Variation in stem bark conductance to water vapor in Neotropical plant species

Eleinis Ávila-Lovera*† and Klaus Winter

Smithsonian Tropical Research Institute, Balboa, Ancón, Panama

Bark conductance to water vapor (g_{bark}) is an important determinant of drought tolerance in tropical plants. Examining species differences in bark conductance can provide useful information about the resilience of tropical trees to ongoing climate change. Values of g_{bark} are positively related to stem photosynthetic rate in desert species, showing that increased stem photosynthesis capacity is associated with increased bark conductance to water vapor. We determined whether stem morphometric traits, bioclimatic variables (e.g., temperature and precipitation), and shared evolutionary history help explain variation in g_{bark} among tropical plant species. We surveyed 94 species (90 trees and 4 liana species) from lowland and mid-elevation forests in Panama and estimated g_{bark}, stem diameter, specific stem area, bark thickness, sapwood area, and bark and wood density. Climate data were extracted from CHELSA 2.1 and Instituto de Meteorología e Hidrología de Panamá. Phylogenetic signal was estimated using Blomberg's K statistic and Pagel's λ. Bark conductance decreased with an increase in bark thickness and relative bark thickness, and was positively related to mean annual precipitation and mean annual temperature. We also determined the temperature response of g_{bark} of six plant species (five trees and one liana) from a lowland forest. In all six species, g_{bark} decreased as air temperature increased from 20 to 50°C. There was a significant phylogenetic signal in g_{bark}, with closely related species resembling each other more than distantly related species. We conclude that interspecific differences in g_{bark} of Neotropical tree species depend on all three factors studied: stem morphometry, climate, and evolutionary history.

KEYWORDS

bark traits, climate change, functional traits, morphoanatomy, tropical forest, water loss

Introduction

Water is the most limiting resource to plant productivity in many terrestrial ecosystems (Schulze et al., 1987; Chaves and Pereira, 1992). With anthropogenic climate change, we expect alterations in water availability in many regions of the world (IPCC, 2023), even in currently mesic ecosystems. The way plants acquire, use, and conserve water is important for their survival, especially in seasonally dry ecosystems. For some time, leaf minimum conductance ($g_{min, leaf}$) has been considered the last barrier to water lost in plants experiencing drought. For example, it has been proposed that when all other drought survival traits are exhausted, the rate at which water is lost from the leaves operating at minimum conductance should determine when leaves and plants die (Santiago et al., 2016). However, some plants lose their leaves when faced with water deficit stress (e.g., drought-deciduous species), and many species are able to hydraulically isolate themselves from drying soil by root shrinkage (Nobel and Cui,

1992). Furthermore, the outer surface of stems can continue transpiring as it is a semi-permeable barrier to water vapor, CO_2, and O_2 movement, and the rate of water loss through this outer bark may ultimately determine mortality. The bark is typically defined as all the tissues outside of the vascular cambium of trees, shrubs, and lianas and includes secondary and primary phloem, cortex, and the periderm, which is made up of phelloderm, phellogen (cork cambium), and phellem (cork) (Angyalossy et al., 2016). The periderm and rhytidome (successive development of periderms) are also called outer bark (Angyalossy et al., 2016). Wolfe (2020) showed that bark conductance (g_{bark}) is related to drought performance in Neotropical trees, as stem water deficit and mortality during drought were positively associated with g_{bark} in tree saplings growing in a greenhouse in central Panama.

The rate at which leaves desiccate after stomatal closure ($g_{min, leaf}$) has been of interest in recent years, with a meta-analysis showing no clear link between $g_{min, leaf}$ and taxonomic associations, climate of origin, or leaf type, but rather that $g_{min, leaf}$ was linked to growth conditions (Duursma et al., 2019). Less effort has focused on the minimum conductance of stem bark. Values of g_{bark} are usually in the same order of magnitude as $g_{min, leaf}$ (Ávila-Lovera et al., 2017, 2019); hence, the contribution of g_{bark} to total plant water loss can be considerable, especially when leaves are absent. However, the lack of large data sets on g_{bark} deters us from understanding the variability in g_{bark} among plants and its contribution to whole-plant water loss. In this study, we seek to understand the drivers of g_{bark} variation in Neotropical plant species.

Traits that determine $g_{min, leaf}$ include the structure and composition of the cuticle. For example, the cutin matrix and the cuticular waxes (intra- and epicuticular) are known to influence $g_{min, leaf}$ in desert plants (Bueno et al., 2019). In stem bark, multiple cells make up the limiting barrier for water movement, the multilayered periderm with live and dead tissues. Bark conductance was recently reviewed in the context of stem photosynthesis of woody plants (Berry et al., 2021), where the authors suggested that properties that make stem periderms more permeable to CO_2 movement for photosynthesis also make periderms more permeable to water vapor movement. Indeed, two studies have linked the ability to perform stem photosynthesis with properties of the bark: either g_{bark} in desert ecosystems (Ávila-Lovera et al., 2017) or outer bark (defined as the rhytidome or the phellem by the authors) thickness in species ranging from xerophytic shrublands to tropical rainforests (Rosell et al., 2015). A recent study in a Brazilian savanna showed that morphoanatomical traits of the outer bark influence variation in g_{bark}, that high g_{bark} is associated with a fast-resource-acquisitive strategy, and that the effect of g_{bark} on whole-plant water balance depends on the hydraulic vulnerability of leaves (Loram-Lourenço et al., 2022). These studies highlight the need to include g_{bark} in future studies of plant functional strategies.

Even though interest in understanding the cost of water loss through the bark has increased in recent years, we are still far from completely understanding the drivers of g_{bark} variation among species from Neotropical forests. For example, climate of origin may influence g_{bark}, as sites with lower precipitation, higher temperature, and drier atmospheres may select for species with low g_{bark}. If communities are phylogenetically structured in these sites, the shared evolutionary history of species may also contribute to variation in g_{bark}, as some families are known to share certain traits regarding their morphology and anatomy. For example, peeling outer bark is common in families

such as Burseraceae and Myrtaceae. Furthermore, a recent review showed that plant-water relation traits that are considered to be structural were more likely to exhibit phylogenetic signal than physiological traits (Ávila-Lovera et al., 2023), suggesting that g_{bark} could exhibit phylogenetic signal. This would indicate that similar drivers of g_{bark} are acting similarly in closely related species.

In this study, we asked what are the factors that underlie the variation of g_{bark} among Neotropical woody species. We tested whether stem morphometric traits, climate of origin, and/or shared evolutionary history play a role in explaining variation in g_{bark}. We expected that increases in bark thickness or density would negatively influence g_{bark} by increasing the path resistance for water movement. We also expected that species from warmer and drier sites, more seasonal sites, or sites with low precipitation in the driest month, would have lower g_{bark}. Finally, we expected that there would be phylogenetic signals in g_{bark} and other morphometric traits if common drivers of variation in g_{bark} act similarly in closely related species. We also explored whether g_{bark} would differ in different functional groups of differing leaf habits, as g_{bark} has been previously found to be associated with different growth strategies.

Materials and methods

Study species and sites

We sampled 94 plant species from 27 families at six Neotropical sites in Central Panama. Since some species were present at more than one site, we have 131 species-at-site combinations (Supplementary Table S1). The sites included: (1) a seasonally dry secondary forest in Parque Natural Metropolitano (PNM), Panama City; (2) natural spaces in Panama City (PC); (3) a moist forest in Parque Nacional Soberanía (PNS), Gamboa; (4) a common garden in Gamboa (GCG); (5) a mid-elevation forest in Parque Nacional Altos de Campana (PNAC), Panama Oeste; and (6) a mid-elevation forest in Nueva Arenosa (NAR), Panama Oeste. More information about the study sites can be found in Table 1.

To test whether site climate influences g_{bark} variation, we downloaded climate data (mean annual temperature and monthly precipitation and temperature) from CHELSA 2.1 (Karger et al., 2017, 2021). We also used mean annual precipitation (MAP) data from the Instituto de Meteorología e Hidrología de Panamá (IMHPA), which has meteorological stations in the country (data can be accessed).[1] We were interested in testing the effect of mean annual temperature (MAT), MAP, the precipitation of the driest month, which was February at all sites, and precipitation seasonality, which we calculated from the monthly precipitation as the coefficient of variation.

Bark conductance measurements

During the dry season of 2021 from January to April, we sampled one to 10 individuals per species (mean = 3.81, median = 4, and SD = 1.55) from 94 plant species, for a total of 354 branches, to

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1   https://www.imhpa.gob.pa/es/

TABLE 1 Geographic coordinates, elevation, and climatic characteristics of the six study sites.

Site	Number of species	Latitude	Longitude	Elevation (m)	MAP (mm)	MAT (°C)
GCG	21	9.12	−79.70	42	2,146	25.9
PNS	64	9.12	−79.70	42	2,152	25.8
PNAC	16	8.68	−79.93	810	1,586	23.0
NAR	13	8.86	−79.92	126	2,360	25.4
PC	5	9.00	−79.57	23	1,916	26.1
PNM	12	8.99	−79.55	47	1,790	26.0

Gamboa Common Garden (GCG), Parque Nacional Soberanía (PNS), Parque Nacional Altos de Campana (PNAC), Nueva Arenosa (NAR), Panama City (PC), and Parque Natural Metropolitano (PNM). Mean annual precipitation (MAP) is taken from Instituto de Meteorología e Hidrología de Panamá (IMHPA), whereas mean annual temperature (MAT) is from CHELSA 2.1 (Karger et al., 2017, 2021).

measure g_{bark} following the bench dehydration and gravimetric method (Sack and Scoffoni, 2011). We collected 1 m long branches from each individual, placed them in a dark plastic bag with wet paper towels, and transported them to a laboratory in Gamboa, Panama. A 10-cm long segment was cut at 10 cm from the apex, i.e., a segment between 10 and 20 cm from the apex was excised. In most cases, these segments corresponded to stems that had both a secondary xylem and a thin periderm. In some species, for example, *Lindackeria laurina* (Achariaceae), *Hirtella racemosa* (Chrysobalanaceae), and *Aiouea montana* (Lauraceae), secondary xylem was present, but the epidermis with stomata had not yet been shed; hence, the stems were covered by an epidermis and not by a periderm. Delayed periderm formation is common in species with green photosynthetic stems (Gibson, 1983; Lindorf et al., 2006). Nonetheless, for all species studied, we use the term 'bark conductance' to describe the stem surface conductance to water vapor, as this term has been used consistently by others (Cernusak and Marshall, 2000; Wolfe, 2020; Loram-Lourenço et al., 2022). The cut ends were covered with two layers of melted candle wax and taped to a clothesline. When leaves were present, they were removed, and the wounds were covered with fast-drying glue (ethyl cyanoacrylate, Krazy Glue, Elmer's Products, Westerville, OH, USA). Three fans were directed at the segments so that the segments slightly swayed in the breeze, and a thermohygrometer (ID-16S Casio, US) was placed close to the segments within the breeze (Supplementary Figure S1). The stem segments were allowed to dehydrate for ~1 h before starting recordings to ensure complete stomatal closure in those segments with stomata (most of the stem segments had lenticels instead). Once the hour had elapsed, stems were weighed at regular intervals using a balance (0.0001 g, H110, Sartorius, Göttingen, Germany), and air temperature and relative humidity (RH) were monitored. The stem segment fresh mass loss was plotted versus time, and the slope of the curve was used to estimate the transpiration rate standardized by stem surface area. Transpiration rate and the mole fraction air vapor pressure deficit [the driving force for gas phase diffusion (Jones, 1983)], calculated from air temperature and RH, were used to estimate g_{bark}.

As in other studies using the gravimetric method to determine stem surface conductance (Wolfe, 2020; Loram-Lourenço et al., 2022; references therein), the internal air spaces of stems were assumed to be water-vapor saturated. We did not determine the water potential of stems under investigation. The reported midday minimum values of stem water potential for several species at two of our study sites

were −1.5 to −0.6 MPa (Meinzer et al., 2008). These values are expected to be closer to zero during the early morning hours when stems were sampled for the study presented here. Under our experimental conditions, the water potential of air was *ca.* –71 MPa (calculated for 28.2°C and 60% RH, see Supplementary Figure S1), vastly more negative than the likely water potential of stems. This suggests that the water potential of stems had little influence on the rate of stem water loss and that the stem-air vapor pressure difference was the principal driving force for stem water loss. However, it needs to be mentioned that the idea that internal spaces of leaves are always water-vapor saturated has recently been challenged (Buckley and Sack, 2019) and that in instances where unsaturation would occur, leaf conductance to water vapor transfer would be underestimated. Similar arguments could be made for g_{bark}. Values of g_{bark} are presented in Supplementary Table S1.

Bark conductance responses to temperature

After the field survey and given the potential role of air temperature on g_{bark}, we ran temperature response curves for six species from PNS. The species were: *Amaioua glomerulata* (Lam. Ex Poir.) Delprete & C.H.Perss. (Rubiaceae), *Coccoloba acuminata* Kunth (Polygonaceae), *Lindackeria laurina* C.Presl (Achariaceae), *Mabea occidentalis* Benth. (Euphorbiaceae), *Piper reticulatum* L. (Piperaceae), and *Serjania mexicana* (L.) Willd. (Sapindaceae). These species were selected because of their size and abundance, ensuring that we could sample multiple stems from multiple individuals across various days. The temperatures used were: 20, 30, 35, 40, 45, and 50°C. Different stem segments from three individuals were used for each temperature. The g_{bark} values at 20°C were obtained by following the protocol mentioned above in the laboratory at STRI's Tupper Center in Panama City. The range of temperatures from 30 to 50°C was achieved using drying ovens (DKN816, Yamato Scientific America, USA).

Morphometric traits

From each stem segment used for g_{bark} measurements, we determined the stem surface area and stem diameter using photographs analyzed with ImageJ (Abràmoff, 2004; Schneider et al., 2012). The following traits were measured in a subset of 61 species:

bark thickness (mm) using a digital caliper (IP67, Mitutoyo, Aurora, IL, USA), by calculating the difference between whole stem diameter and wood diameter divided by two; relative bark thickness (%) as the ratio between stem bark thickness and stem radius multiplied by 100; sapwood area (cm^2) by measuring the diameter of the wood to calculate the area of a circle and subtracting from it the pith area; bark density ($g\,cm^{-3}$) and wood density ($g\,cm^{-3}$) were estimated by calculating the volume of a cylinder using the diameter and length of a 1-cm long stem segment (wood) and the volume of a hollow cylinder (bark) and the dry mass of the wood and bark sections, respectively, after drying at 70°C for 72 h. From this 1-cm stem segment, we also estimated the ratio between stem surface area and stem bark dry mass (specific bark area, $cm^2\,g^{-1}$) and the ratio between stem surface area and stem dry mass (specific stem area, $cm^2\,g^{-1}$) (Cernusak and Marshall, 2000; Ávila-Lovera et al., 2017). We also calculated the ratio between sapwood area and stem surface area as an analog for the Huber value. The Huber value is the ratio of sapwood area to distal leaf area, i.e., the leaf area supplied by the sapwood area (Tyree and Zimmermann, 2002). For methodological reasons, bark thickness and bark density determined by us include the vascular cambium, which is difficult to separate from the phloem and the rest of the cortex in fresh samples.

Phylogenetic signal

We first built a phylogenetic tree using the 'phylo.maker' function in the 'PhyloMaker' R package (Jin and Qian, 2019). The tree had 94 species. We then estimated the phylogenetic signal of bark conductance and other morphometric traits as Blomberg's K using the 'phylosig' function of the 'phytools' package (Revell, 2012), and Pagel's λ by changing the method in the phylosig function to "lambda." We also used the phylogenetic tree to map g_{bark} onto it using the 'contMap' function of the 'phytools' package (Revell, 2012). All analyses were done in R v.4.3.0 (R Core Team, 2023).

Statistical analyses

Before performing statistical analyses, we removed outliers above 25 mmol m^{-2} s^{-1} as most $g_{min,\,leaf}$ reported in the literature range from 0 to 25 (Duursma et al., 2019). These were five values above 30 mmol m^{-2} s^{-1}, with two being between 55 and 60 mmol m^{-2} s^{-1}, and one surpassing 80 mmol m^{-2} s^{-1}. The outliers corresponded to few species-at-site means that did not affect the total number of species studied (94 species). These abnormally high values may have resulted from damage to the outer bark, incomplete sealing of leaf petiole wounds, or other causes not accounted for in this study.

Statistical analyses and plots were performed using R v.4.3.0 (R Core Team, 2023). We ran multiple linear mixed models using the function 'lmer' from the 'lmerTest' R package (Kuznetsova et al., 2017) to estimate the effect of morphometric traits or climatic variables on g_{bark}, using species as a random effect (random intercept only) and the species-at-site means. For morphometric traits, we evaluated the significance of a model with all the traits as fixed factors and models with one trait at a time. We compared significant models using the 'compare_performance' function in the 'performance' package (Lüdecke et al., 2021) to select the best model based on r^2 (conditional and marginal), intraclass correlation

coefficient (ICC), root mean squared error (RMSE), Sigma, and Akaike information criterion (AIC), corrected AIC (AICc), and Bayesian information criterion (BIC) weights. The rank argument of the 'compare_performance' function provides a ranking of models based on normalizing all the indices (i.e., rescaling them to a range from 0 to 1) and taking the mean value of all indices for each model. We used this ranking to select the best model (Lüdecke et al., 2021). We made the same type of comparison for the models with climatic variables. Furthermore, for the climate models, we used $\log(g_{bark})$ instead of g_{bark} because of heteroscedasticity in residual variance. Mixed models with one or multiple explanatory variables took the following form:

$$g_{bark} <- lmer\ (explanatory\ variable\ 1 + explanatory\ variable\ 2 + \ldots + (1|Species),\ data)$$

Linear models using temperature as a fixed factor were used to test the relationship between g_{bark} and air temperature for the temperature response curves for each species.
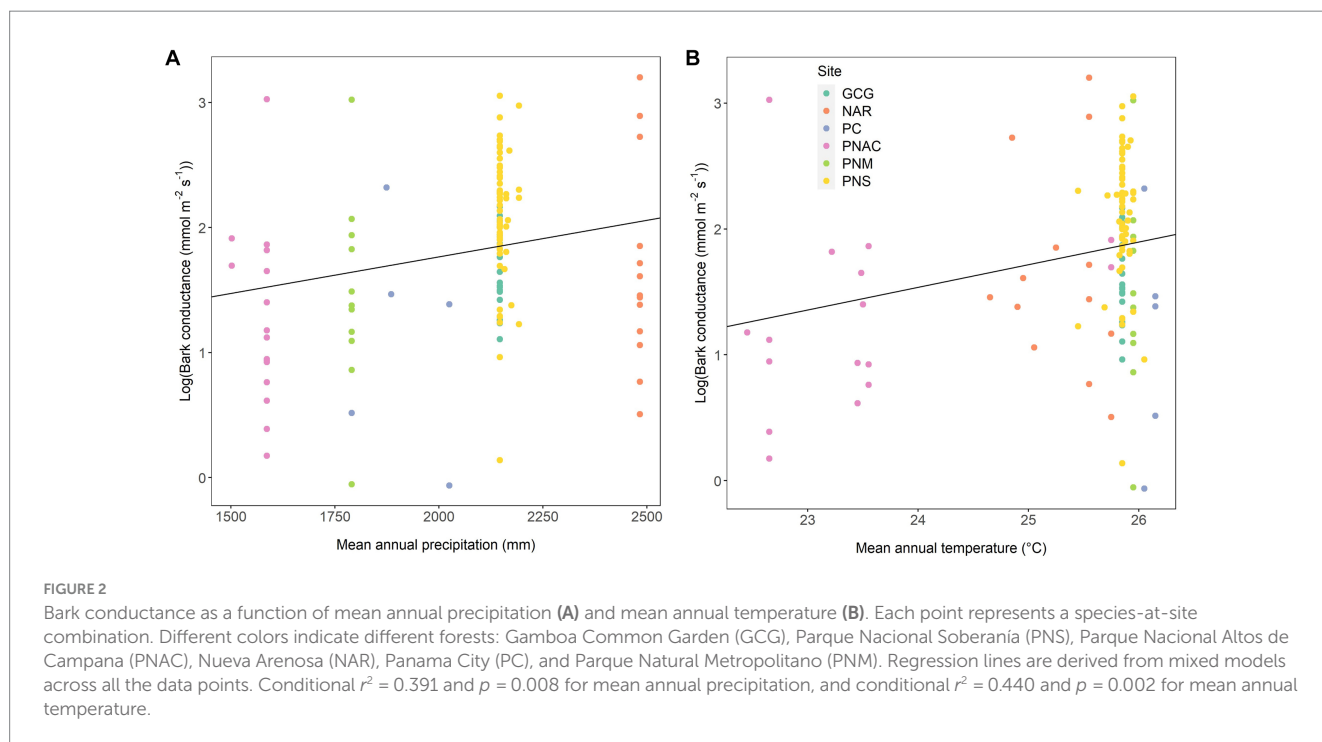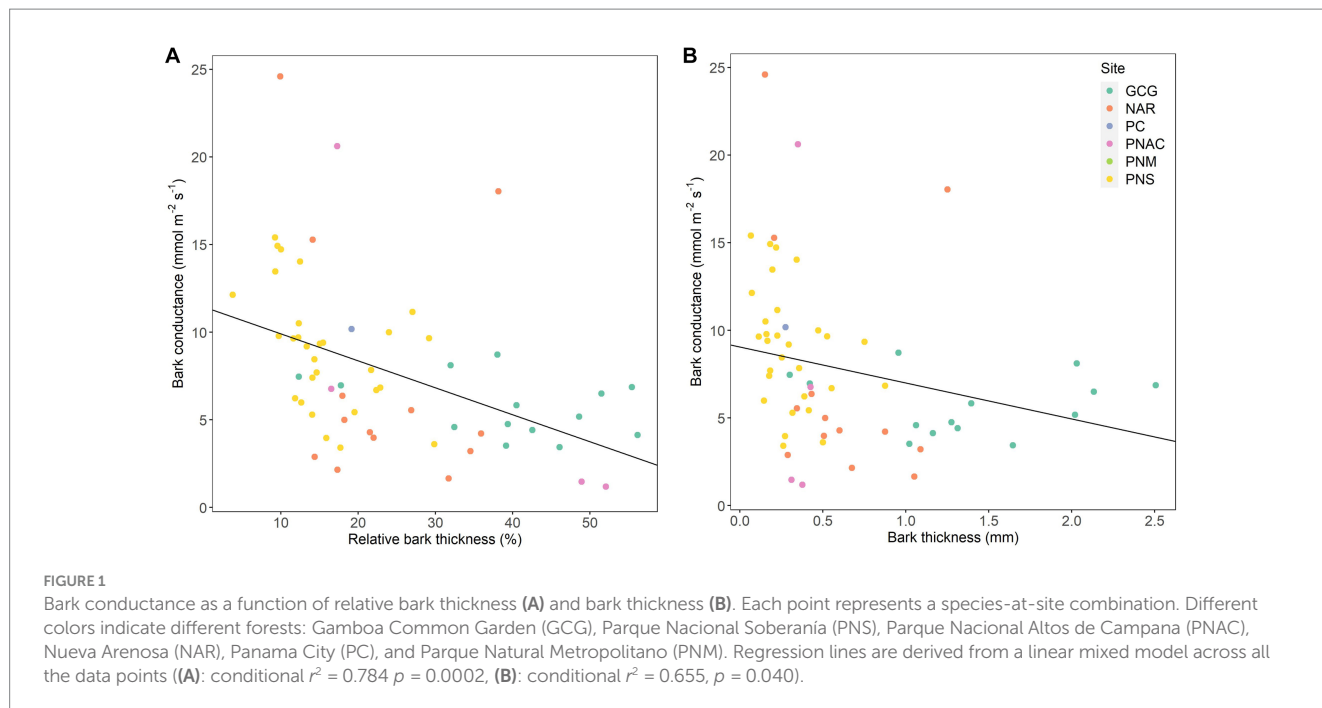
Results

Across all species-at-site combinations, g_{bark} varied from 0.94 to 24.60 mmol m^{-2} s^{-1} with a slightly skewed distribution toward low values (Supplementary Figure S2). Some families were more variable than others ($F_{26,291} = 2.33$, $p = 3.85 \times 10^{-4}$). For example, Anacardiaceae, Euphorbiaceae, Fabaceae, and Meliaceae showed the largest variation in g_{bark} (Supplementary Figure S3). We found no difference in g_{bark} between evergreen and deciduous species ($F_{1,124} = 0.917$, $p = 0.340$, Supplementary Figure S4).

From the morphometric traits measured and linear mixed models run, one was selected as the best model, a model with relative bark thickness as the fixed effect (conditional $r^2 = 0.784$, $p = 0.0002$), with the highest g_{bark} values at the lowest relative bark thickness (Figure 1A). Other models with relatively high ranking indicated that stem diameter and bark thickness were also related to g_{bark} (stem diameter: conditional $r^2 = 0.535$, $p = 0.011$; bark thickness: conditional $r^2 = 0.655$, $p = 0.040$, Figure 1B), but these two traits are highly correlated ($r = 0.623$, $p = 8.388 \times 10^{-8}$). In the following, we primarily discuss relative bark thickness.

Bark conductance was also highly influenced by site, MAP and MAT (Figure 2). Values of $\log(g_{bark})$ increased with both MAP (conditional $r^2 = 0.391$, $p = 0.008$) and MAT (conditional $r^2 = 0.440$, $p = 0.002$), but there was no relationship with the precipitation of the driest month ($p = 0.516$) or precipitation seasonality ($p = 0.977$), as these two variables were very similar across sites (Supplementary Figure S5).

In addition to morphometric traits having an impact on g_{bark}, as well as site climate, there was also a significant phylogenetic signal in g_{bark}, evidenced by both Blomberg's K of 0.19 ($p = 0.006$) and Pagel's λ of 0.25 ($p = 0.014$) (Table 2) indicating that closely related species are more similar in terms of g_{bark} than distantly related species. We also found a significant phylogenetic signal, as evidenced by both Blomberg's K and Pagel's λ indexes, in relative bark thickness and bark density (Table 2) and, as evidenced by Pagel's λ only, in bark-specific area (Table 2). The phylogenetic signal in g_{bark} can also be observed when mapping the trait onto a phylogenetic tree of the study species

FIGURE 1
Bark conductance as a function of relative bark thickness **(A)** and bark thickness **(B)**. Each point represents a species-at-site combination. Different colors indicate different forests: Gamboa Common Garden (GCG), Parque Nacional Soberanía (PNS), Parque Nacional Altos de Campana (PNAC), Nueva Arenosa (NAR), Panama City (PC), and Parque Natural Metropolitano (PNM). Regression lines are derived from a linear mixed model across all the data points (**(A)**: conditional r^2 = 0.784 p = 0.0002, **(B)**: conditional r^2 = 0.655, p = 0.040).

FIGURE 2
Bark conductance as a function of mean annual precipitation **(A)** and mean annual temperature **(B)**. Each point represents a species-at-site combination. Different colors indicate different forests: Gamboa Common Garden (GCG), Parque Nacional Soberanía (PNS), Parque Nacional Altos de Campana (PNAC), Nueva Arenosa (NAR), Panama City (PC), and Parque Natural Metropolitano (PNM). Regression lines are derived from mixed models across all the data points. Conditional r^2 = 0.391 and p = 0.008 for mean annual precipitation, and conditional r^2 = 0.440 and p = 0.002 for mean annual temperature.

(Figure 3), where species in the Bixaceae, Salicaceae, and Sapindaceae show the highest g_{bark} values and species in the Clusiaceae the lowest.

In all six species studied for temperature response, g_{bark} decreased as air temperature increased (Figure 4).

Discussion

We studied the possible factors that underlie variation in g_{bark} among Neotropical plant species from six forest sites in Panama. Bark conductance was strongly influenced by relative bark thickness.
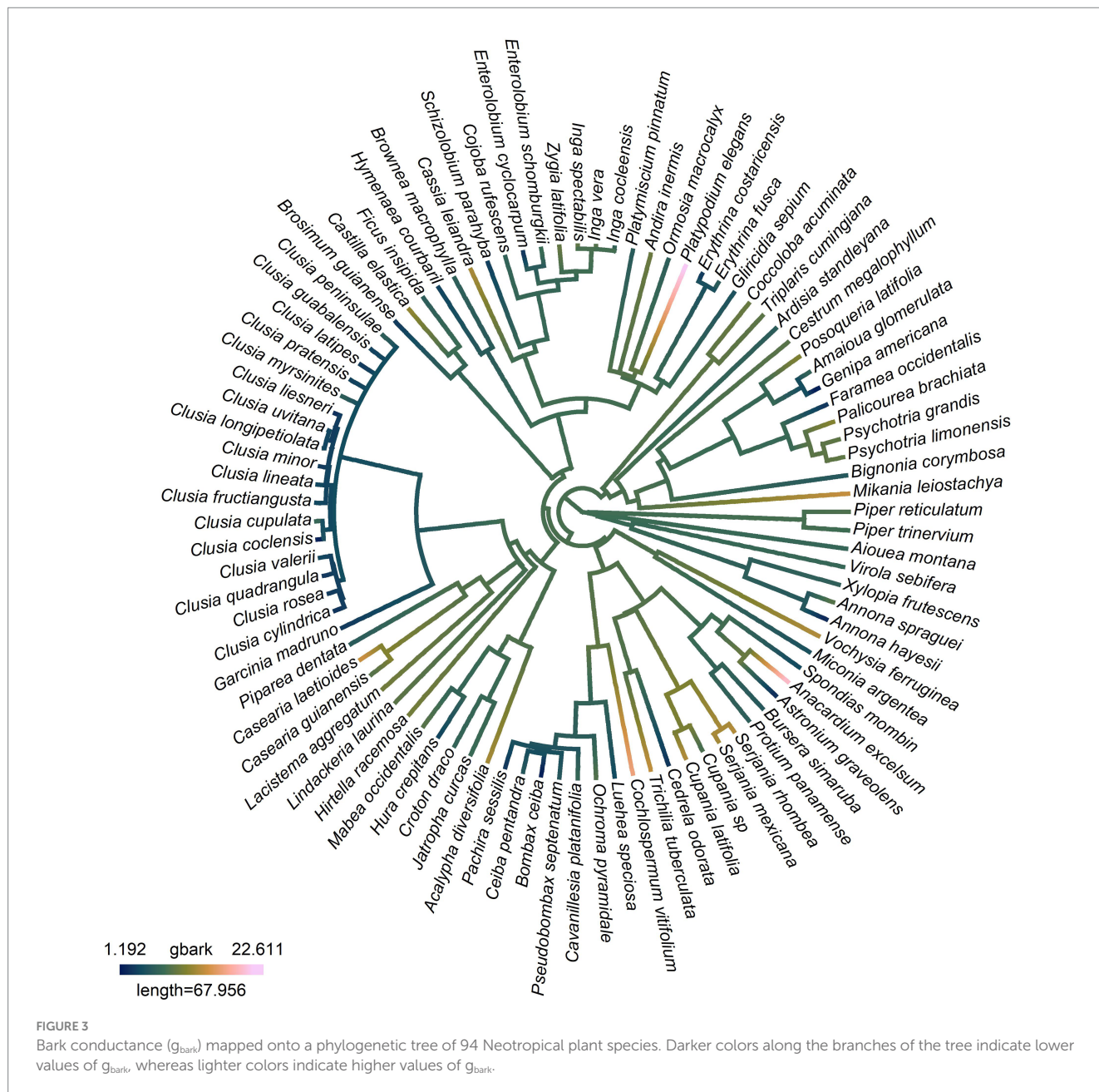
We also found that site climate, mainly MAP and MAT, influenced g_{bark}. Finally, closely related species were more similar regarding g_{bark} than distantly related species, i.e., there was phylogenetic signal in g_{bark} evidenced by both Blomberg's K and Pagel's λ.

As reported for many other species (Poorter et al., 2014; Rosell, 2016; Rosell et al., 2017), bark thickness was positively related to stem diameter. We found that relative bark thickness was a key morphometric trait related to g_{bark}. Even though we did not measure inner and outer bark thickness separately, we expect the outer bark to be more limiting to g_{bark} than the inner bark as has been reported for Cerrado plants (Loram-Lourenço et al., 2022). Rosell et al. (2017)

TABLE 2 Phylogenetic signal of bark conductance and associated morphometric traits.

Trait	Blomberg's K	p	Pagel's λ	p
Bark conductance	**0.19**	**0.006**	**0.25**	**0.014**
Relative bark thickness	**0.25**	**0.015**	**0.48**	**4.864×10^{-8}**
Stem-specific area	0.09	0.520	0.17	0.494
Bark-specific area	0.09	0.587	**0.27**	**0.043**
Wood density	0.11	0.314	7.344×10^{-5}	1
SA to stem surface area ratio	0.10	0.395	0.20	0.219
Bark density	**0.30**	**0.005**	**0.653**	**1.984×10^{-5}**

Values include Blomberg's K and Pagel's λ. Significant phylogenetic. signal values at $p \leq 0.05$ are in bold.

FIGURE 3

Bark conductance (g_{bark}) mapped onto a phylogenetic tree of 94 Neotropical plant species. Darker colors along the branches of the tree indicate lower values of g_{bark}, whereas lighter colors indicate higher values of g_{bark}.

demonstrated that the metabolically active inner bark is not related to g_{bark}. Our observations of the relationship between relative bark thickness and bark thickness and g_{bark} (Figures 1A,B), respectively, are consistent with a previous study by Wolfe (2020) on Panamanian tree species and other studies that have demonstrated that low investment in structural carbon facilitates both stem CO_2 exchange (photosynthetic and respiratory) and water loss in thin stems with thin bark in tropical and non-tropical species (Ávila-Lovera et al.,
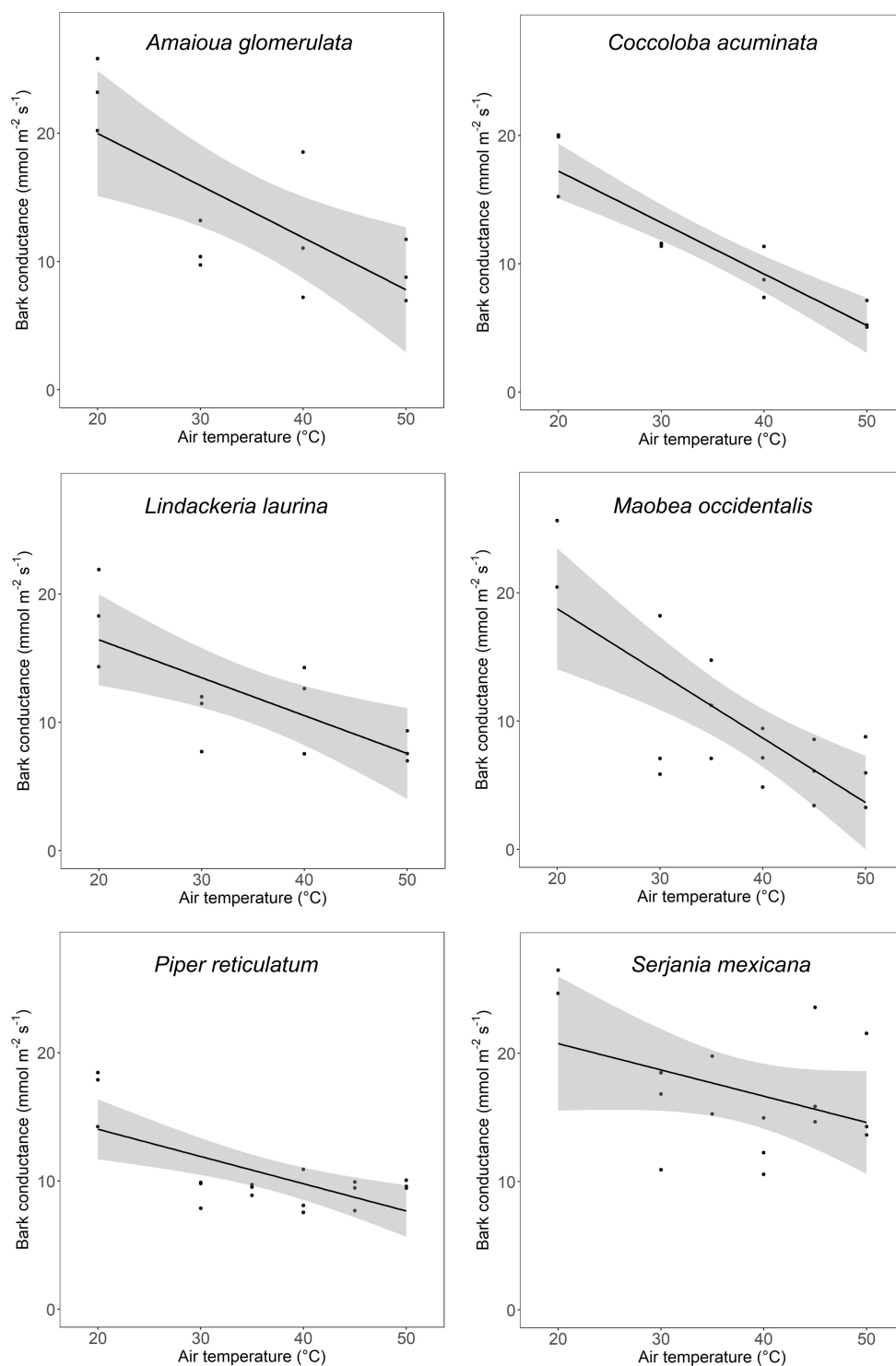
FIGURE 4
Temperature response curves of bark conductance in six plant species from Parque Nacional Soberanía. Each point is a different stem subjected to the specified temperature. Lines are from linear models fit to every species. *Amaioua glomerulata* ($r^2 = 0.547$, $p = 0.006$), *Coccoloba acuminata* ($r^2 = 0.858$, $p = 1.50 \times 10^{-5}$), *Lindackeria laurina* ($r^2 = 0.548$, $p = 0.006$), *Mabea occidentalis* ($r^2 = 0.553$, $p = 4.07 \times 10^{-4}$), *Piper reticulatum* ($r^2 = 0.465$, $p = 0.002$), and *Serjania mexicana* ($r^2 = 0.275$, $p = 0.026$).

2017; Berry et al., 2021; Loram-Lourenço et al., 2022). A small relative bark thickness shortens the path length that water must travel from the xylem to the surface of the stem during transpiration. Similarly, in a thin bark, it is expected to find fewer cell walls and cell membranes that water must pass through. These may be two reasons why we found

a negative relationship between g_{bark} and relative bark thickness. In a comparison of photosynthetic vs. non-photosynthetic stems from six different ecosystems, the relative bark thickness of branches and the outer bark thickness of the main stem were smaller in photosynthetic than in non-photosynthetic stems (Rosell et al., 2014, 2015), further

supporting the fact that thin bark, especially a thin outer bark, increases photosynthetic capacity and facilitates water movement. Overall, it seems that both CO_2 and water vapor movement are not only linked in organs with stomata but also in organs without stomata, such as stems with periderm and lenticels.

Species from wetter and warmer forests, i.e., lowland forests, in Panama had greater g_{bark} values than species from drier and slightly cooler forests supporting the idea of plant trait variation along climatic gradients (Wright et al., 2004; Moles et al., 2009, 2014; Blonder et al., 2017), which may be an indication of the adaptive significance of the trait. While it is unclear what the advantage would be of having a relatively high g_{bark} in a wet and warm tropical forest, the adaptive value of having a low g_{bark} in a dry tropical forest seems obvious. The situation changes completely when the precipitation gradient includes woody shrubs of Mediterranean-type drylands and deserts characterized by highly active green stems with an epidermis instead of a periderm (Gibson, 1983; Yiotis et al., 2006; Ávila et al., 2014); these stems attain high rates of net photosynthesis and transpiration (Ávila-Lovera et al., 2017).

As more phylogenetic information becomes available, the usage of phylogenetic trees to answer questions about the role of evolutionary relatedness on trait variation has become more relevant (for example, Ackerly and Reich, 1999; Maherali et al., 2004; Ávila-Lovera et al., 2023). Despite the strong effect of climate on many plant-water relations traits, phylogenetic signal is also common among these traits (Sanchez-Martinez et al., 2020; Ávila-Lovera et al., 2023), especially structural traits. The fact that we found the phylogenetic signal in g_{bark} and morphometric traits, such as relative bark thickness and bark density, indicates that bark traits are influenced by the evolutionary history of closely related species. For example, the Clusiaceae species had the lowest g_{bark} values measured. Consistent with observations of low g_{min} of leaves of *Clusia rosea*, *Clusia pratensis,* and *Garcinia intermedia*, all species of Clusiaceae from Panamanian forests (Slot et al., 2021), the stems of Clusiaceae species in our study also had relatively low values of g_{bark}. Even though the photosynthetic physiology of *Clusia* stems is quite well understood (Kocurek et al., 2015, 2020), detailed studies of the structure and chemistry of *Clusia* stems are required to fully assess the reasons for their relatively low g_{bark}, although it is clear that members of Clusiaceae we examined were those with the thickest barks (Figure 1).

Contrary to our expectations and the results of the field survey, in the laboratory, g_{bark} decreased as air temperature increased. In leaves, an increase in air temperature leads to an increase in air temperature can lead to an increase in cuticular conductance (Schuster et al., 2016; Bueno et al., 2019; but see Slot et al., 2021), due to the fact that the cutin matrix and epicuticular waxes lose their stability at high temperatures, except in the highly thermostable cuticles of some desert plants (Schuster et al., 2016; Bueno et al., 2019). In stems, the barrier that water needs to pass through is a suberized periderm. We do not know whether higher air temperatures and greater VPD caused dehydration and shrinkage of the periderm leading to lower g_{bark} values at high temperatures, although at all temperatures we observed linear decreases of stem fresh mass with time. Decreasing g_{bark} with increasing air temperature and VPD has also been found in the study of Wolfe (2020), although the temperature range was narrower in that study compared with ours. More research is needed to disentangle the effect of air temperature and VPD on g_{bark}.

Taken together, these results indicate that several factors contribute to the variation in g_{bark} in Neotropical woody species. In a warmer and partly drier world with increased frequency of extreme weather events, including heat waves, g_{bark} may determine the ability of plants to survive drought periods, as water loss through the stem bark is the remaining path for whole-plant dehydration after stomatal closure and loss of leaves and fine roots.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

EÁ-L: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – original draft. KW: Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2023.1278803/full#supplementary-material

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