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Global dominance of lianas over trees is driven by forest disturbance, climate and topography

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Abstract

Growing evidence suggests that liana competition with trees is threatening the global carbon sink by slowing the recovery of forests following disturbance. A recent theory based on local and regional evidence further proposes that the competitive success of lianas over trees is driven by interactions between forest disturbance and climate. We present the first global assessment of liana–tree relative performance in response to forest disturbance and climate drivers. Using an unprecedented dataset, we analysed 651 vegetation samples representing 26,538 lianas and 82,802 trees from 556 unique locations worldwide, derived from 83 publications. Results show that lianas perform better relative to trees (increasing liana-to-tree ratio) when forests are disturbed, under warmer temperatures and lower precipitation and towards the tropical lowlands. We also found that lianas can be a critical factor hindering forest recovery in disturbed forests experiencing liana-favourable climates, as chronosequence data show that high competitive success of lianas over trees can persist for decades following disturbances, especially when the annual mean temperature exceeds 27.8°C, precipitation is less than 1614 mm and climatic water deficit is more than 829 mm. These findings reveal that degraded tropical forests with environmental conditions favouring lianas are disproportionately more vulnerable to liana dominance and thus can potentially stall succession, with important implications for the global carbon sink, and hence should be the highest priority to consider for restoration management.

KEYWORDS

carbon, climbers, competition, ecosystem function, forest succession, liana–tree interaction, plant–climate interaction, plant–plant interaction, restoration, vines

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1 | INTRODUCTION

Trees are undoubtedly central to forest structure and function, yet other plant guilds like lianas also influence the dynamics and resilience of forests (Schnitzer, 2018; Schnitzer & Bongers, 2002). Lianas are woody vines that depend on standing trees for mechanical support to access the forest canopy (Rowe, 2018). Along with trees and other vascular plant guilds, lianas are integral to many forest ecosystems, notably via their contributions to and impacts on primary productivity, canopy turnover and carbon sequestration (Durán et al., 2015; Phillips et al., 2005) as well as on forest recovery following disturbance (Campbell et al., 2015; Marshall et al., 2020).

In past decades, there has been a marked shift towards the relative success (dominance) of lianas over trees in forests across the globe (Jones et al., 2017; Londré & Schnitzer, 2006; Phillips et al., 2002; Wright et al., 2004). This increasing liana dominance impacts not only forest processes (Laurance et al., 2014; Schnitzer et al., 2015) but also their function (Campbell et al., 2018; van der Heijden et al., 2015) and trajectories of recovery (Ladwig & Meiners, 2010). This has drawn growing interest and speculation about the future and fate of global forests (Schnitzer & Bongers, 2011; Verbeeck & Kearsley, 2016), where changes in atmospheric carbon dioxide (Granados & Körner, 2002; Phillips et al., 2002; but see Marvin et al., 2015), climate regimes (DeWalt et al., 2015; Gentry, 1991; van der Heijden & Phillips, 2008) and increasingly persistent disturbances (Laurance et al., 2001; Letcher, 2015; Putz, 1984; Schnitzer et al., 2021) could favour lianas over trees.

Lianas influence forest ecosystem processes through complex mechanisms of intense competition with trees for above and belowground resources (Schnitzer et al., 2005; Toledo-Aceves, 2015), benefitting from faster resource acquisition strategies compared to trees (Jones et al., 2017; Putz, 2023). As a result, lianas typically play a much more significant functional role than their relatively smaller contribution to biomass in most forests. Lianas are known to reduce tree recruitment and survival (Marshall et al., 2017; Schnitzer et al., 2000, 2014), create structural stresses on host trees and suppress their growth (van der Heijden et al., 2013, 2015; van der Heijden & Phillips, 2009), increase tree mortality (Ingwell et al., 2010; Phillips et al., 2005) and slow forest regeneration (Lai et al., 2017; Estrada-Villegas et al., 2020, 2022; Schnitzer & Carson 2010). Lianas also increase the susceptibility of trees to being killed by lightning, an important agent of forest disturbance, by facilitating damage to additional trees (Gora et al., 2023). In addition, forests with abundant lianas have far lower stand biomass and carbon than forests with few lianas (see Chave et al., 2001; Durán & Gianoli, 2013).

However, lianas are not only detrimental. They maintain and enhance forest biodiversity (Gentry, 1991; Schnitzer & Bongers, 2002; Schnitzer & Carson, 2001) and boost soil fertility and carbon cycling through their leaf-litter productivity and turnover, which are consistently higher than those of trees per unit

biomass (Estrada-Villegas & Schnitzer, 2018; Schnitzer, 2018; Tang et al., 2012). Additionally, lianas can benefit other plants, animals, soils and overall ecosystem function in both intact and disturbed forests by providing them with a wide range of protective services or 'bandage effects' (Marshall et al., 2020). This is particularly important for forest management, where increasing consideration of liana cutting may help tree growth but harm other vital ecosystem functions (Finlayson et al., 2022). Therefore, investigating how disturbances and competition from lianas affect trees is deemed essential for successfully restoring the world's forests (Marshall et al., 2023).

Climatic factors, alongside forest disturbances, are hypothesised as the primary drivers of the global distribution of lianas and their increasing dominance over trees (DeWalt et al., 2015; Marshall et al., 2020; Ofosu-Bamfo et al., 2022; Schnitzer & Bongers, 2011). For instance, Schnitzer et al. (2005) and Schnitzer and Bongers (2011) suggested that disturbances leading to increased light, higher temperatures and water deficits are conducive to liana proliferation, which could foster liana dominance over trees (Marshall et al., 2020). Lianas tend to thrive in forests with reduced precipitation and climatic water availability (DeWalt et al., 2015; Gentry, 1991; Schnitzer, 2018). Their dominance over trees is further enhanced by the greater light penetration in the understorey of disturbed forests and increased insolation during longer and more severe dry seasons (DeWalt et al., 2010, 2015). Hence, adverse shifts in climate, such as prolonged droughts, could potentially tip the ecological balance in favour of lianas (Schnitzer & van der Heijden, 2019; van der Heijden et al., 2019), fundamentally alter forest dynamics (Phillips et al., 2005) and potentially lead to arrested natural succession or alternate stable states in forest ecosystems (Marshall et al., 2020). This understanding underscores the importance of considering the influences of climatic factors and disturbances when examining the competitive success of lianas over trees.

However, a critical gap persists in the assessment of liana dominance over trees at the global scale. While numerous local and regional studies have contributed valuable insights into liana ecology (Lobos-Catalán & Jiménez-Castillo, 2019; Phillips et al., 2005; Schnitzer, 2005; Schnitzer & Bongers, 2011), there is a tendency to extrapolate these findings to global contexts, often overlooking the variability in environmental drivers across different regions. This pattern has resulted in the frequent identification and adoption of specific local or regional trends and factors as the primary influences and drivers behind the competitive advantages of lianas worldwide. To date, no study has comprehensively combined data on lianas and trees in a simultaneous quantitative analysis at the global scale to assess their proportional successes and the underlying driving factors. Addressing this gap is pivotal for a more nuanced understanding of forest dynamics and for guiding forest management strategies in the face of global environmental changes.

Our study aims to identify the global drivers of liana dominance over trees. We use a newly compiled dataset of measurements of

liana and tree relative stem densities, basal areas (BA) and aboveground biomass (AGB) from 83 published studies on all six forested continents. We test how relative measures of liana–tree attributes vary with climate, topography and both the presence of disturbance and the time since the disturbance occurred. We then further assess interactions between these variables to test a recent hypothesis that the effects of disturbance on liana–tree competition vary with climate suitability for lianas (Marshall et al., 2020).

2 | METHODS

2.1 | Literature survey and data extraction

We gathered data from literature searches in publicly accessible databases: Web of Science, Scopus, Google Scholar, ResearchGate and JSTOR. Our search strings included all records from June 1939 to December 2019, using the following keywords/expressions: liana AND tree AND (abundance OR density OR basal area OR biomass OR species OR diameter OR diversity OR productivity OR carbon OR competition OR growth OR mortality OR recruitment OR survival OR phenology OR presence OR occurrence OR succession OR recovery OR ecology OR load OR infestation OR prevalence OR turnover OR litterfall OR tolerance OR burden).

Searches for published literature were conducted mainly in English. However, data of interest were also extracted from publications that were available only in French, Spanish or Portuguese. Materials found were then imported into Mendeley <www.mendeley.com>, and duplicates were discarded. Reference lists from every study were also examined for additional suitable articles. This process yielded 1351 publications. Titles, abstracts, methods and results of each retained publication were then screened to check their relevance while looking for explicit liana and tree measurements based on metrics described in Table 1.

Studies were automatically excluded if they: (1) did not provide the specific geographic location of data collection; (2) did not report at least one measure of stem density (SD), BA, AGB or aboveground carbon (Table 1) for both lianas and trees at plot or habitat scale; (3) focussed on a single tree and/or liana species or a single taxonomic group of trees and/or lianas, instead of whole forest communities for both guilds; (4) did not provide the unit sample plot size and the total number of plots sampled per habitat; or (5) did not specify minimum diameters sampled for both lianas and trees.

Data extracted from the selected articles included measures of liana and tree community structure (Table 1) and study site names, geographical coordinates, habitat type, elapsed time since disturbances occurred (for disturbed forests), type of disturbances and sampled plot size per habitat type. Where the required data were not available directly from the selected papers or their published supplemental information, we obtained unpublished data from the authors. The exception was the Gentry dataset (Gentry, 1988), which we accessed through the Missouri Botanical Gardens (<www.mobot.org>) and updated growth form and species nomenclature information by matching voucher codes with the TROPICOS database (<www.tropicos.org>), as in van der Heijden and Phillips (2008). Data associated with Phillips et al. (2002) were also accessible via ForestPlots.net (ForestPlots.net et al., 2021).

2.2 | Data processing and standardisation

We used habitat descriptions in the articles to categorise observations into undisturbed and disturbed forests based on whether any previously reported disturbance had occurred in the area. The main forest disturbances included logging, clearing, farming, pasture, wildfire, hurricane, fragmentation, encroachment or mixed (any combination of two or more). Time since disturbance was also recorded to assess the persistence of lianas relative to trees over time. For studies that reported aboveground carbon instead of biomass, a conversion factor of 0.47 was used to convert carbon into biomass equivalents, following guidelines from the IPCC (2006).

For each forest category (disturbed or undisturbed) and sample unit, we calculated liana-to-tree ratios (hereafter LTRs) of SD (LTR_{SD}), BA (LTR_{BA}) and AGB (LTR_{AGB}), which were then used as response variables in statistical models to assess liana dominance—that is the competitive success of lianas relative to trees (see Marshall et al., 2020). For each data point that had multiple samples, we aggregated LTRs according to plot size, category of forest and diameter cut-off. In these instances, we calculated area-weighted mean observations for each metric of LTR to facilitate further analyses.

The above data selection and standardisation resulted in 651 observations from 83 case studies (details in Table S1), representing 556 unique sample points (Figure 1) in 44 countries across five continents. Each sample point had at least one metric of SD ($n = 610$), BA ($n = 462$) and/or AGB ($n = 396$) for both lianas and trees in disturbed ($n = 279$) or undisturbed ($n = 372$) forests (Table S2).

TABLE 1 Response variables extracted from publications.

Metric	Description	Unit
Stem density	Stems per unit area	Stem per ha
Basal area	Sum of cross-sectional stem surface area reported per unit area	m ² per ha
Aboveground biomass	Aboveground standing dry mass expressed as a mass per unit area	Mg per ha
Aboveground carbon	Aboveground carbon fraction of the standing dry mass expressed as a mass per unit area	Mg C per ha

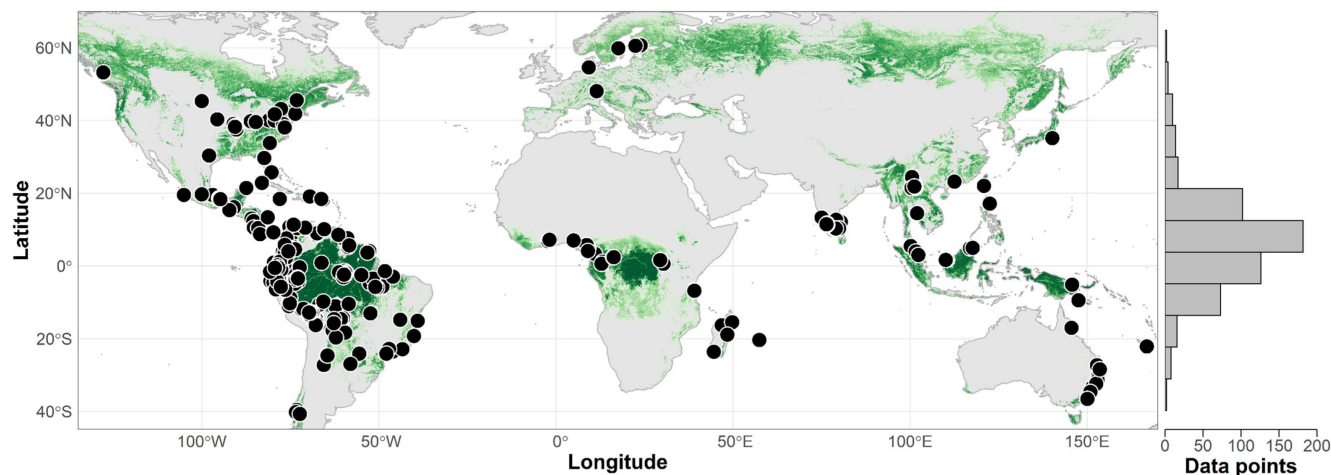


FIGURE 1 Distribution of data sources used for this study. The green gradient shades indicate areas with $\geq 30\%$ tree cover, as derived from Global Forest Change v1.9 (Hansen et al., 2013).

2.3 | Spatial data

For each unique data point (Figure 1), we extracted bioclimatic variables from WorldClim v2.1 (Fick & Hijmans, 2017) at 30-arcsec (~ 1 km) spatial resolution. Maximum climatic water deficit, that is the length and severity of seasonal drought (Pfeifer et al., 2018; also known as dry-season water stress), was calculated as the greatest cumulative deficit in mean monthly rainfall, where a deficit is less than 100 mm per month—that is wet period (Platts et al., 2010; Silva Junior et al., 2021). Likewise, topographic variables (elevation and slope) were obtained at a similar spatial resolution as climate variables after aggregating the Digital Elevation Model (SRTM v4.1) data from their original 3-arcsec (~ 90 m) spatial resolution (Jarvis et al., 2008).

2.4 | Modelling approach

To identify the major predictors of the dominance of lianas over trees (LTR) at the global scale, we separately tested for key drivers expected to alter LTR in disturbed and undisturbed forests. To avoid the confounding effects between climate and topography, we fitted two models for each response variable: one with topographic predictor variables and another comprising climatic predictor variables. Forest disturbance was included as a two-level factor ('disturbed forests' and 'undisturbed forests') in both models to assess LTRs along climate and topographic gradients as modified by disturbance.

Specifically, we assessed LTR as a function of topography (STRM elevation and slope; Jarvis et al., 2008) across forest disturbance categories to validate the long-held view that lianas are more competitive versus trees at low elevations (Schnitzer, 2005). Likewise, we also assessed LTR against disturbance categories and climate variables to investigate whether forest disturbance and climate (WorldClim bioclimatic variables and MWD; Fick & Hijmans, 2017) combine to influence the dominance of lianas over trees. We assessed the effect of

topography (elevation and slope) on LTR for completeness and consistency with previous works (DeWalt et al., 2015; Lai et al., 2017; Marshall et al., 2020; Schnitzer, 2005; Schnitzer & Bongers, 2011). This aimed to better place the relevance of our work in landscape science and practice.

In the absence of repeat measurements in the majority of studies, we used a chronosequence approach to assess the variation of LTR in disturbed forests over time. Specifically, we tested for effects of time since disturbance to evaluate the hypothesis that tree growth does not increase with time relative to lianas at locations where climate favours lianas (Marshall et al., 2020). To do this, we fitted separate models using only data from disturbed forests, incorporating the recorded time since disturbance for each observation as a numeric predictor.

2.5 | Statistical analysis

Data were analysed in R version 4.2.2 (R Core Team, 2022), using mixed-effects models. To meet assumptions of normality and prevent heteroscedasticity before modelling, LTR values were subjected to a natural logarithm transformation. To allow effect size comparisons, all numeric covariates were standardised by centring and scaling them to a mean of zero and unit standard deviation, using the built-in 'scale' R function (R Core Team, 2022).

To account for anticipated variations among different minimum sampled stem diameter thresholds (for instance, a lower cut-off might lead to higher estimates of SD, BA and AGB), we categorised liana–tree minimum diameter cut-offs into groups (Table S2), then included discrete random intercepts for these groups in all models. We also incorporated the names of study sites as an additional grouping random factor to account for potential effects arising from an unbalanced sample distribution among the study site groups.

The effect of plot size on the variation in LTR was accounted for by weighting observations by a power transformation of plot size using a

non-linear term, that is assuming that plot size increases variation in SD, BA and AGB when smaller but having reduced or no effects when plots are larger (see Cuni-Sanchez et al., 2021). Variance weighting was included in the structure of 'lme' models using the 'varPower' function in the 'nlme' R package (Pinheiro et al., 2022). Subsequently, models were refitted with the 'lmer' function in the 'lme4' package (Bates et al., 2015), incorporating these estimated weights.

Spatial autocorrelation patterns were addressed by incorporating correlation terms constructed using geographic coordinates of sample points, in line with the approach by Dormann et al. (2007) using the 'corSpatial' function in the 'nlme' R package (Pinheiro et al., 2022). To further complement and minimise the potential effects of spatial patterns, we used the best distance-based Moran's eigenvector maps (MEMs), generated for each LTR response metric, as a covariate in each model (Bivand & Wong, 2018). The MEM sets were generated using the 'dbMEM' function in the 'adespatial' R package (Dray et al., 2022). We used 'listw.candidates' and 'listw.select' functions to select the best ones among spatial weighting matrix candidates, which we built, tested and compared following the nearest-distance neighbours' method as in Bauman et al. (2018).

We used the standardised variance inflation factors (VIF) following a stepwise approach to select predictors and avoid multicollinearity (Peng & Lu, 2012). By assessing both the marginal R -squared (R_m^2) and conditional R -squared (R_c^2) based on Nakagawa et al. (2017), we identified and removed predictors with the highest $VIF > 4$ and lowest R_m^2 values. This process was repeated until all remaining predictors had a $VIF \leq 4$. This procedure was carried out using the 'car' package (Fox & Weisberg, 2019).

Bootstrapping (1000 iterations) was executed on best-fitted models to estimate parameters using the 'bootMer' function (Bates et al., 2015). We further undertook hierarchical partitioning of variance in these models (Chevan & Sutherland, 1991; Jaeger et al., 2019) to dissect the individual contributions of each predictor to variation in LTRs. This was executed using the 'glmm.hp' (Lai

et al., 2022) and 'partR2' (Stoffel et al., 2021) R packages. Since our best models did not retain any interaction terms, we used a subset of disturbed forest data to fit separate models. This allowed us to assess the interactive effects of time since disturbance and each environmental predictor on liana-to-tree ratios within disturbed forests.

We quantified the effect sizes of retained predictors on LTRs through multimodel inference and averaging (Zhang et al., 2016). To do this, we generated all potential combinations of predictors from the best-fitted models. We then restricted all model subsets to a 95% confidence set, where the Akaike Information Criterion (AIC) weights of the models sum to 0.95, thus excluding highly unlikely models. Following this, we averaged the coefficients of predictors, using the AIC weights from each generated model subset.

The multimodel inference and averaging were carried out using the 'dredge' and 'model.avg' functions from the 'MuMIn' R package (Barton, 2022). This method allows variables with limited support to shrink towards zero and accounts for the relative importance and contribution of each predictor across combinations of all model subsets. It also takes into consideration uncertainties and the variability in coefficients and effect sizes among the best-selected models (Dormann et al., 2018).

3 | RESULTS

3.1 | Forest disturbance

Forest disturbance was the most influential predictor of LTRs, demonstrating the highest individual contribution to the fixed-effect variance explained (R_m^2) in both topography and climate models (Figure 2). In topography-based models, disturbance stood out by individually explaining 23%, 19% and 1% of the variance of LTR_{AGB} ($R_m^2 = .34$; $R_c^2 = .59$), LTR_{SD} ($R_m^2 = .21$; $R_c^2 = .90$) and LTR_{BA} ($R_m^2 = .02$; $R_c^2 = .71$), respectively. In parallel, the climate-based models also

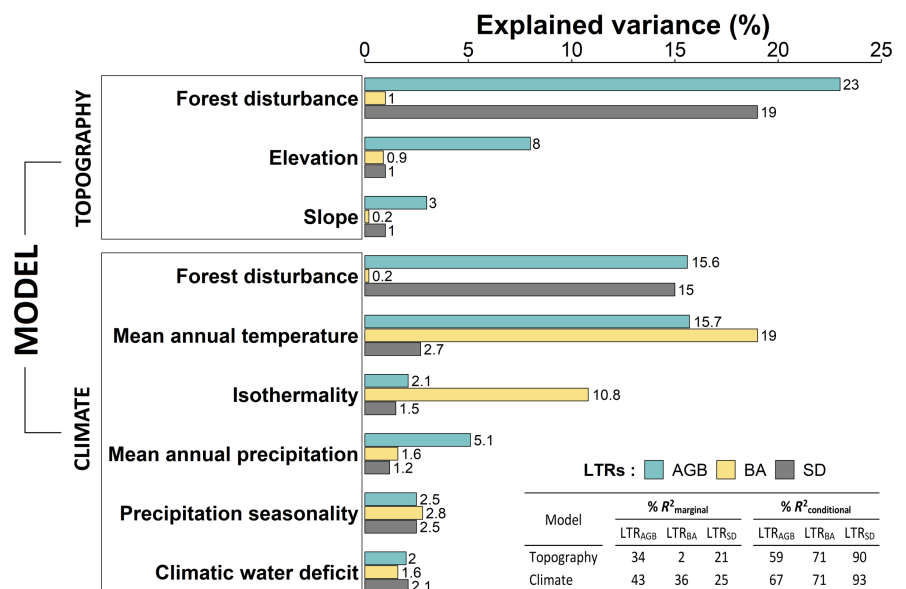


FIGURE 2 Individual contributions of each predictor to the explained variance in best-fitted mixed-effects models predicting liana-to-tree ratios (LTRs) of aboveground biomass (AGB), basal area (BA) and stem density (SD). The table insert shows the total proportions of variance explained in each model.

showed the importance of forest disturbance in predicting LTRs, with corresponding individual contributions of 15.6%, 15% and 0.2% to the variations in LTR_{AGB} ($R_m^2 = .43$; $R_c^2 = .67$), LTR_{SD} ($R_m^2 = .25$; $R_c^2 = .93$) and LTR_{BA} ($R_m^2 = .36$; $R_c^2 = .71$), respectively.

Forest disturbance had a significant positive effect on LTRs (Figures 3 and 4). The values of LTR_{SD} ($p < .001$; Figures 3a and 4a), LTR_{BA} ($p < .001$; Figures 3b and 4b) and LTR_{AGB} ($p < .001$; Figures 3c and 4c) were 114% (95% confidence interval 95%–132%), 40% (16%–63%) and 245% (210%–279%) higher in disturbed forests than in undisturbed forests, respectively.

Across all studies with disturbed forest data points, sampling occurred 0–60 years post-disturbance, and yet, in these disturbed forests, LTRs did not change significantly with the time elapsed since disturbance ($R_m^2 = .03$ –.11; $R_c^2 = .27$ –.71; $p = .249$ –.761; Figure 3d–f).

3.2 | Climate

Apart from forest disturbance, climate variables also appeared as important predictors of LTRs (Figure 2). Mean annual temperature (MAT) had the highest explanatory power of all climate predictors, individually explaining 19%, 15.7% and 2.7% of the variance of LTR_{BA} ($R_m^2 = .36$; $R_c^2 = .71$), LTR_{AGB} ($R_m^2 = .43$; $R_c^2 = .67$) and LTR_{SD} ($R_m^2 = .25$; $R_c^2 = .93$), respectively. We found overall positive effects of MAT on LTRs in all

forests (Figures 3a–c and 5d–f). LTR_{SD} increased by 1.5% (0.4–2.5%; $p = .004$; Figures 3a and 5d), LTR_{BA} by 10% (8.2%–12%; $p < .001$; Figures 3b and 5e) and LTR_{AGB} by 9.9% (7.8%–12%; $p < .001$; Figures 3c and 5f) for each 0.5°C increase in MAT. The positive effects of MAT on LTR_{SD} persisted in disturbed forests ($R_m^2 = .08$; $R_c^2 = .48$; $p < .001$; Figure 3d). However, in undisturbed forests, LTR_{SD} did not show a significant trend with MAT ($R_m^2 = .05$; $R_c^2 = .97$; $p = .89$; Figure 5d).

The diurnal temperature variability relative to the annual temperature range (i.e. isothermality) was another important climatic predictor of LTRs (Figure 2). It respectively explained 10.8%, 2.1% and 1.5% of the variations in LTR_{BA} ($R_m^2 = .36$; $R_c^2 = .71$), LTR_{AGB} ($R_m^2 = .43$; $R_c^2 = .67$) and LTR_{SD} ($R_m^2 = .25$; $R_c^2 = .93$). Isothermality also showed positive effects on LTRs (Figures 3 and 5). We found that lianas relatively had greater SD and BA than trees in highly isothermal regions (Figure 3a,b), increasing respectively by 10% (4.7%–15.3%; $p < .001$; Figure 5g) and 35.3% (25.3%–46.7%; $p < .001$; Figure 5h) for an increase in isothermality of 10. The relationship was less clear for LTR_{AGB} , which showed no significant association with isothermality ($p = .734$; Figure 3c). Isothermality was not retained in the best models fitted using disturbed forest data subsets.

Mean annual precipitation (MAP) explained 5.1%, 1.6% and 1.2% of the variances in LTR_{AGB} (2.5%, $R_m^2 = .43$; $R_c^2 = .67$; Figure 2), LTR_{BA} ($R_m^2 = .36$; $R_c^2 = .71$; Figure 2) and LTR_{SD} ($R_m^2 = .25$; $R_c^2 = .93$; Figure 2), respectively. Lianas showed significantly greater BA

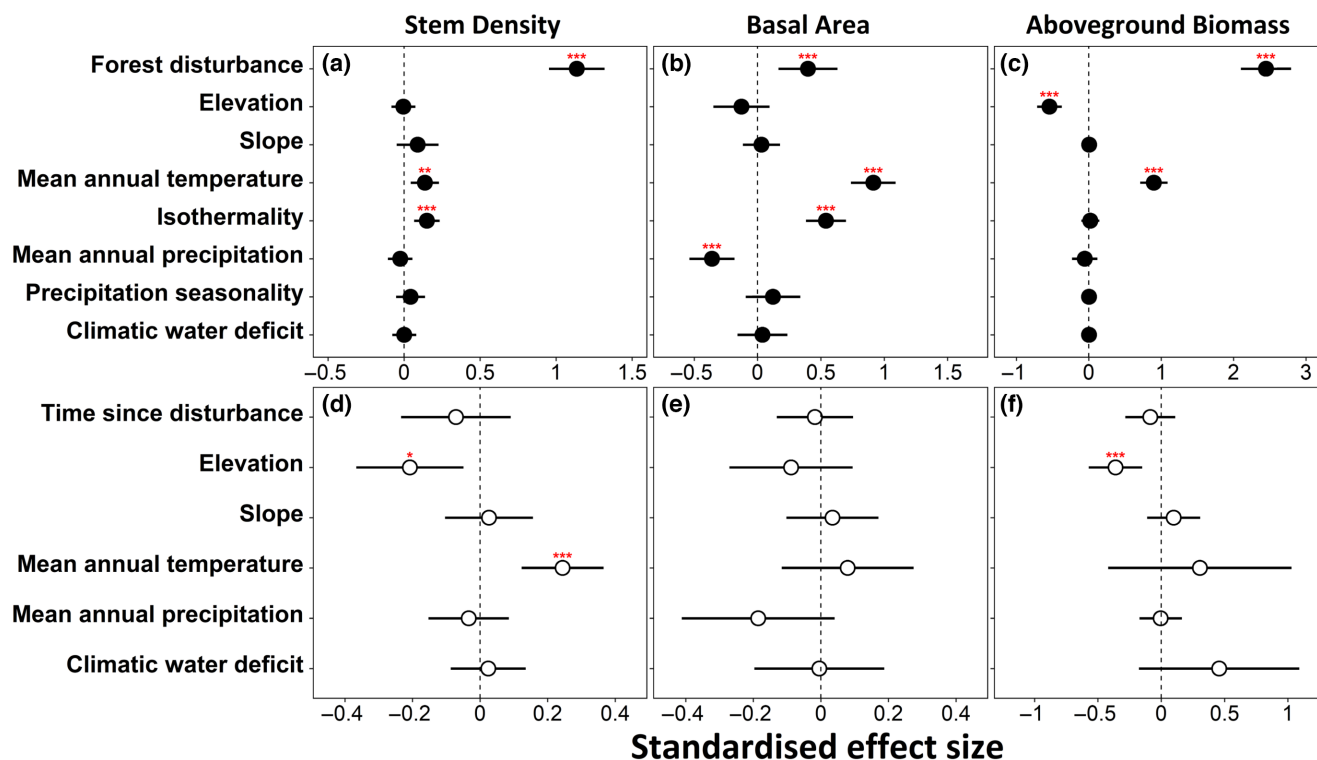


FIGURE 3 Effect sizes of change in liana-to-tree ratios (LTRs). Points indicate coefficients ($\pm 95\%$ confidence intervals) calculated from best-fitted linear mixed-effects models using multimodel inference across all forests (filled symbols) and disturbed forest subsets (open symbols). Effect sizes are standardised to show the change in LTR for stem density (a and d), basal area (b and e) and aboveground biomass (c and f) per unit SD of each predictor. Asterisks indicate significant effects ($*p < .05$, $**p < .01$, $***p < .001$). Coefficient values can be found in Tables S3 and S4.

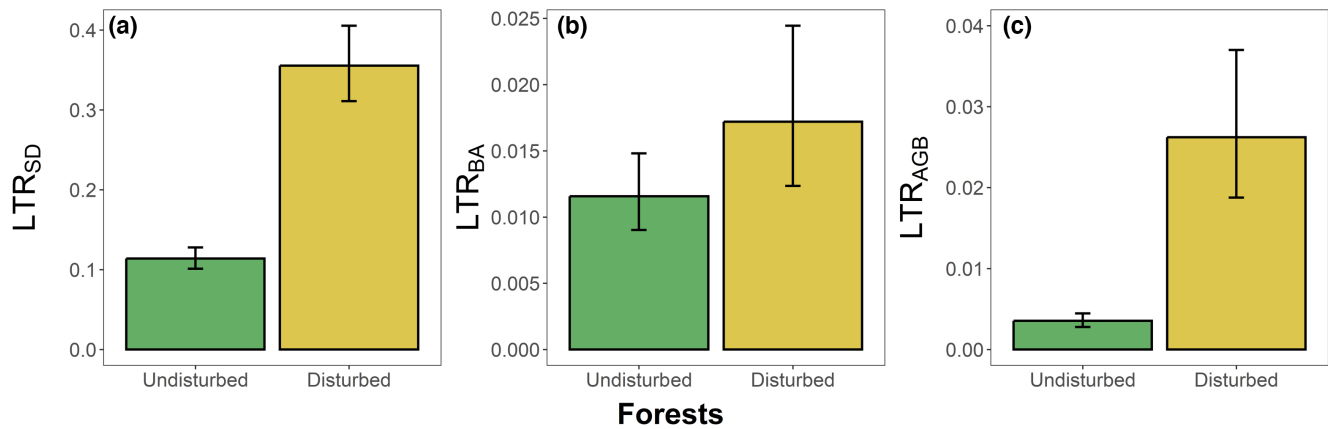


FIGURE 4 Mean liana-to-tree ratio (LTR) of (a) stem density (SD), (b) basal area (BA) and (c) aboveground biomass (AGB) across forest categories predicted by mixed-effect models. Error bars denote bootstrapped 95% confidence intervals (1000 iterations).

relative to trees in drier forests (i.e. with decreasing MAP, Figure 3b). In fact, LTR_{BA} decreased by 4.2% (2.1%–6.2%; $p < .001$) with each 100 mm increase in MAP (Figure 5i).

Precipitation seasonality explained 2.8% of the variance in LTR_{BA} ($R_m^2 = .36$; $R_c^2 = .71$; Figure 2). It also had equal contributions to explained variances in LTR_{AGB} (2.5%, $R_m^2 = .43$; $R_c^2 = .67$; Figure 2) and LTR_{SD} (2.5%, $R_m^2 = .25$; $R_c^2 = .93$; Figure 2). No significant effects of precipitation seasonality were found on LTRs ($p \geq .266$; Figure 3).

The maximum climatic water deficit (MWD) individually contributed 2.1%, 2% and 1.6% to the variances explained for LTR_{SD} ($R_m^2 = .25$; $R_c^2 = .93$; Figure 2), LTR_{AGB} ($R_m^2 = .43$; $R_c^2 = .67$; Figure 2) and LTR_{BA} ($R_m^2 = .36$; $R_c^2 = .71$; Figure 2), respectively. It showed no significant relationships with LTRs ($p \geq .157$; Figure 3).

3.3 | Topography

Topographical predictors, namely elevation and slope, exhibited smaller individual contributions to LTR variations when compared to forest disturbance (Figure 2). Specifically, elevation accounted for 8% and 1% of the variability in LTR_{AGB} ($R_m^2 = .34$; $R_c^2 = .59$) and LTR_{SD} ($R_m^2 = .21$; $R_c^2 = .90$), respectively. The contributions of slope to LTR_{AGB} and LTR_{SD} variances were 3% and 1%, respectively. Both elevation and slope had very negligible individual contributions to LTR_{BA} (Figure 2) variance explained.

LTR_{AGB} significantly varied with elevation ($p < .001$; Figure 3c,f), displaying a non-linear trajectory as it decreased, depending on forest disturbance (Figure 5c). For each increase in elevation of 100 m above sea level, LTR_{AGB} declined by 25.4% (17.4%–33.3%) in disturbed forests, while showing no significant change in undisturbed forests (Figure 5c). Meanwhile, neither LTR_{SD} ($p = .910$; Figures 3a and 5a) nor LTR_{BA} ($R_m^2 = .02$; $R_c^2 = .71$; $p = .263$; Figures 3b and 5b) varied significantly with elevation. However, LTR_{SD} showed a significant negative relationship with elevation in disturbed forests ($p = .01$; Figure 3d). LTRs did not change significantly with slope ($p = .201$ –.901; Figure 3).

3.4 | Interactions between time since disturbance and climate

The effect of climate variables on LTR_{BA} was modified by time since disturbance ($R_m^2 = .13$; $R_c^2 = .36$; $p \leq .002$; Table 2; Figure 6). LTR_{BA} showed a steady decrease with time since disturbance (Figure 6a) at cooler temperatures (MAT $< 23.4^\circ\text{C}$) but increased with time at higher temperatures (MAT $> 27.8^\circ\text{C}$), while no change was observed at mid-temperature values ($23.4^\circ\text{C} \leq \text{MAT} \leq 27.8^\circ\text{C}$). LTR_{BA} increased with time since disturbance in sites with lower annual precipitation (MAP < 1614 mm) but decreased with time for higher precipitation sites (MAP > 3334 mm), while no change was observed around average precipitations ($1614 \text{ mm} \leq \text{MAP} \leq 3334$ mm; Figure 6b). LTR_{BA} decreased with time since disturbance in sites with low water deficit (MWD > -140 mm) but increased with time when MWD < -829 mm, while no significant change was observed around mid-values of MWD ($-140 \text{ mm} \geq \text{MWD} \geq -829$ mm; Figure 6c). The interactions between topographic variables and the elapsed time since disturbance did not show any significant effect on LTR_{BA} ($R_m^2 = .03$; $R_c^2 = .28$; $p \geq .313$; Table 2). However, no interactive effects between time since disturbance and climatic or topographic variables were found to be significant for either LTR_{SD} ($R_m^2 = .01$ –.04; $R_c^2 = .61$ –.64; $p \geq .138$; Table 2) or LTR_{AGB} ($R_m^2 = .25$ –.34; $R_c^2 = .82$ –.89; $p \geq .245$; Table 2).

4 | DISCUSSION

This study is the most geographically extensive and data-rich assessment of the competitive success of lianas over trees to date. It provides fundamental new information supporting recent hypotheses regarding environmental drivers of liana-mediated forest recovery following disturbance. Independent disturbance and environmental effects on liana dominance are clear in the models (Figure S1; Tables S5 and S6).

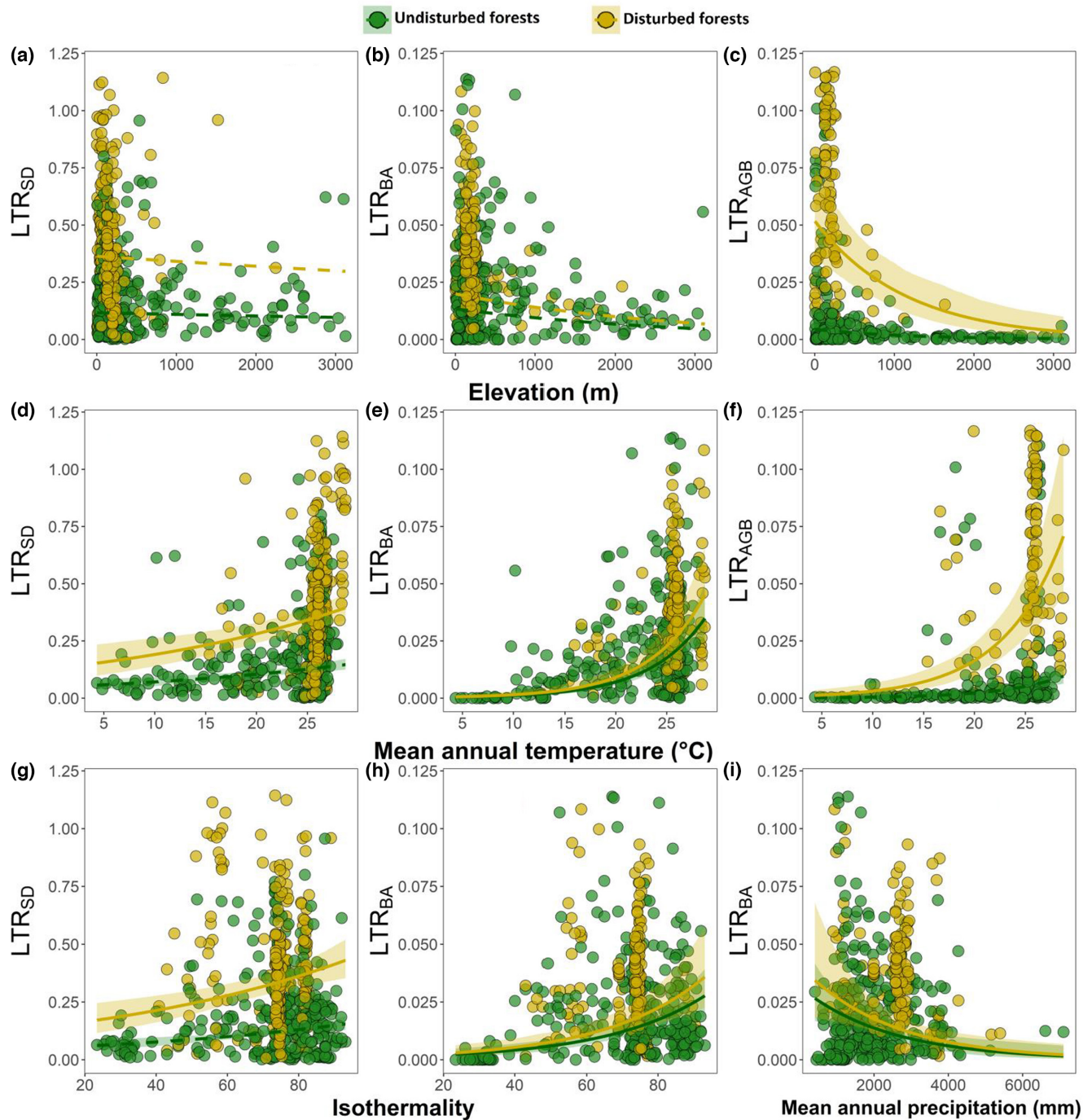


FIGURE 5 Liana-to-tree ratios (LTR) and predictors across all forests. Lines and ribbons show fitted slopes ($\pm 95\%$ bootstrapped confidence intervals, 1000 iterations) for SD, stem density (a, d and g), BA, basal area (b, e, h and i) and AGB, aboveground biomass (c, f), predicted by best-fitting mixed-effects models with restricted maximum-likelihood estimation using data from all forests. Dashed lines indicate non-significant effects.

4.1 | Effects of forest disturbance

Relative to trees, lianas exhibited increased SD, BA and AGB in disturbed forests. This, and our observation that disturbance consistently was the best predictor in all models, supports previous assertions that increasing light resulting from canopy loss may be a main driver of liana abundance (Phillips et al., 2002; Schnitzer

et al., 2021; Schnitzer & Bongers, 2011), suggesting that increased competition with trees in disturbed forests may impact forest recovery (Lai et al., 2017). The increase in LTRs in disturbed forests is most likely a consequence of liana proliferation post-disturbance (Schnitzer, 2015, 2018), whether through natural—for example cyclones and treefalls—or anthropogenic activities—for example logging and shifting agriculture (see Campbell et al., 2018; Laurance

TABLE 2 Averaged interactive effects of the time since disturbance and moderator variables on liana-to-tree ratios (LTRs) of stem density (SD), basal area (BA) and aboveground biomass (AGB) in disturbed forests.

Moderator	Response	n	Coefficient	95% CI	z	p
Elevation	LTR _{SD}	270	0.03	-0.05 to 0.11	0.35	.504
	LTR _{BA}	163	-0.02	-0.07 to 0.04	0.54	.587
	LTR _{AGB}	131	0.09	-0.17 to 0.26	0.94	.698
Slope	LTR _{SD}	270	0.06	-0.02 to 0.15	1.48	.138
	LTR _{BA}	163	-0.03	-0.10 to 0.03	1.01	.313
	LTR _{AGB}	131	-0.19	-0.60 to 0.23	0.89	.375
Mean annual precipitation	LTR _{SD}	270	0.05	-0.05 to 0.15	0.97	.332
	LTR _{BA}	163	-0.51	-0.76 to -0.26	4.03	<.001
	LTR _{AGB}	131	-0.15	-0.20 to 0.18	0.42	.679
Mean annual temperature	LTR _{SD}	270	-0.02	-0.08 to 0.04	0.69	.489
	LTR _{BA}	163	0.27	0.46-1.69	3.15	.002
	LTR _{AGB}	131	0.38	-0.23 to 0.98	1.41	.245
Maximum climatic water deficit	LTR _{SD}	270	0.005	-0.11 to 0.12	0.09	.932
	LTR _{BA}	163	0.64	0.24-1.04	3.15	.002
	LTR _{AGB}	131	0.04	-0.51 to 0.56	0.35	.886

Note: Bold text denotes significant effects.

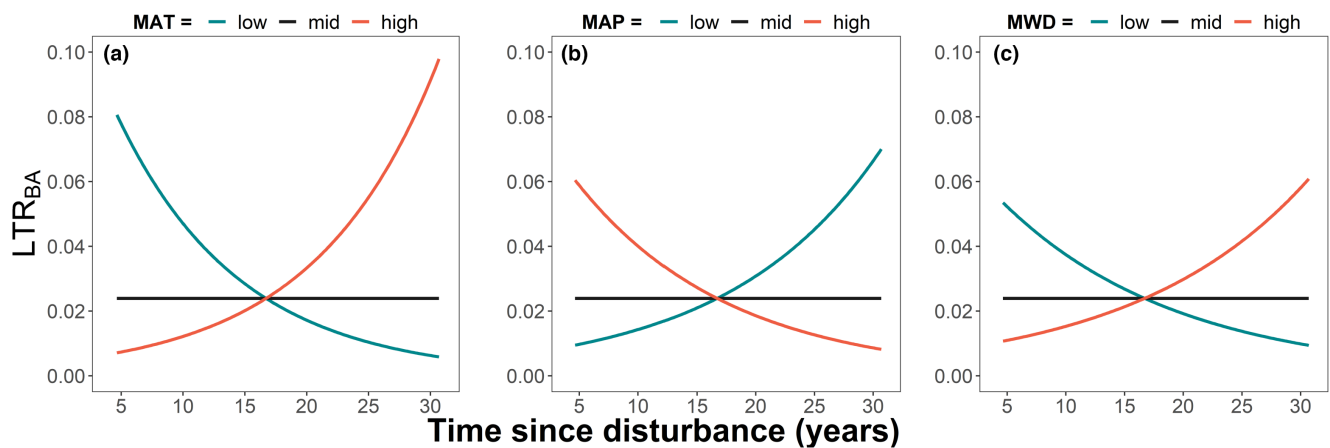


FIGURE 6 Interactive effects on liana-to-tree ratio of basal area (LTR_{BA}) of the time elapsed since disturbance, with (a) MAT (mean annual temperature); (b) MAP (mean annual precipitation); and (c) MWD (maximum climatic water deficit) as moderator variables. Moderator categories (i.e. low, mid and high) denote the observed 16th (mean-SD), 50th (mean) and 84th (mean+SD) percentiles.

et al., 2001; Schnitzer et al., 2000). This highlights the central role of forest disturbance in shaping liana dominance (Marshall et al., 2020) and underscores the necessity of integrating lianas and disturbance dynamics in forest recovery models (Campbell et al., 2015; Heinrich et al., 2023; Poorter et al., 2021).

Disturbances that open up the canopy enhance light availability and indirectly affect other crucial resources such as water and soil nutrients (Marvin et al., 2015; Schnitzer & Bongers, 2011; Schnitzer et al., 2021). These changes can provide lianas with competitive advantages (di Porcia e Brugnera et al., 2019; Putz, 2023) and boost their relative success over trees in disturbed forests (Ledo & Schnitzer, 2014; Schnitzer, 2018). Lianas are also known to exhibit relatively higher abundance and biomass recovery rates than trees in early forest successions, where disturbances are more recent and

have stronger effects (Estrada-Villegas et al., 2020; Lai et al., 2017; Letcher & Chazdon, 2009; Umaña et al., 2020).

4.2 | Effects of climate

Our findings offer further insights into how climate impacts liana dominance. Temperature (MAT) is consistently shown among our models to be the main environmental driver of liana dominance over trees. Given its consistent relationship with elevation, MAT is also likely to be the principal reason for the observed elevational trends. Previous studies investigating patterns and drivers of liana success across world forests have also attributed higher liana abundance with higher temperatures (DeWalt et al., 2015; Schnitzer, 2005; van der Heijden & Phillips, 2008).

Increased temperatures afford lianas strong competitive physiological advantages over other forest growth forms (Schnitzer, 2018). For instance, lianas thrive better than trees at higher temperatures, as is the case during lengthy seasonal droughts (Schnitzer & van der Heijden, 2019; van der Heijden et al., 2019), which cause an increase in evapotranspiration demand from the atmosphere (Slot et al., 2014). Positive temperature change has also been shown to affect tree communities across tropical forests both compositionally and structurally (Bennett et al., 2021; Feeley et al., 2007; Sullivan et al., 2020).

The positive relationship observed between metrics of LTRs and isothermality—a measure that also captures temperature seasonality across the year (Fick & Hijmans, 2017; Noce et al., 2020)—indicates that lianas, relative to trees, are more likely to show increased SD (LTR_{SD}) and BA (LTR_{BA}) in tropical regions. These regions are characterised by a greater uniformity in diurnal temperature ranges and less variation over the year (Visher, 1923). Lianas are most abundant, and likely most dominant, in forests experiencing the highest seasonality (DeWalt et al., 2010, 2015; Schnitzer, 2005). This relationship is also consistent with recent explanations (Schnitzer, 2018; Schnitzer & van der Heijden, 2019) and conceptual hypotheses (Marshall et al., 2020).

In contrast to the patterns observed with temperature and isothermality, LTRs were more weakly and negatively associated with MAP, as this relationship was significant only for LTR_{BA} . Our findings indicate that as MAP decreases, lianas are more likely to show an increase in BA relative to trees. This aligns with earlier observations of lianas thriving in drier forest conditions (DeWalt et al., 2015; Gentry, 1991; Schnitzer, 2005; Schnitzer & Bongers, 2011), compared with trees that appear limited by lower precipitation, occurring mostly in wetter climates (Schnitzer & van der Heijden, 2019). Our results also follow predictions that the competitive effects of lianas over trees should be greater under conditions of increased water scarcity (Marshall et al., 2020; Schnitzer, 2018). However, in a pantropical meta-analysis, Estrada-Villegas et al. (2022) found no significant increase in liana impacts on tree performance at lower MAP. Their finding is consistent with van der Heijden et al. (2019), who previously observed that the negative effect of lianas on trees remained strong in both drier and wet conditions.

Our global findings contrast with results from the Neotropics, where previous studies found no significant relationship between liana abundance and mean annual precipitation (van der Heijden & Phillips, 2008). In this same region, Estrada-Villegas et al. (2021) also found that lianas did not negatively affect tree biomass accumulation in young successional dry forests. However, other studies (Estrada-Villegas et al., 2020; Lai et al., 2017), which used the same experimental design as Estrada-Villegas et al. (2021), have found that lianas do inhibit tree biomass accumulation in humid early successional forests. Our results also appear inconsistent with those of Durigon et al. (2013), who found that lianas were more prevalent in wetter forests at the global scale, noting that this latter analysis was based only on liana occurrence data and had fewer sample points, all from undisturbed forests. We could, therefore, attribute

the observed disparity to differing scales and methods or regional variations.

4.3 | Effects of time since disturbance under varying climate conditions

Strikingly, we found an increase in liana relative BA over time since disturbance with higher MAT ($>27.8^{\circ}\text{C}$), greater MWD ($<-829\text{ mm}$) and lower MAP ($<1614\text{ mm}$). It has been acknowledged that, compared to trees, lianas have better morphological and physiological adaptations to stress induced by rising temperature and water scarcity (Asner & Martin, 2012; Schnitzer, 2018; Schnitzer & Bongers, 2011). It is therefore plausible that in disturbed forests with less precipitation, rising temperatures or pronounced climatic water deficits (e.g. lengthy seasonal droughts), lianas gain more competitive advantages over trees (Schnitzer & van der Heijden, 2019). However, in the longer term, lianas might experience a higher mortality than trees due to their greater susceptibility to drying hydroclimates (Willson et al., 2022).

Understanding how liana dominance in disturbed forests varies over time under different climate regimes is crucial for predicting the responses of degraded forest landscapes to climate change. Based on the trends in LTRs, the results suggest that some disturbed forests, with persistent high liana dominance, may not easily be able to return to a stable climax state with increasing time since disturbance. This result supports the hypothesis that under climates favouring lianas, the effects of liana dominance often persist long after disturbance, stalling forest recovery for decades as a result of liana feedbacks and tipping point thresholds (Marshall et al., 2020).

4.4 | Elevational change in liana dominance

Global patterns of liana dominance assessed in our study were similar to those predicted by Marshall et al. (2020) based on local data that is showing a decline in liana dominance towards higher elevation. Like this earlier local work, we also observed that LTR_{AGB} were disproportionately greater towards lowland disturbed forests, as suggested by the non-linear trend. This observation fills an important knowledge gap, as prior studies mostly focused on the individual effects of elevation on lianas or trees (e.g. Jiménez-Castillo et al., 2007; Schnitzer, 2005), leaving effects on relative dynamics between the two largely theoretical until now (Schnitzer, 2018).

4.5 | Implications and limitations of our models

Our study demonstrates the drivers and patterns of liana–tree relative forest attributes. Associated findings have considerable implications for global forest models aiming to understand how lianas affect ecosystem functioning and the recovery of forests from disturbance under a changing climate (Campbell et al., 2015). For instance, by

providing global evidence, our analyses allow us to validate the empirical hypothesis that the dominance of lianas over trees was consistently driven by forest disturbance interacting with climate factors (Marshall et al., 2020). Assessing various attributes of forest stands and adding topographic variables to our analyses permit us to extend our understanding of the interaction between liana and trees beyond current perspectives, using a larger sample size than previous studies (DeWalt et al., 2015; Durán et al., 2015; Gentry, 1988; Schnitzer, 2005; Schnitzer & Bongers, 2011). The observations provide fundamental new information about global forest successional dynamics while also indicating that forest management may be able to better prioritise action towards regions and elevations that are disproportionately more vulnerable to liana dominance.

Despite including broad geographical coverage of forests globally, there remain some limitations to our study. First, the locations included in our dataset are mostly tropical (and especially from the neotropics) and are dominated by low-elevation sites, especially for disturbed forest samples. This sample bias might potentially obscure some patterns and affect relationships between response metrics and climate variables. Additionally, the uneven distribution of observations across forest disturbance categories might skew certain trends. This is particularly important because sample observations are unbalanced between the forest stand metrics used in our analyses, with some response measures unavailable at some locations. Finally, the spatial distribution of samples is not completely random. Despite accounting for spatial autocorrelation, the lack of true independence among samples might jointly affect patterns in predictors and their relationships with response variables (Berdugo et al., 2017).

We believe that relying on single metrics might be insufficient for assessing the effects of climate and forest disturbance on the relative success of lianas over trees. This is because no single metric appears to consistently capture the variation in liana–tree ratios across different climatic or topographic gradients, irrespective of whether the forests are disturbed or undisturbed. To develop more nuanced, holistic models that predict patterns and drivers of liana–tree dynamics, we recommend the use of comprehensive, geographically balanced datasets. These datasets should encompass diverse ecologically pertinent variables, such as liana load and burden (Muller-Landau & Visser, 2019), net primary productivity (Meunier et al., 2022), wood density (Chave et al., 2009, 2014) and other functional traits (Kattge et al., 2020). Moreover, assessing liana dominance should involve extensive site investigations (Ichihashi & Tateno, 2015; Wright et al., 2004, 2015).

5 | CONCLUSIONS

In this study, we confirmed that forest disturbance and climatic factors are major drivers of liana dominance in global forests. We also found that the competitive effects of lianas on trees vary with time since disturbance and along climate gradients in disturbed forests. Lianas tend to have a higher relative BA than trees in disturbed

forests subjected to less precipitation, high temperature or conditions of increased climatic water deficit. Overall, we provide global insights into how lianas affect forest dynamics and recovery through structural attributes. Quantifying the global patterns and drivers of liana–tree competition through forest stand attributes is crucial for understanding their impacts on the global carbon sink, forest recovery from disturbance, timber yields and resilience to climatic change. Our findings advance the current knowledge of the causes and consequences of liana dominance in forest ecosystems under global climate and land-use change. This can support the development and implementation of forest management and restoration measures worldwide that may be targeted towards regions and elevations with climate disproportionately favouring lianas to enhance carbon sequestration, biodiversity and other ecosystem services in degraded forest landscapes.

AUTHOR CONTRIBUTIONS

Alain Senghor K. Ngute: Data curation; formal analysis; investigation; methodology; resources; validation; visualization; writing – original draft; writing – review and editing. **David S. Schoeman:** Methodology; supervision; validation; visualization; writing – review and editing. **Marion Pfeifer:** Conceptualization; funding acquisition; methodology; resources; supervision; validation; writing – review and editing. **Geertje G. F. van der Heijden:** Data curation; resources; writing – review and editing. **Oliver L. Phillips:** Data curation; resources; writing – review and editing. **Michiel van Breugel:** Data curation; resources; writing – review and editing. **Mason J. Campbell:** Data curation; writing – review and editing. **Chris J. Chandler:** Data curation; writing – review and editing. **Brian J. Enquist:** Data curation; resources; writing – review and editing. **Rachael V. Gallagher:** Data curation; resources; writing – review and editing. **Christoph Gehring:** Data curation; resources; writing – review and editing. **Jefferson S. Hall:** Data curation; writing – review and editing. **Susan Laurance:** Data curation; writing – review and editing. **William F. Laurance:** Data curation; resources; writing – review and editing. **Susan G. Letcher:** Data curation; resources; writing – review and editing. **Wenyao Liu:** Data curation; resources; writing – review and editing. **Martin J. P. Sullivan:** Methodology; writing – review and editing. **S. Joseph Wright:** Data curation; resources; writing – review and editing. **Chunming Yuan:** Data curation; writing – review and editing. **Andrew R. Marshall:** Conceptualization; funding acquisition; methodology; resources; supervision; validation; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interest.

DATA AVAILABILITY STATEMENT

All primary data sources have been provided and described in Table S1. All raw and processed data supporting the results in this study are openly available in Zenodo <https://doi.org/10.5281/zenodo.10428833> and Figshare <https://doi.org/10.6084/m9.figshare.24879021>. Direct access to the original and raw data might be restricted due to ethical considerations and data privacy agreements with our data contributors. All requests to access specific raw data should be directed to the original data sources listed in Table S1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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