIM} = 0.9771$, $\beta_{NES} = 0.0046$). We also calculated β_{SOR} for each pairwise plot combination and compared this to the pairwise difference in MAT (ΔMAT). A Mantel test indicated a significant positive relationship between β_{SOR} and ΔMAT, indicating higher plot dissimilarity with larger differences in air temperature (Mantel statistic $r = 0.32$, $p = 0.001$, Table S5). This relationship held when controlling for geographic distance and topography using a partial Mantel test (Mantel statistic $r = 0.31$, $p = 0.001$, Table S5). Furthermore, the distribution of β_{SOR} indicates that plots with similar temperatures (i.e., small ΔMAT) can exhibit a range of compositional similarity, but plots with large temperature differences (i.e., large ΔMAT) are always compositionally dissimilar (Figure S18).

To further explore compositional changes along the thermal gradient, we performed an ordination using non-metric multidimensional scaling (NMDS) based on Bray-Curtis community dissimilarities. The resulting NMDS showed a relationship between the composition of woody plants and air temperature (Figure 4; Figure S19). Together, these results indicate that plots in the hotter portions of the Boiling River gradient are more compositionally similar to each other than they are to plots in the cooler portions of the gradient and that air temperature is associated with a shift in the composition of woody plant species.

We tested if changes in composition along the Boiling River's thermal gradient were associated with differences in species' thermal affiliations by calculating the community temperature
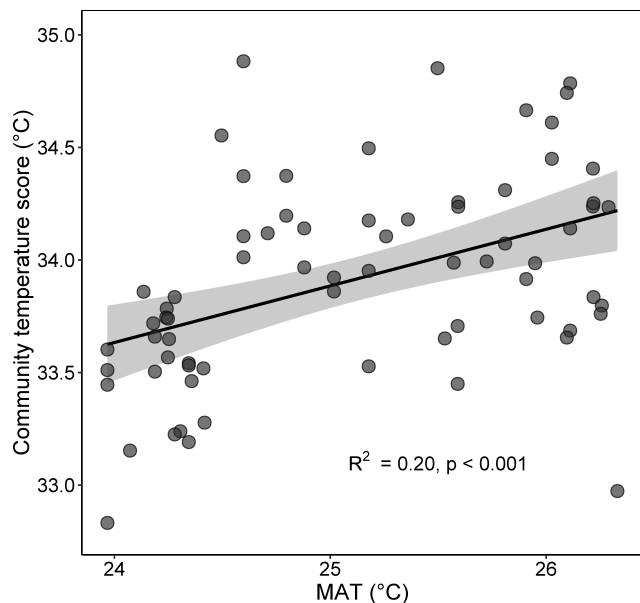
FIGURE 5 | Scatterplot showing the relationship between community temperature scores of woody plant inventory plots along the Boiling River's thermal gradient and the plots' estimated mean annual temperature (MAT). Each point is a plot. The line shows the linear relationship between the two variables, and the shaded area is the 95% confidence interval.

scores for each of our 70 forest inventory plots. A linear regression shows a significant positive relationship between MAT and community temperature scores ($R^2 = 0.20$, $p < 0.001$, Figure 5). In other words, the hotter plots contain greater relative abundances of more thermophilic species whose geographic ranges include higher maximum air temperatures. Conversely, plots with lower MAT predominantly contain species whose geographic ranges are restricted to cooler regions of the Amazon.

4 | Discussion

The Boiling River and its surrounding forest are a valuable system to examine the effects of rising temperatures on lowland tropical plants and their associated communities. Indeed, this model system alleviates many of the limitations that typically complicate the application of experimental warming studies to natural tropical forests (Cavaleri et al. 2015). First, the high diversity of tropical forests makes it challenging to study whole-ecosystem responses to experimental warming. The Boiling River, which includes over 2 km of contiguous riparian forest, features both a cool "control" forest and a "heated" forest (Figure 1), which enables research into above-ground community-level, species-level, and individual-level responses to high temperatures (Kullberg et al. 2023; Kullberg and Feeley 2024). A corresponding gradient of soil temperatures (Figure S11) suggests the possibility of studying below-ground responses to high temperatures as well. Another major limitation posed by warming experiments is the inability to warm entire adult trees (Cavaleri et al. 2015). At the Boiling River, trees have been exposed to augmented temperatures since germination, providing an unprecedented opportunity to study whole-tree and whole-lifetime responses to high temperatures.

Finally, time is a limiting factor in warming experiments, which do not cover the time frame necessary to study long-term responses to warming. Therefore, the current state of warming experiments precludes our ability to understand how increasing temperatures influence multi-generational community dynamics that may result from changes in recruitment or mortality (Doughty et al. 2023). The Boiling River is estimated to be at least 10,000 years old (A. Ruzo, unpublished data), which provides insight into how air temperature might affect long-term, multi-generational processes that drive changes in community composition. The extended duration of elevated temperatures at the Boiling River may have allowed species to locally adapt or for communities to reach a stable state in the hotter forests. As a result, plant responses to increased temperatures at the Boiling River may actually be muted compared to responses that result from more rapid ongoing climate warming. In summary, the Boiling River is a unique and invaluable system to study the effects of elevated temperatures on organisms and communities in a diverse lowland tropical rainforest.

4.1 | Changes in Woody Plant Diversity and Composition Across the Thermal Gradient

Tropical forests and their constituent species are widely predicted to be vulnerable to rising temperatures, but the effects of high temperatures on lowland tropical plant communities remain largely unexplored. Here, we show that elevated air temperature markedly effects the diversity and composition of lowland tropical woody plant communities. At the Boiling River, woody plant diversity declined significantly across the thermal gradient (Figure 3; Table S4). Indeed, species richness declined from an average of 8.6 species per plot on the cooler end of the gradient to an average of 5.7 species on the hotter end, translating to a 33.5% reduction in woody plant diversity across the entire gradient. In other words, there is an 11.3% reduction per 1°C increase in MAT, or a 3.6% reduction per 1°C increase in maximum temperature. Our results are in accord with previous estimates of biodiversity loss due to warming. One previous study estimated a 21%–32% loss of plant and animal species under maximum climate change, a scenario that expects a mean global temperature increase of > 2°C by the year 2050 (Thomas et al. 2004), and another study focused on a few groups of plants and insects found that nearly half of species are candidates for biotic attrition in the lowlands (Colwell et al. 2008). Likewise, across the entire lowland Amazon, there is a ~50% decrease in tree diversity (species per hectare) across a 5°C gradient in maximum temperature (Colwell and Feeley 2024). Losses of diversity of this magnitude could disrupt a wide array of ecosystem processes, especially if expanded to larger spatial scales due to global warming (ter Steege et al. 2023). It is important to note that changes of diversity due to increases in temperature are almost certainly non-linear: rising temperatures may actually increase diversity in some cooler areas due to species immigration (Steinbauer et al. 2018; but see Harrison 2020), and the potential for tipping points can lead to rapid and/or unpredictable changes.

More research is still required to determine the specific mechanisms and demographic processes behind the observed losses of diversity in hotter forests. However, one potential explanation is that in the lowland tropics, many species are already near their

thermal threshold (Doughty et al. 2023) and any rapid increases in temperature in an already hot environment may be too great for most species to overcome. In addition, because there are no hotter rainforests than the lowland Amazon (Feeley and Silman 2010), any colonization by more heat-tolerant species that would ameliorate heat-induced diversity loss is unlikely (Colwell et al. 2008). Although diversity in the Neotropics was actually higher during periods of past warmth (Jaramillo, Rueda, and Mora 2006) and many extant species originated during these periods (Dick et al. 2013), previous warming and cooling cycles happened over millions of years, which allowed species to adapt to changes in temperature and which promoted the diversification of species due to increased habitat heterogeneity (Jaramillo 2023; van der Hammen and Hooghiemstra 2000). Current and future increases in temperature are likely too rapid for species to tolerate through adaptation (Feeley et al. 2023), thereby precluding future diversification of lowland tropical forest species due to warming. In summary, lowland tropical forests will likely experience losses in diversity due to warming because (1) many of their constituent species are already near their upper thermal limit, (2) there are no analogous forests where temperatures are higher that could serve as origins of species immigrations, and (3) warming rates are too fast for species to adapt and diversify.

At the Boiling River, elevated temperatures were also associated with marked and directional changes in species composition, with an overall pattern of increased relative abundances of more thermophilic woody plant species in hotter parts of the thermal gradient (Figures 4 and 5). We detected a significant effect of air temperature on species composition such that the relative abundances of thermophilic species were greatest in plots with higher MAT. It is worth emphasizing that the observed differences in diversity and composition all occur within a single continuous forest over a distance of < 2 km. The observed compositional changes corroborate previous studies that have found similar patterns across much more expansive gradients or that have observed thermophilization of tree communities through time associated with rising temperatures in montane forests (Duque, Stevenson, and Feeley 2015; Fadrique et al. 2018; Feeley et al. 2013; Tanner et al. 2022). In these other studies, thermophilization was driven primarily by increased mortality of the less thermophilic species (Duque, Stevenson, and Feeley 2015; Feeley et al. 2013; Tanner et al. 2022), increasing the relative abundances of thermophilic species in subtropical and temperate regions (Osland et al. 2021; Rosenblad, Baer, and Ackerly 2023; Vesperinas et al. 2001), and lineage filtering rather than adaptation to environmental changes over evolutionary time (Donoghue 2008). Although it is difficult to identify the specific mechanisms behind the observed compositional changes in our study, the putative drivers of thermophilization seen in these previous studies should inspire future investigations at the Boiling River and elsewhere. The increase in community temperature scores of woody plant communities along the Boiling River's thermal gradient suggests that ongoing and future warming may similarly lead to widespread thermophilization of other tropical lowland forests.

Although the mechanisms driving compositional change across the Boiling River's thermal gradient are still unclear, there could be a potential link between a species' thermal maximum and its ability to acclimate to increased temperatures. For example, a previous study found that two species at the Boiling River, *Ochroma pyramidale* (Malvaceae) and *Warszewiczia coccinea* (Rubiaceae), acclimated their photosynthetic thermal tolerances at increased temperatures (Kullberg et al. 2023). Both of these species are common in the hotter forests at the Boiling River and have relatively high thermal maxima based on our analyses (Table S6). Conversely, some species, including *Syagrus smithii* (Arecaceae) and *Tetrathylacium macrophyllum* (Salicaceae), are common in cooler forests at the Boiling River and virtually absent from hot forests; both of these species also have relatively low thermal maxima (Table S6). In the hot forests at the Boiling River, some species may have a competitive advantage by exhibiting more trait plasticity than other species, and this trait plasticity may be correlated with species' thermal maxima.

It is important to note that plot community temperature scores were calculated based on the species' large-scale geographic distributions, which may be influenced by spatial biases in sampling and yield imprecise estimates of species' thermal maxima. Taxonomic uncertainty and misidentifications of botanical specimens could also influence the characterization of thermal niches. Additionally, there is a potential mismatch between plot community temperature scores (reflecting macroclimate data derived from WorldClim) with plot air temperature (reflecting microclimate data).

4.2 | Limitations of the Temperature Gradient

We acknowledge several limitations in our characterization of climate at the Boiling River site. First, our temperature loggers only measured the soil and air temperatures up to 1 m above the ground, so it is uncertain how the thermal gradient varies across the vertical strata of the forest. However, Landsat LST estimates of canopy temperatures were highly correlated to the air temperatures recorded in the understory (Table S1), providing evidence of a similar pattern in relative temperatures throughout the vertical profile of the forest, although the heating effect is likely weaker at increasing heights and distances from the river.

Similarly, given that temperature loggers were not directly associated with each of the 70 inventory plots, it was not possible to assess the impact of microclimatic variations on woody plant diversity and composition. We characterized the daily temperature fluctuations (T_{diff}) for each of the temperature loggers and found that, on average, the hottest sites had greater T_{diff}, especially during the dry season, potentially due to a thinner canopy and/or increased deciduousness, which would increase solar radiation in the understory of the hotter forests. The greater variability in microclimate (and potentially greater understory solar radiation) at the hotter sites may have an impact on germination and recruitment, which we were unable to account for here. Indeed, increasingly open canopies in European forests are leading to thermophilization of the forest understory due to decreased buffering of macroclimatic conditions (Zellweger et al. 2020). Currently, tropical forests show the greatest capacity to buffer macroclimatic air temperature maxima globally (De Frenne et al. 2021). Given current knowledge gaps regarding physiological thresholds across Amazonian taxa, potential thermal tipping points for

Amazonian vegetation, and the projected outcomes of said tipping points (Doughty et al. 2023), it is not possible to predict future microclimatic regimes in the Amazon, as these are largely dependent on canopy cover in tropical forests (De Frenne et al. 2021). As such, the conditions at the Boiling River may not exactly match future conditions for much of the Amazon; nonetheless, they do provide a unique and valuable opportunity to study lowland tropical plant communities under elevated temperatures.

Another limitation is the inconsistency of the thermal gradient throughout the year. The water temperatures of the Boiling River are not constant as the river's flux is significantly supplemented by rainwater and runoff that temporarily cools the hottest portions of the river by up to ~45°C during the wet season (Kullberg and Feeley 2024). Although the relative thermal gradient is maintained throughout the year (Figure S10), the seasonal temperature fluctuations are greater in the hotter areas of the forest and may confound the effects of greater mean and maximum temperatures (Figure S13). Therefore, the effect of maximum temperatures may be inflated since plants in hotter areas must also survive a wider breadth of conditions.

Recognizing these limitations, we compared the hottest 25 plots to the coldest 25 plots since this characterization should be robust to most potential errors or inaccuracies. This coarse comparison confirmed the plot level analyses and showed markedly higher species diversity in the cool plots than in the hot plots, even controlling for differences in stem numbers (Figure S4).

4.3 | Conclusions

Our study suggests that rising temperatures may lead to decreases in plant diversity and drive thermophilization of plant communities across the lowland Amazon. Such widespread changes could lead to biotic attrition as many species disappear entirely from low elevations (Colwell et al. 2008; Colwell and Feeley 2024) and potentially even contribute to a wholesale transition from rainforest to savannah biomes (i.e., Amazonian dieback (Malhi et al. 2009)). Changes in plant diversity and communities due to warming will likely be compounded by other changes in climate. Indeed, shifting precipitation regimes and intensifying droughts have already altered species composition (Esquivel-Muelbert et al. 2019) and rates of carbon sequestration (Bennett et al. 2023) in the Amazon. These other changes in climate and their impacts on Amazon plant communities could magnify any direct effects of temperature alone (Bennett et al. 2023; Malhi et al. 2009). Ongoing and future changes in climate will also be accompanied by deforestation and other forms of habitat loss throughout the Amazon, which will undoubtedly contribute to additional declines in plant diversity and compositional changes (Feeley et al. 2012; Feeley and Rehm 2012; Hubbell et al. 2008). Increasing temperature, shifting precipitation regimes, intensifying drought, habitat loss, and land-use change will all independently lead to changes in lowland Amazon forest communities. These drivers of change, how they interact, and their consequences must all be taken into consideration when predicting ecosystem responses to global change and when formulating conservation strategies.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.13929535 and Github at https://github.com/alyssakullberg/BoilingRiver_ThermalGradient_TreeDiversity. Landsat 9 imagery is available on the USGS EarthExplorer website (https://earthexplorer.usgs.gov/, https://doi.org/10.5066/P975CC9B). Updated species occurrence data can be downloaded from the Botanical Information and Ecology Network (BIEN, https://bien.nceas.ucsb.edu/bien/biendata/) using the BIEN package in R statistical software (https://cran.r-project.org/web/packages/BIEN/index.html). Climate data used to calculate thermal maxima are available from the WorldClim database (https://www.worldclim.org/data/worldclim21.html).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.