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Plant modulation on daytime ground surface temperature: An overlooked mechanism in climate warming regulation

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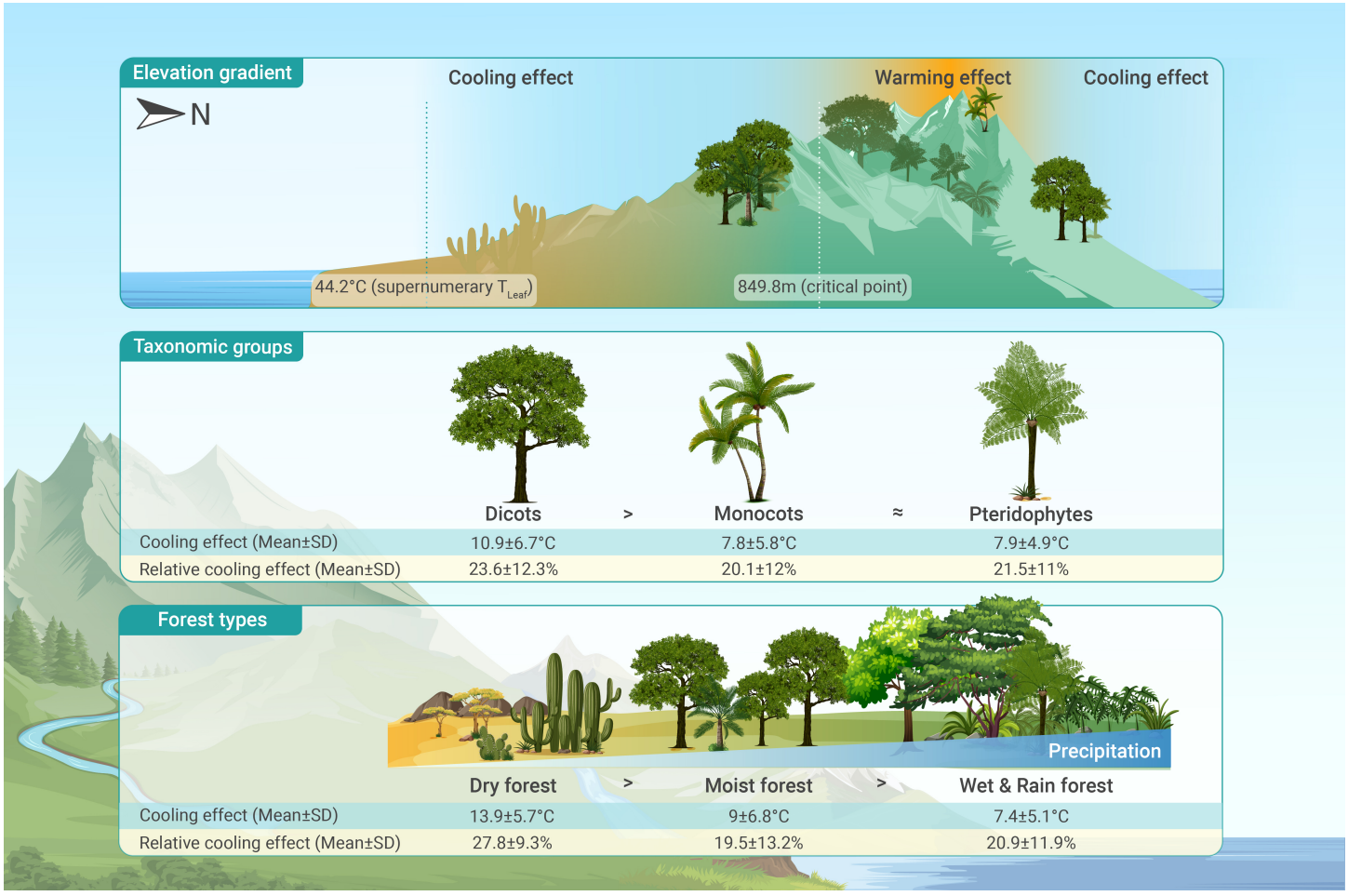
GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Plants influence global warming by altering surface infrared radiation.
- The cooling effect of tropical forests depends on elevation, species composition, and forest types.
- Sustainable strategies, such as tropical reforestation, can help mitigate climate change.

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Plant modulation on daytime ground surface temperature: An overlooked mechanism in climate warming regulation

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Despite the widely recognized greenhouse effect caused by greenhouse gases, atmospheric temperature is also directly driven by ground surface temperature. Tropical forests cover 7% of terrestrial land and likely play a noticeable and disproportionate role in regulating the temperature of the ground surface that emits infrared radiation available for the subsequent greenhouse effect. Here, we evaluated the role of plant leaves in modulating daytime ground surface temperature across tropical dry-rain forests in Puerto Rico. We found that leaf midday temperature decreased with altitude following a logistic function. In contrast, bare ground surface temperature linearly reduced with altitude. Canopy cooling effect ranged from 34.5°C to -10.2°C, with the strongest cooling observed in low-altitude forests and diminishing at higher elevations. Further, dicotyledons exhibited a stronger cooling effect on ground surface temperature than pteridophytes and monocotyledons. Dry forests showed the greatest cooling effect at high temperatures, whereas wet-rain forests exhibited the most effective cooling when temperatures were below 10°C. These findings highlight the critical yet often overlooked role of tropical forests in regulating daytime surface temperatures and call for greater attention to the biophysical impacts of deforestation on climate change beyond the carbon-centric discourse.

INTRODUCTION

Global warming is predicted to continue increasing, with the global average atmospheric temperature having risen by 1.1°C since the industrial era.[1] Greenhouse gases released from human activities have long been considered the dominant driving factor in global warming, as they can capture and retain infrared radiation before it escapes directly from the atmosphere to space.[2] Although it is undeniable that the greenhouse effect, as a direct driver, plays an important role in regulating atmospheric temperature, alteration in the infrared radiation from the ground surface resulting from land-use changes, as another direct driver of atmospheric temperature, has been largely overlooked.

Rationales for supporting greenhouse gas emissions as the main driver of climate warming rely on the facts that (1) greenhouse gases have a greenhouse effect, and (2) there is a positive correlation between atmospheric CO_2 concentration and air temperature.[3-5] While it is true that the increase in atmospheric concentration of greenhouse gases will enhance the greenhouse effect, leading to an increase in atmospheric temperature, however, a correlation does not necessarily mean a full causal relationship. Further, there exists abundant evidence that does not support greenhouse gases being the only primary driver of climate change, including (1) The concentration of CO_2 in the atmosphere does not always correlate with atmospheric temperature;[6,7] (2) Historical periods of high atmospheric CO_2 concentrations have not consistently resulted in proportional warming;[6] (3) CO_2 alone cannot explain historical atmospheric minimum and maximum temperatures;[8] (4) Atmospheric CO_2 exhibits variable climate change sensitivity/efficiency of the greenhouse effect;[9-12] And (5) recent studies have shown that the ground surface temperature influences atmospheric temperature.[13] Most importantly, the Earth system cannot support a positive feedback between greenhouse gas emissions and climate warming, as numerous studies have demonstrated that the increase in temperature will lead to an increase in soil CO_2 emissions.[14-16] All these suggest that there are other major drivers for climate warming in addition to the recognized greenhouse effect by greenhouse gases, and that ground surface radiation, as the other direct driver, may have an underappreciated impact on atmospheric temperature.

Vegetation cover not only affects atmospheric temperature by reducing greenhouse gas concentrations through photosynthesis but also regulates ground surface temperature through biophysical and physiological processes, thereby influencing local climates.[17-19] According to the surface energy balance, the net radiation reaching the ground surface (*Rn*) mainly flows into the soil heat flux (*G*), sensible heat flux (*H*), and latent heat flux (*LE*). Vegetation can change various physical properties of the land surface, such as albedo, evapotranspiration, and surface roughness, thereby affecting the values and distribution of heat fluxes (Figure 1).[20] Forests typically have lower surface albedo than non-forested areas, allowing them to absorb more solar radiation.[21] However, forests have strong evapotranspiration and high canopy roughness, leading to a large latent heat flux, thus bringing a significant cooling effect on ground surface temperature,[21,22] especially in tropical forests. The annual total evaporation in the Amazon region can reach 1300 mm with an integrated daily Bowen ratio of 0.17 throughout the year, indicating a larger proportion of incoming solar energy is used for evapotranspiration.[23] A global study reveals an asymmetric land surface temperature response to tree cover changes, with cooling from tree cover gain due to enhanced evapotranspiration outweighing warming from tree cover loss.[24] Additionally, the high evapotranspiration of forests provides a large amount of water vapor, thereby supporting cloud and precipitation formation at large scales.[20,21,25] The formation of clouds can make the atmosphere brighter, increasing albedo, which can offset the decrease in surface albedo caused by vegetation.[20,22] In some tropical regions, such as the Amazonian rainforest, the top of the atmosphere shows a significantly higher albedo, ultimately reducing incoming solar radiation and net ground surface radiation, leading to a cooling effect.[23]

Further, forests have strong photosynthesis, accounting for 50% of the total net primary productivity on land.[26] During photosynthesis, vegetation not only absorbs carbon dioxide but also consumes energy. The combination of vegetation's carbon cycling and biophysical effects demonstrates a global potential cooling capability,[25] which has been supported by many studies. Remote sensing data analysis of global land surface temperature (LST) and leaf area index from 2001 to 2018 showed that regions with higher vegetation cover had lower surface air temperatures.[27] Cooling associated with greening could offset approximately 20% and 40% of the warming trends resulting from the increased atmospheric CO_2 concentration in China and

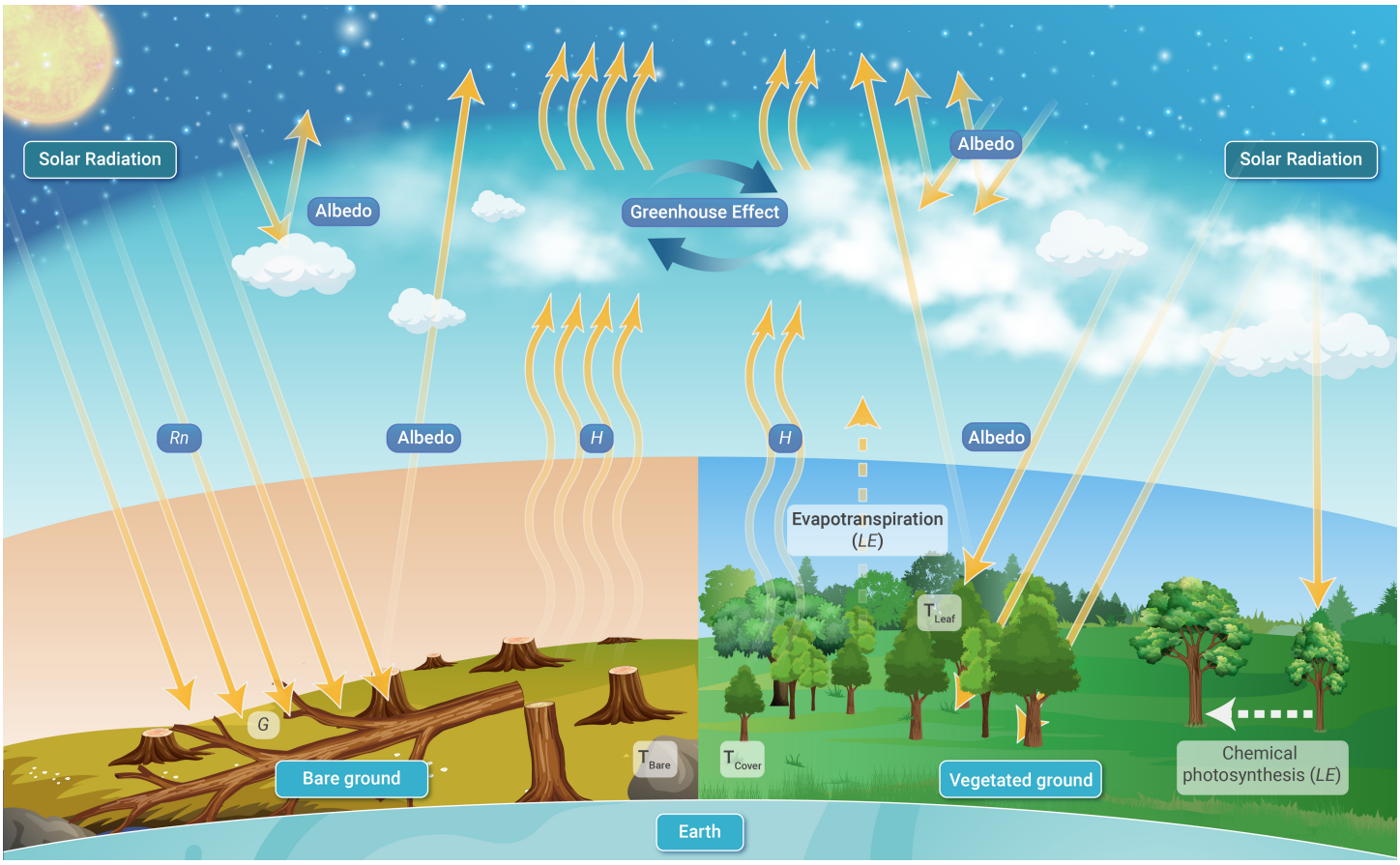

Figure 1. Diagram illustrating energy balance in the atmosphere comparing bare and forested ground A fraction of net solar radiation is reflected into outer space through the albedo effect that varies between bare and vegetated ground. The remaining solar energy (*Rn*) is absorbed by bare or vegetated ground surface (*G*) and irradiated as long wave energy (*H*) that causes the greenhouse effect, or by ground vegetation distributed between chemical photosynthates and water evapotranspiration (*LE*). T_{Bare} stands for the temperature of bare ground and T_{Cover} temperature of vegetated ground. T_{Leaf} is the temperature of the forest canopy leaves. The number of lines resembles the amount of energy flow.

India, respectively.[27] Trees in forests and pastures in Latin America and Africa are shown to provide substantial cooling benefits, with each hectare sequestering 10 metric tons of woody carbon associated with a linear decrease in temperature ranging from 0.32°C to 2.4°C.[28] Another study on LST in Chinese afforestation areas and adjacent grasslands or farmland found that afforestation could lead to an average daytime surface temperature reduction of approximately 1.1±0.5°C (mean ± 1 SD) and an average nighttime surface temperature increase of approximately 0.2±0.5°C.[29] Conversely, deforestation can accelerate surface temperature increases, leading to accelerated climate warming and reduced climate stability. In a canopy trimming experiment imitating hurricane defoliation in the tropical wet forest of Puerto Rico, soil temperatures significantly rise by >1°C even in 30 X 30 m plots that were surrounded by undefoliated forest, but as vegetation gradually recovers, soil temperatures gradually decrease back to the level prior to hurricane disturbance.[30]

At the same time, air temperature feeds back to the biophysical and physiological processes of vegetation. Tropical forests have a high-temperature threshold because once the temperature of plant leaves approaches or exceeds the critical temperature of 46.7°C (T_{Crit}), photosynthesis-related enzymes become inactive, causing a significant impact on primary production.[31-33] Plants that have undergone natural selection prevent leaf temperature from exceeding T_{Crit} through accelerated transpiration, which indicates a non-linear response of leaf metabolism temperature to solar radiation or air temperature.[34] Unlike plant-regulated leaf temperatures, bare ground temperature responds linearly to solar radiation or air temperature due to the absence of plant physiological regulation processes. Furthermore, because of the characteristics of high average temperatures and minimal diurnal and seasonal temperature variations in tropical forests, even slight temperature changes can have a significant impact on plants. Therefore, tropical forests are more sensitive to temperature increases compared to other regions.[31] Some studies suggest that certain tropical forests are already approaching or have exceeded the high-temperature threshold.[31-33,35]

Plants vary in physiological processes such as transpiration and in physical characteristics of leaves, such as size, shape, thickness, anatomical structure, optical properties, etc. These variations can influence leaf temperature. Therefore, different species have different abilities to regulate leaf temperature.[33,36,37] The effectiveness of plants in regulating their leaf temperature varies with the environment. Plants in arid and hot regions typically exhibit smaller leaves, lower absorptivity, and higher reflectivity, likely resulting in stronger physical cooling effects compared to those in wet and moist regions.[18] These plants often have higher leaf vein density and stomatal area, leading to higher transpiration rates when water becomes available. It is noteworthy that the effect of vegetation cover on surface temperature also varies at different latitudes. In mid to low-latitude regions, especially in tropical areas, higher solar radiation allows for more energy for photosynthesis and evapotranspiration, resulting in an overall cooling effect.[17] In high-latitude regions, solar radiation absorption by photosynthesis and transpiration is highly seasonal, resulting in a weakened cooling effect. Further, the low albedo of forests relative to snow-covered bare ground retains more radiation in high-latitude regions, leading to an insulating and even a warming effect.[17] Thus, we can infer that both plant taxonomy and environmental conditions can influence the effectiveness of plants in controlling ground surface temperature.

To elucidate the possible role of tropical forests over ground surface temperatures in mitigating global warming, we designed this study to examine the cooling effect of plant canopy on ground surface temperature and explore the variations among plant species and forest types on temperature regulation. We measured leaf temperatures (T_{Leaf}), corresponding canopy-covered ground temperatures (T_{Cover}), and adjacent bare ground temperatures (T_{Bare}) from nine tropical forests across dry to wet environmental condi-

Table 1. Geographic data, sampling date, and meteorological data for the tropical forests in Puerto Rico. Weather information is based on Preliminary Monthly Climate Data (CF6) from National Oceanic and Atmospheric Administration (NOAA, https://www.weather.gov/wrh/Climate?wfo=sju).

Sampling sites	Average Elevation(m)	Long. (°)	Lat. (°)	Forest Type	Sampling Date	Wind (Beaufort scale)	Weather Obersed
El Yunque National Forest (EY)		-65.8000	18.2951			1-Light air	Sunny
—Tabonuco forest (EV)	~425	-65.8199	18.3223	Wet	14, Aug, 2023	1-Light air	Sunny
—Palo Colorado forest	~500	-65.8199	18.3223	Rain	15, Aug, 2023	1-Light air	Sunny
—Palm forest	~750	-65.8199	18.3223	Rain	15, Aug, 2023	1-Light air	Sunny
—Dwarf forest	~950	-65.8199	18.3223	Rain	15, Aug, 2023	1-Light air	Cloudy/Sunny
Guayama Research Area (GY)	~235	-66.1690	18.0384	Moist	16, Aug, 2023	1-Light air	Sunny
Rio Abajo State Forest (RA)	~325	-66.3863	18.4236	Moist	20, Aug, 2023	1-Light air	Sunny
Vega Baja Nature Reserve (VB)	~12	-66.3918	18.4891	Moist	20, Aug, 2023	1-Light air	Sunny
Guanica State Forest (GN)	~338	-66.8686	17.9716	Dry	16, Aug, 2023	1-Light air	Sunny
Cabo Rojo Wildlife Refuge (CR)	~60	-67.1088	18.0102	Dry	19, Aug, 2023	1-Light air	Sunny

tions in Puerto Rico and at various altitudes. We hypothesize that (1) Leaf temperature has a supremum value and thus responds non-linearly to altitude across an elevational gradient, whereas bare ground temperature responds linearly to altitude; (2) Taxonomic plant groups vary in cooling effects on ground surface temperature; and (3) Forests in different moisture environments vary in cooling effects on ground surface temperature.

MATERIALS AND METHODS

Site information

Samples were collected from plants growing in seven regions in the Commonwealth of Puerto Rico (Table 1) between 10 am and 4 pm. We measured the longitude and latitude of every region via the handheld GPS terminal, and the data are presented in World Geodetic System 1984 (WGS84). We categorized all the measured regions into three groups based on wide life zones in the tropics.[38] The dry forest receives 600-1100 millimeters of rainfall per year, the moist forest receives 1000-2200 millimeters of annual rainfall, and the wet-rain forests receive more than 2000 millimeters of annual rainfall. Elevations, T_{Bare}, and T_{Cover} were measured at the same time as the samples were taken. Hence, for each site, those data may vary, depending on the specific location of the sampling point and the weather condition of the sampling time. Previous studies have shown that under field conditions, within a certain wind speed range (0 to 2 m/s), changes in wind speed has almost no effect on leaf temperature,[18,39] but for the sake of seriousness, we still got wind speed data from ERA5.[18,39,40]

Species selection and sample collection

We collected samples from 67 tropical species (Table S1) from lowlands up to montane-forest including monocots (monocotyledonous plants), dicots (dicotyledonous plants), and ferns (pteridophytes). In order to choose the species that are beneficial to the research, we have followed the principle of preferential selection to include widespread species such as *Hedychium coronarium* (White ginger lily), *Cyathea arborea* (West Indian tree-fern), and *Prestoea acuminata* var. *montana* (Sierra palm).[41] Species included primarily trees, but also woody shrubs and herbaceous plants.

At each sampling site, the sun-exposed outer canopy leaves were selected for T_{Leaf} measurement. Our measuring time was from 2 p.m. to 4 p.m. each day to ensure stable lighting conditions. The reachable leaves were measured directly with the infrared thermometer (Etekcity Infrared Thermometer 774) on the top side of the leaf surface. The leaves in the high canopy were cut using pole pruners and immediately measured within five seconds. For each plant, we randomly chose at least five different leaves that fit the criteria and measured them separately to obtain an average to improve the reliability and repeatability of the data.

T_{Cover} and T_{Bare} were also measured by the infrared thermometer. T_{Bare} refers to the temperature of the sun-exposed ground/soil surface. T_{Cover} refers to the temperature of the ground/soil surface that is covered by vegetation. Due to the heterogeneity of the environment, we measured a set of ground temperature values for every five leaf temperature measurements. All measurements were carried out while avoiding areas that were either inundated or covered with dry leaves.

Forest function parameters

We computed two forest function parameters to quantify the magnitude of the impact of forests on ground temperature. The two forest function parameters are the forest cooling effect (FCE) and the relative forest cooling effect (RFCE). Both forest function parameters are determined by the T_{Bare} and the T_{Cover}. The equations are:

$$\text{ForestCoolingEffect (FCE)} = T_{Bare} - T_{Cover}$$

$$\text{RelativeForestCooling Effect (RFCE)} = \frac{T_{Bare} - T_{Cover}}{T_{Bare}} \times 100\%$$

With two forest function parameters, we can consistently evaluate the extent to which forests influence the local ground environment in different regions. For FCE, it measures the absolute control ability of the ground temperature by plants, standing for the integrated cooling capacity of the entire forest ecosystem, including direct biophysical processes (canopy shading, evapotranspiration) and indirect microclimate regulation (humidity stabilization, soil moisture retention). For RFCE, we considered it as a reflection of forest cooling/warming sensitivity or the sensitivity of forest cooling/warming ability. It represents the proportional sensitivity of vegetation to mitigate or amplify ground temperature extremes, which enables cross-environment comparisons by accounting for variations in initial thermal conditions. Moreover, due to the presence of the numerator term, these parameters are positive when forests act as cooling factors and negative when they act as warming factors.

Data processing and statistical analysis

To test hypothesis (1), all data and images were recorded electronically, and species information was identified and classified. Due to the discrete nature of the elevation data obtained at each site, curve fitting posed a challenge. Hence, we reorganized the data as follows: (i) We initially divided the temperature range from 20 to 67.5°C (which is the lowest and the highest temperature we observed) into small intervals of 0.75°C. (ii) The temperature data points we got were then allocated to these intervals. Subsequently, (iii) we computed the average elevation data corresponding to the temperature data points within these intervals. This average value was used as the elevation value corresponding to that specific temperature interval. Consequently, (iv) we obtained the elevation-temperature correspondence data and used these data for plotting and fitting purposes. We employed the Levenberg-Marquardt (LM) algorithm and linear fitting (Origin Pro 2023b) for the regression analyses using the ordinary least squares (OLS) method. Moreover, we applied a similar method to that used for temperature-elevation data to assess the variation of leaf parameters-elevation data. Thus, we segmented

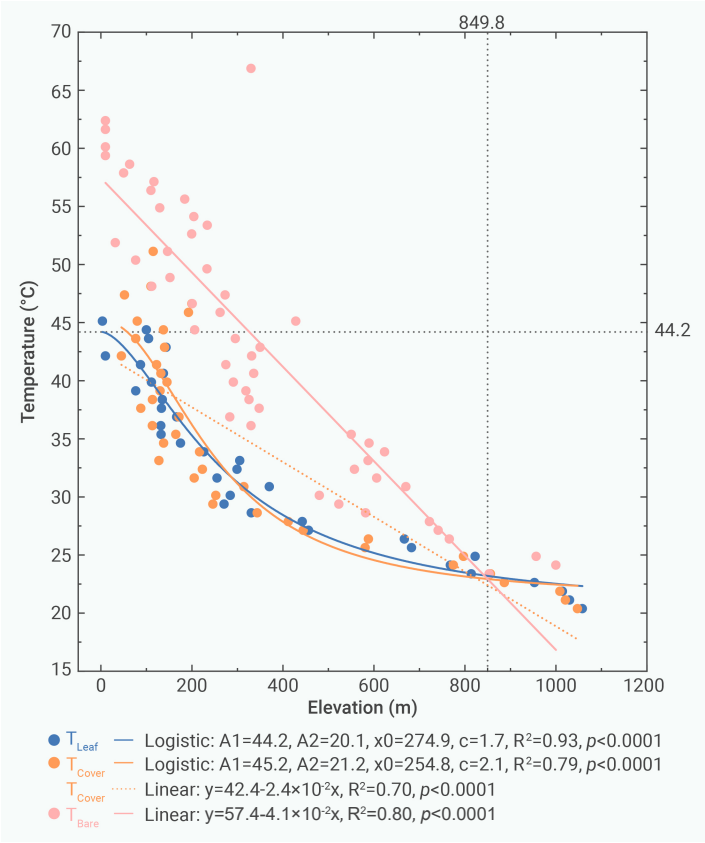

Figure 2. T_{Leaf}, T_{Bare}, and T_{Cover} **as a function of elevation in the logistic model and linear model** The equation of the Logistic model is $\mathbf{y} = \mathbf{A}2 + (A1 - A2)/[1 + (x/x0)^p]$, where A1, A2, x0, and p are fitted constants.

the FCE and RFCE range from -11°C to 35°C and -26% to 60%, respectively, into small intervals of 0.75°C or 1%. The obtained leaf parameter data points were subsequently assigned to these intervals. Subsequently, we calculated the average elevation data corresponding to the temperature data points within these intervals. Using this data, we conducted linear regression analysis and other statistical methods.

To test hypothesis (2), we first analyzed the relationship between taxonomy and leaf function parameters in all sampling sites. We carried out the two-sample t-tests on the data with elevation and taxonomic groups as independent variables, while cooling and relative cooling effects as dependent variables.

To test hypothesis (3), based on the usual practice,[38] the sampling sites are divided into three dry-wet gradients. Cabo Rojo and Guanica represent the dry gradient category, Guayama, Rio Abajo and Vega Baja represent the moist gradient category, and El Verde, El Yunque represent the wet and rain gradient category. Since temperature data at each elevation can be considered normally distributed, according to the linearity property of normal distribution, we can verify that the sum of temperature data in different sampling sites should also follow a normal distribution. Therefore, we first tested the homogeneity of variances of the collected data and found that the condition was satisfied, so we conducted the following analyses: (1) We performed the two-sample t-tests (Origin Pro 2023b) on the T_{Bare} and T_{Cover} within each category to preliminarily verify our prediction that forests control ground surface temperature, regardless of the dry-wet classification. (2) We created boxplots, indicating the maximum, minimum, and mean values, to examine the distribution of T_{Bare} and T_{Cover} data within the three dry-wet categories and compare the temperature distribution differences among them. (3) To quantify the absolute control ability of forests on ground surface temperature and the response sensitivity of ground surface temperature in different dry and wet environments, two-sample t-tests were executed among three distinct forest types (Figures 5A-B) where FCE and RFCE were employed as metrics. To further elucidate the relationship between T_{Bare} or T_{Cover} and T_{Leaf} in different sampling sites with varying dry-wet conditions, we conducted linear regression analysis (Origin Pro 2023b), with leaf surface temperature as the independent variable and either T_{Bare} or T_{Leaf} as the dependent variable.

RESULTS

Temperature and cooling effect changes along the elevation gradient

There were significant differences among T_{Leaf} ($F_{25,685}$=80.1, p <0.0001), T_{Cover} ($F_{25,685}$=81.1, p < 0.0001), and T_{Bare} ($F_{25,685}$=52.0, p < 0.0001), all of which decreased significantly with elevation as expected. We attempted fitting with 21 different curve equations, among which the logistic model yielded highly satisfactory fitting results (Table S2) for T_{Leaf} with a supremum value of 44.2°C and T_{Cover} with a supremum value of 45.2°C (Figure 2). In contrast, T_{Bare} decreased linearly with the elevation, and the linear correlation between T_{Cover} and elevation was also significant, albeit with a lower R^2 compared with its logistic fitting result. Further, T_{Bare} values were greater than T_{Cover} or T_{Leaf} till T_{Bare} (liner fitting) and T_{Cover} (logistic fitting) intersected at an altitude of 849.8m (Figure 2).

Our data showed that leaf response to elevation was not linear, which was different from the linear bare-elevation pattern (Figure 2). Moreover, plant leaf temperature showed a weakening of response to altitude at both high and low elevations as characterized by lower curve slopes. It also revealed that the fitting function value was approaching the supremum values of 44.2±1.0°C ($A1$) near sea level (at 0 m elevation).

It was apparent that T_{Bare} had a wider variation than T_{Cover} and T_{Leaf} (Figure 3A). The distribution of FCE for each elevation interval exhibits a normal distribution pattern within each elevation interval and shows a decreasing trend as elevation increases (Figure 2B). Meanwhile, the change in FCE with elevation exhibited two distinct patterns (Figure 3C). FCE values greater than zero (indicating an apparent cooling effect) decreased linearly with elevation, while FCE values less than zero (indicating an apparent warming effect) increased with elevation. The highest absolute values of both cooling and warming effects occurred at coastal forests, reaching 34.5 and 10.2°C, and decreased at the rate of 5.0 and 1.0°C for every 100 m increase in altitude, respectively. Similarly, the RFCE (Figure 3D) exhibited an identical cooling and warming pattern, with the cooling and warming slopes of 4.9% and 3.9% for every 100 m increase in altitude, respectively. Both the highest relative cooling and warming effects occurred at coastal forests, reaching 52.1% and 25.1%, respectively.

Taxonomic groups and plant cooling effects

We found that dicots had a greater cooling effect than monocots and ferns (Figure 4A). The cooling effect of the monocots and ferns did not differ. The mean cooling effect of dicots was 10.9°C with a range of -7.7°C~34.5°C. The mean cooling effect of monocots was 7.8°C with a range of -10.2°C~27.4°C. The mean cooling effect of ferns was 7.9°C with a range of -1°C~19.1°C. Further, dicots had a greater relative cooling effect than monocots, and ferns did not differ with either (Figure 4B). The mean relative cooling effects of dicots, monocots, and ferns were 23.6%, 20.1%, 21.5%, with a range of -13.9%~52.1%, -25.1%~46.8%, and -4.3%~42.6%, respectively.

Forest types and plant cooling effects

FCE and RFCE varied with forest types. Dry forests exhibited the most pronounced cooling effect, followed by moist forests, and lastly, wet-rain forests (Figure 5A). The mean cooling effect in the dry forests was 13.9°C with a range of 1.2°C~34.5°C. The mean cooling effect in the moist forests was 9.0°C with a range of -10.2°C~32.2°C. The mean cooling effect in the wet-rain forests was 7.4°C with a range of -1.0°C~19.6°C. Further, dry forest plants had a greater relative cooling effect than plants in the moist and wet-rain forests, and the latter two forest types did not differ from each other (Figure 5B). Mean plant relative cooling effects of the dry, moist, and wet-rain forests were 27.8%, 19.5%, and 20.9% with a range of 3.7%~51.6%, -25.1%~52.1%, and -4.3%~43.8%, respectively. Dry forest has the highest and wet-rain forests have the lowest T_{Bare} temperatures (Figure 5C). While the wet-rain forests have the lowest T_{Cover} temperatures, the dry and moist forests did not differ. T_{Bare} temperatures were higher than T_{Cover} temperatures across all forest types. Variations of T_{Bare} were greater than those of T_{Cover} across all three forest types, especially for the dry and wet-rain forests.

There existed robust correlations between $T_{Leaf}$and T_{Cover} or $T_{Bare}$for all forests together (Figure 6). These correlations also existed within the dry,

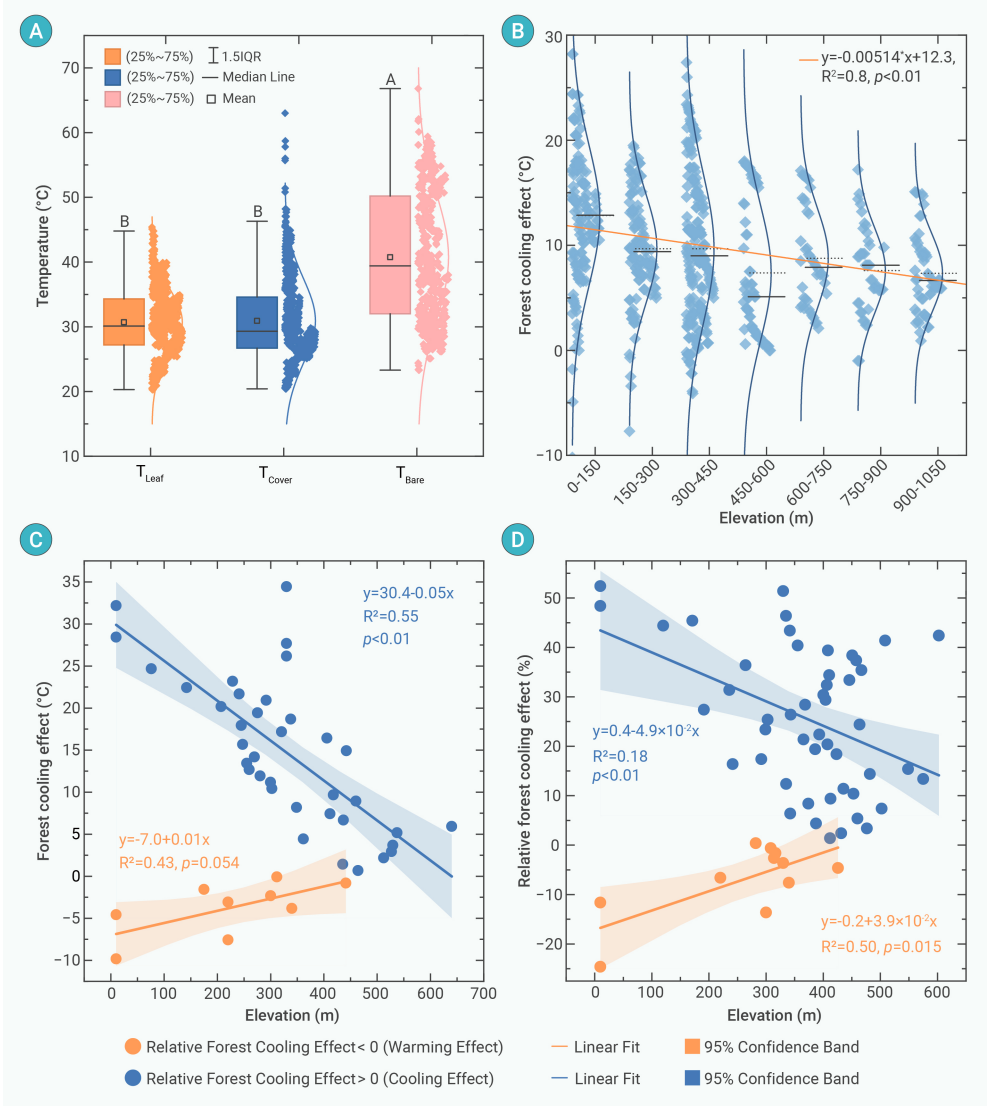

Figure 3. Regression analysis and distribution of T_{Leaf}, T_{Bare} and T_{Cover}, FCE and RFCE with altitude variation (A) The box plot illustrates all the T_{Leaf}, T_{Bare} and T_{Cover} data we obtained. T_{Bare} is significantly higher than both T_{Leaf} and T_{Cover} with different letters on the boxplot representing significant differences among T_{Leaf}, T_{Bare} and T_{Cover} temperatures by the LSD-t test at α=0.01 level. (B) Distribution of FCE for each elevation interval, the curve next to the data points represents the normal distribution line, the short horizontal dashed line on the curve represents the data median, and the short horizontal solid line on the curve represents the average of the data. The average FCE for each elevation interval was used for linear fitting. (C) FCE and (D) RFCE as a linear function of elevation. The data depicted in this figure underwent processing using the same approach applied to Figure 2.

moist, or wet-rain forests. The tightness of these linear correlations between T_{Cover} and T_{Leaf} consistently surpassed that of T_{Bare} and T_{Leaf} as evidenced by their R-squared values hovering beyond 0.6, whereas the latter was less than 0.6. Further, the difference between slopes for T_{Bare} and T_{Leaf} in the dry forests is substantially greater than those in the moist and wet-rain forests, substantiating the assertion that the dry forest has a stronger cooling effect than the moist and wet-rain forests. At the leaf T_{Crit} of 46.7°C, [32] cooling effects reach 17.1, 13.9, and 11.8°C for the dry, moist, and wet-rain forests according to the linear regression model, respectively. In comparison to the low range of tropical temperature of 10°C, cooling effects are 0.84, 2.6, and 9.5°C for the dry, moist, and wet-rain forests, respectively, signifying the pivotal role of the wet-rain forest in regulating ground surface temperature towards the low-temperature endpoints.

DISCUSSION

The temperature of leaves plays a crucial role in shaping the microenvironment and influencing various physiological processes.[18] Our data show that the fluctuation of T_{Cover} and T_{Leaf} is noticeably smaller than T_{Bare} (Figure 3A), confirming that the presence of vegetation plays an important role in regulating the ground surface temperature during the daytime. The investigation of these factors offers us new insights into the understanding of the roles of tropical forests in regulating ground surface temperature and managing the climate crisis in tropical regions.

Temperature along the elevation gradient and leaf supremum temperature

It is noteworthy that according to the linear fitting results (Figure 2), the slopes of the regression lines for T_{Bare} and T_{Cover} do not run parallel with elevation, suggesting an apparent vegetation influence. Our data have demonstrated significant differences in the values of T_{Bare} and T_{Cover} further indicating the role of forests in regulating ground temperature. Vegetation influence on T_{Cover} are reflected by the better logistic fitting curve than the linear model, and the curve shape is very similar to the T_{Leaf} curve, which indicates the strong correlation between T_{Leaf} and T_{Cover}. According to our regression results, the trend lines of T_{Bare} and T_{Cover} intersect at around 849.8 m of altitude, implying that vegetation has a cooling effect below 849.8m of altitude and a warming effect above 849.8m of altitude.

The atmospheric temperature is expected to decrease linearly by about 0.6°C for every 100-meter rise in elevation.[42] Causes for this decrease mainly include the reduced infrared radiation density and CO_2 concentration as elevation increases. In oceanic mountains, this decrease in atmospheric temperature is further strengthened by increased precipitation as elevation increases. This is because water and water vapor have quite higher specific heat capacities of 4.2 and 1.9 J/g·°C, respectively, than dry air (1.0 J/g·°C). Although solar radiation remains strong, warmer air near the ground constantly rises and is replaced by colder air surrounding the mountain slopes. Thus, bare ground surface temperature is strongly influenced by air temperature in oceanic mountains till the formation of predominant clouds that substantially increase the albedo effect and decrease the amount of solar radiation reaching the ground. In the Luquillo Mountains of Puerto Rico, this cloud formation occurs in the dwarf (i.e. cloud) forest around 900 m.a.s.l.[43] where T_{Bare} becomes lower than T_{Cover} or T_{Leaf}. Thereafter, atmospheric temperature shall be cooled by T_{Bare} and warmed by the presence of vegetation above this elevation.

Our data support the negative linear function between T_{Bare} and elevation, but with a slope of -0.04, i.e., 4°C decrease in bare ground temperature for every 100-meter rise in elevation which is much steeper than the expected slope of -0.006 between atmospheric temperature and elevation, suggesting a substantial effect of precipitation and clouds on T_{Bare} on montane slopes. In contrast, although T_{Cover} decreases with elevation, their logistic fitting is the best in the multiple models we use. This corresponds to the logistic fitting between T_{Leaf} and elevation, suggesting a strong influence of vegetation on T_{Cover}.

The negative correlation between T_{Leaf} and elevation has been observed in previous studies that focused on variations in the heat tolerance of species at different altitudes.[33,35] In this study, we further explored this relationship by fitting it with a logistic equation. The nonlinear relationship suggests that leaves can regulate their temperature and have a supremum temperature.[44]

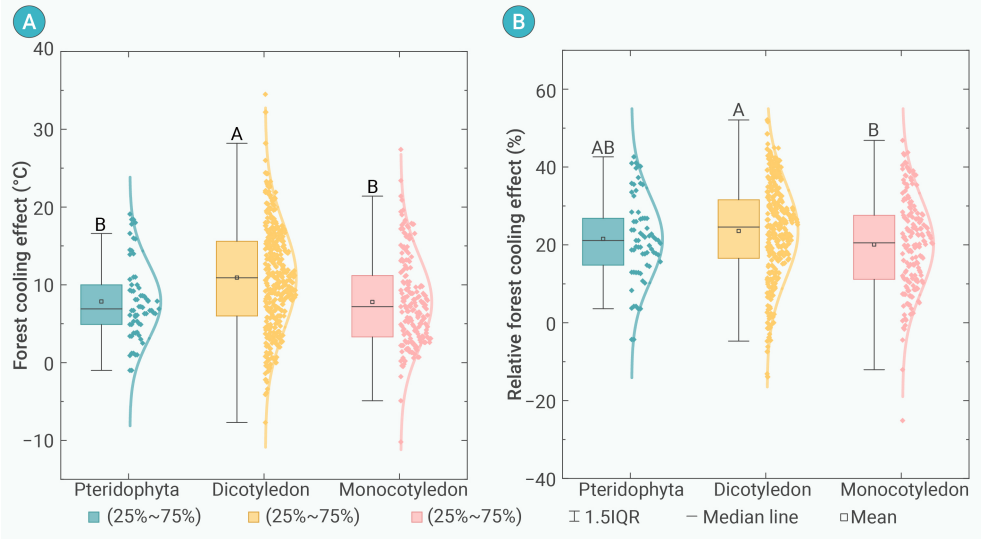

Figure 4. The differences in cooling effects among taxonomic groups (A) FCE and (B) RFCE among taxonomic groups. Different letters on the boxplot represent significant differences among Pteridophyta, Dicotyledon, and Monocotyledon by the LSD-t test at α=0.01 level.

In line with hypothesis (1), leaf temperature reaches a supremum value of approximately 44.2°C at sea level. This temperature is within the range of the leaf critical temperature (T_{Crit}) at which the photosynthetic system begins to deteriorate for 13 mangrove species (T_{Crit} = 40.7°C)[45] and 147 tropical tree species (average T_{Crit} = 46.7°C).[33] The fitted curve flattens out at 0 m.a.s.l., possibly due to the dying of leaves at temperatures exceeding 44.2°C, indicating the average thermal tolerance of the measured plants. Our finding suggests that plants in low-altitude regions of Puerto Rico might be approaching the heat threshold point, consistent with previous findings that tropical plants survive if leaf temperature exceeds the T_{Crit} threshold for less than 1.3% of the photosynthetic active time.[32]

It is worth mentioning that T_{Bare} reaches 57.4°C at an altitude of 0 m.a.s.l. according to the fitted equation, significantly surpassing the supremum leaf temperature. In contrast, T_{Cover} at sea level is 45.2°C, comparatively closer to the extreme of T_{Leaf}. Moreover, the trend of T_{Cover} closely aligns with that of T_{Leaf} rather than T_{Bare}. These results indicate that leaves not only possess the ability to self-regulate temperature but also exhibit significant regulation on T_{Cover}. Therefore, tropical forests influence the longwave radiation at the ground surface, which in turn affects the radiation absorption by greenhouse gases. The potential mechanism underlying this phenomenon is the descent of cooler air formed around the leaves, which exerts a direct influence on T_{Cover}, in addition to the leaves' ability to directly block solar radiation, a further enhancement of the cooling impact.

Forest cooling effect along the elevation gradient

Similar to temperature changes, the forest cooling effect and the relative cooling effect decreased as elevation increased. Surprisingly, there was an apparent divergence in cooling and warming effects along the elevation gradient, with the cooling effect prevailing. Compared with the cooling effect, the warming effect appeared to be weakened in magnitude and frequency. One possible cause for the warming effect was that those measurements were taken immediately after rain showers that cooled the bare ground more than the forest canopy.

The intersection of the T_{Bare} and T_{Cover} curves occurred approximately at 850 m.a.s.l., above which dwarf/cloud forest dominates,[43] indicating a possible effect of the frequent rain showers with often saturated soil water content above this altitude. Plant metabolic activities release heat and warm the forest canopy in forests with a high level of cloud albedo effect and high moisture content. This warming effect coincides with the observation that forests at latitudes greater than 50°N, where the snow albedo effect prevails, have a warming effect.[27]

Furthermore, variation in forest community structure may be another cause for the observed elevation gradient in the cooling effect. Notably, many other microclimate variables, such as wind speed, humidity, and canopy height, could influence ground surface temperature dynamics.[46] Forests at lower altitudes often exhibit complex communities with high levels of diversity, aboveground biomass, stand density, canopy complexity, canopy cover, canopy height, and soil depth, all of which can strengthen the cooling effects of plants.[47] Taking precipitation as an example, assuming the annual precipitation at the selected altitudes is similar, the amount of precipitation stored by the soil can vary greatly due to variations in processes such as leaf interception, transpiration, surface runoff, and soil water infiltration. Soils with different moisture content have different temperature sensitivity,[48] directly affecting the bare ground temperature and thus influencing the cooling effects exhibited by plants. Soils from the high-elevation dwarf/cloud forest contain high water content and are often saturated, while soils from the low-elevation sites are typically well drained, containing low levels of soil moisture,[49] suggesting a reduced cooling effect as elevation increases. Our field work prioritized replicability across diverse tropical sites, necessitating a simplified yet robust metric (FCE/RFCE) to capture baseline vegetation-driven cooling.

Our result aligns with previous studies that proved the cooling effects of vegetation, including forests, grasslands, and silvopasture lands, on ground surface temperature in tropical regions.[28,50,51] Zeppetello et al. [28] highlight the cooling benefits of agroforestry, particularly silvopasture, in Latin America and Africa. It suggests that increasing woody carbon per hectare can enhance cooling effects, and expanding silvopasture systems could help counteract local temperature increases due to climate change. Prevedello et al.[50] show that changes in forest cover impact local climate through albedo and evapotranspiration. In tropical areas, deforestation generally shows the warming effect, while reforestation shows the cooling effect, which is mediated by albedo, evapotranspiration, soil moisture content changes and historical land use and land cover change (LULCC).[52] Notably, reforestation in high-latitude regions has a warming effect due to the decrease of albedo in winter.[53,54] But none of these studies took altitude gradient into account. Our study focuses on the cooling effect of leaves along an altitude gradient.

Plant species composition affects the forest cooling effect

To test hypothesis (2), we categorized the collected tree species into ferns, monocots, and dicots. Further, we analyzed all the plants in all sites measured in Puerto Rico and made the charts on FCE and RFCE of different taxonomies. We found that dicots exhibited more pronounced cooling effects on the ground surface temperature than monocots and ferns.

Plants vary in vascular tissues among different taxonomic groups. As the primary water transport tissue, the tracheid-based xylem has been evolving throughout plant evolutionary history. Compared to ferns and monocots, dicots possess well-developed secondary xylem.[55] Vascular tissues play a vital role in the transpiration process of leaves.[56] Dicots with well-developed vascular tissues demonstrate higher transpiration efficiency, thereby resulting in superior cooling effects. However, other studies suggest that it is the diversity and richness of plant species, rather than a specific taxonomic group of tree species, that enhances the cooling effect of greening.[57] Our research cannot completely rule out the influence of surrounding vegetation on the temperature of the shaded areas of a particular tree species.

Variation among forest types across the wet-dry gradient

The two-sample t-tests on T_{Bare} and T_{Cover} within a moisture category revealed a statistically significant higher T_{Bare} across wet-rain forest, moist forest, and dry forest gradients. This substantiated the pivotal role of plants in regulating ground surface temperature, demonstrating a noteworthy cooling effect in Puerto Rico throughout August. The slope of the linear regression between T_{Cover} and T_{Leaf} in dry forests closely approximated 1 (slightly exceed-

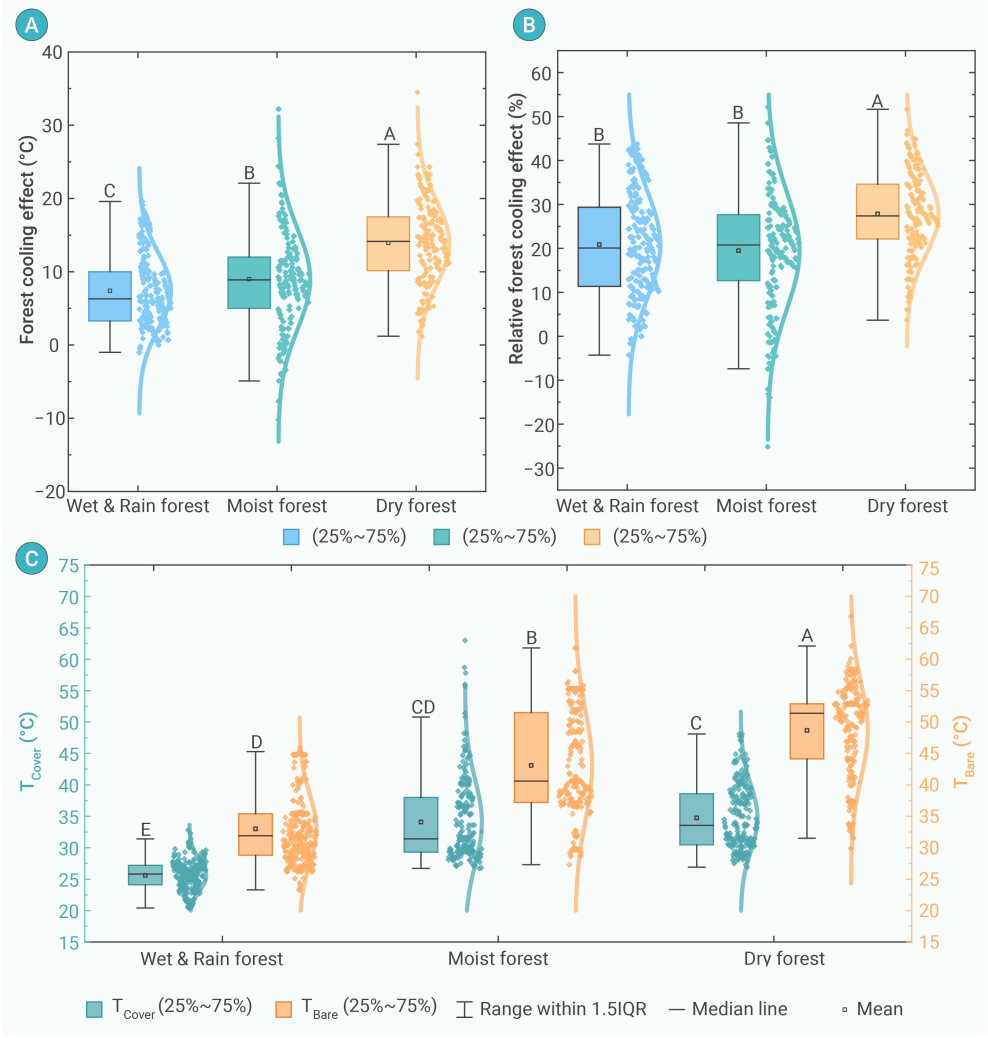

Figure 5. The differences in cooling effects among forest types (A) FCE and (B) RFCE, and (C) bare ground temperature (T_{Bare}) and covered ground temperature (T_{Cover}) across wet-rain forest types, moist forests, and dry forests in Puerto Rico. Different letters on the boxplot represent a significant difference between forest types by the LSD-t test at the α=0.01 level.

ing 1, slope=1.1), signifying a strong correspondence between T_{Leaf} and T_{Cover}. This again underscored the pivotal role of vegetation in regulating land surface temperature, especially in the dry forest. However, this pivotal role of vegetation in regulating land surface temperature does not necessarily manifest as high FCE, because in forests with different wet-dry gradients, variations in baseline T_{Bare} lead to differences in FCE levels. Thus, the strong control between T_{Cover} and T_{Leaf} is more accurately reflected through the RFCE.

When it comes to forest conservation, researchers and the public at large often focus on tropical rainforests.[58] In 1988, Janzen[59] stated that tropical dry forests are the most threatened among all major tropical forest types. By overlaying a new global distribution map of tropical dry forests with spatial data, Miles and his team[60] discovered that 97% of the existing tropical dry forests are under threat from climate change, forest fragmentation, fire, agricultural conversion, and increasing human population. For example, in Latin America and the Caribbean, less than 10% of tropical dry forests remain intact.[61] The dry Chaco woodlands in Africa are also experiencing some of the quickest deforestation rates.[62] The existing research has confirmed that the role of tropical dry forests in maintaining biological evolutionary diversity, providing protection against wind and water erosion, and offering shade for animals has been significantly underestimated.[63] In this study, we report another important function of tropical dry forests, which is their control over land surface temperature. Our data reveal that when the leaf temperature approaches T_{Crit} the temperature-regulating capacity of tropical dry forest is far stronger than that of the tropical rainforest, the latter has traditionally received more attention. However, the protective efforts for tropical dry forests still do not match their significance. For example, only 1.2% of the Caatinga dry forest region in Brazil is adequately protected, while in the Brazilian Amazon, only 9.9% receives sufficient protection.[64]

A notable difference in FCE was observed between wet-rain forests and moist forests (Figure 5). Nevertheless, RFCE remained invariant across all forest types. It could be attributed to the susceptibility of RFCE to bare ground surface composition across diverse dry-wet environments. The ratio of leaf temperature to surface temperature was influenced not solely by the forest cooling effect, but also by the specific heat capacity of the land surface. In addition, the regression coefficients between T_{Leaf} and T_{Cover} varied among wet-rain, moist, and dry forests (Figure 6). The possible reason for the regression coefficient of moist forests being less than 1 suggests that other factors are involved in the cooling process. The regression coefficient of wet-rain forests was greater than 1, reflecting the weakening cooling effect as altitude increases.

Our data show a trend that the cooling effects of plants increase as environmental moisture decreases, with plants in dry forests resulting in the widest gap and most significant difference between T_{Bare} and T_{Cover}. The presence of moist forests as a transitional state between dry and wet-rain forests substantiates the logical basis of the gradient classification for the sampling sites. These findings also imply the existence of some co-evolutionary mechanism between the plants in the dry forest and their surrounding environment to maintain ecological stability. Plant leaves in a hot dry habitat tend to have a smaller size, higher albedo, higher vein density, and higher stomatal area index, which enhances their physical cooling effect and transpiration rate. (Tables S3-S4)[18] Take a specific example, one of the plants measured and identified in Puerto Rico was *Bourreria succulenta*, whose leaves are usually hairy, but twigs are hairy at the dry site and hairless at wet site.[65] Leaf hairs of plants living in dry areas are capable of capturing moisture in the air. Some hair has micro and nanoscale protrusions, which can contribute to filtering out the ultraviolet and infrared rays from the sun.[66,67] These differences in leaf traits can be a possible explanation for the varying cooling effects of plants on the ground surface across the wet-dry gradient. Additionally, the variation in canopy structure between dry and wet forests has garnered our interest. In particular, we found that the leaf area index (LAI) of both lower and upper vegetation in the two dry forests was greater than in other forests (Table S4), contributing to a more intricate canopy structure, which, in turn, also partially explains the higher FCE in dry forests.

Furthermore, detaching leaves from the tall tree canopy may lead to a rapid increase in leaf temperature. Our evaluation showed that leaf temperature rose by 4°C within 50 seconds after detachment, which could lead to an underestimation of the cooling effect (Figure S1). However, this did not affect our overall conclusions. Besides, to obtain data on leaves bathed in light fully, we generally select plants close to the roads for measurement and do not go very deep into the forest. Due to objective factors, it is sometimes difficult to find bare soil during sampling, and the temperatures of paved roads (gravel roads) are used to replace the bare ground temperature, which is probably warmer than the actual bare ground temperature. As a result, both T_{Bare} and T_{Cover} may have been slightly overestimated. However, because these overestimations were applied consistently across the dataset, the differences

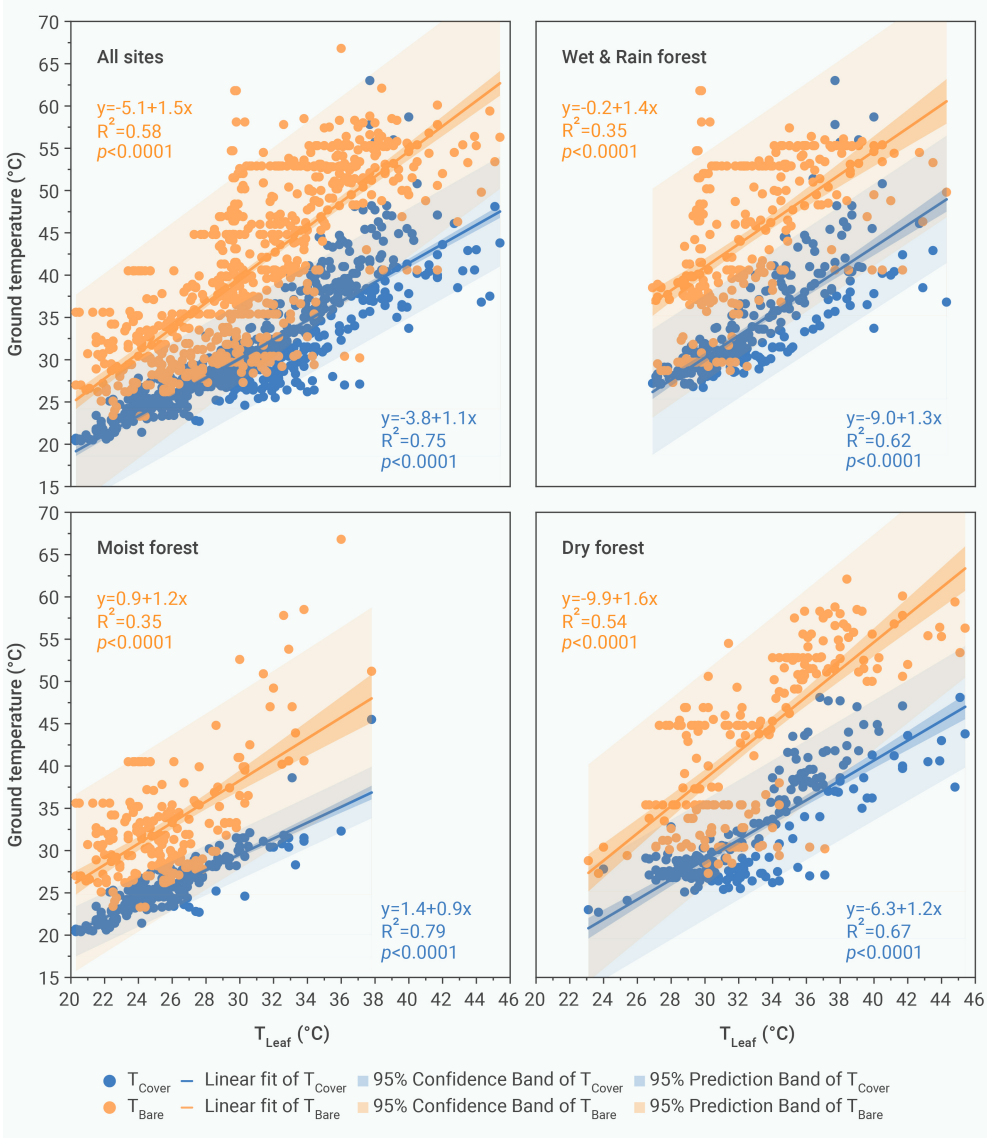

Figure 6. Linear regression analysis of T_{Leaf} and T_{Cover} or T_{Bare} across all sampling sites, wet-rain forests, moist forests, and dry forests in Puerto Rico All the fitted slopes are significantly different from zero at the α=0.0001 level.

between T_{Bare} and T_{Cover}—which determine the cooling effect—were likely unaffected, ensuring the robustness of our conclusions.

Prospects

Tropical forests, which possess the highest amount of aboveground biomass and play a crucial role in carbon sequestration and carbon removal,[68-70] are currently facing substantial deforestation pressures. With rates of deforestation accelerating,[71] 17% of the Amazon had already been deforested by 2021, and the percentage is estimated to rise to 40% by 2050 if this trend continues.[72,73] Deforestation not only leads to extreme local warming[71] but also impacts regional temperatures,[74,75] exerting adverse effects on global climate, agricultural production, public health, and other aspects beyond tropical regions.[71,75] Historically, temperature effects induced by deforestation have been conflated with those caused by CO_2 emissions due to the concurrent onset of both deforestation and substantial CO_2 emissions since the Industrial Revolution. This led to the previous oversight of deforestation. Currently, the respective contributions of the biophysical effect on ground surface temperature and the greenhouse effect of CO_2 emissions of deforestation on atmospheric temperature remain largely unexplored. Subsequent investigations could seek to calculate the respective contributions of biophysical and greenhouse effects to the observed global temperature rise of 1.1°C since the Industrial Revolution.

Reforestation in tropical regions has been proven to be an effective strategy to mitigate global warming.[50] Against the backdrop of global warming, our research demonstrates the midday cooling effect of vegetation on the Earth's surface, which has significant implications for the formulation of future land-use policies. Due to limited land availability, merely expanding green areas is insufficient when planning reforestation projects. This study provides a new insight that land managers can choose to plant proper tree species in tropical environments to achieve superior cooling effects within the same area of land. This could be another potentially more effective and feasible method for mitigating global warming, aside from reducing CO_2 emissions. The greenhouse effect, primarily caused by human-induced carbon dioxide emissions, has conventionally been recognized as the most dominant contributor to global warming. Nonetheless, it is imperative to underscore the direct influence of ground surface radiation on atmospheric temperature. Our results elucidate the capacity of leaves to modulate ground temperature, which implies that ground surface temperature change following deforestation may be underappreciated as an equally important driver of global warming aside from CO_2 emission. In addition to diminishing the cooling effect of leaves, deforestation also influences climate by disrupting the water cycle and water distribution. The loss of forests reduces atmospheric water vapor, and the confirmed reduction in atmospheric water vapor, namely cloud cover, has been identified as the primary cause for the daily maximum temperature's average warming rate being greater than that of the minimum temperature.[76] Furthermore, deforestation diminishes soil water retention capacity, weakening soil's ability to regulate its own temperature. We note that our study supplements the research by Weber et al.,[77] addressing plant cooling mechanisms, which may have significant effects on climate in certain regions. Consequently, under similar solar radiation conditions, deforested areas experience an accelerated warming process, which coincides with the findings of Zhao et al. regarding post-fire forests.[78]

While our results demonstrate significant daytime vegetation-mediated cooling effects, we acknowledge that diurnal 24-hour measurements from all seasons and additional microclimatic variables—such as wind speed, humidity, and canopy structural heterogeneity—likely influence these observed outcomes. Future research should incorporate measurements of these variables to provide a more nuanced understanding. Furthermore, our current findings predominantly reflect vegetation's influence on land surface temperature during daytime conditions, given the timing limitations of our data collection. To gain a comprehensive perspective, future studies should include observations across a broader range of time points, notably nighttime measurements and seasonal variations. Additionally, field observation data could further elucidate how vegetation affects surface temperatures throughout the day and across the year, clarify the underlying biophysical mechanisms, and explore how these surface temperature changes subsequently influence air temperature.

CONCLUSION

We validate the fundamental premise that tropical forests have a substantial midday cooling effect on ground surface temperature. The supremum temperature of the forest canopy is obtained through logistic regression. We

also show that the cooling effect is influenced by factors such as plant species composition, altitude, and environmental moisture. Lowland tropical dry forests have the greatest cooling effect at high ground surface temperature, and tropical wet and rainforests have the greatest cooling effect at the low end of ground surface temperature. These findings highlight the regulatory effect of vegetation on ground temperature and provide potential applications for mitigating global warming.

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AUTHOR CONTRIBUTIONS

Conceptualization, X.Z., X. Tian, J.L., S.G., X.T. and K.X.; Methodology, X.Z., X. Tian, J.L., X.T., K.X., W.C., Y.L. and Y.W.; Software, M.C. and J.L.; Validation, M.C., X.T., B.K., K.X., J.L. and S.Y.; Formal Analysis, J.L., M.C., X.T. and K.X.; Investigation, J.L., S.G., M.C., X.T., Z.J., B.K., W.C., Y.L., Y.W., J. Xia and J.Z.; Data Curation, J.L., M.C., X.T., K.X. and S.Y.; Writing, J.L., S.G., M.C., X.T., Z.J. and K.X.; Visualization, J.L., S.G., M.C., X.T., Z.J. and K.X.; Supervision, X.Z. and X. Tian; Project Administration, X. Tian, X.Z. and J.L. All authors contributed to and approved the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

The August leaf and ground temperature dataset of Puerto Rico and data processing code are available at Science Data Bank (DOI: 10.57760/sciencedb.25293).

SUPPLEMENTAL INFORMATION

It can be found online at https://doi.org/10.59717/j.xinn-geo.2025.100159

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