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Global increase of lianas in tropical forests

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Abstract

Lianas profoundly affect tropical forests dynamics, reducing productivity and carbon storage, which underscores the importance of monitoring change in their abundance in projecting the future of the global terrestrial carbon store. While increasing liana populations are documented within the Neotropics, the global consistency of these patterns is questioned, and remains to be determined. To evaluate pantropical trends in liana abundance comprehensively and quantitatively, we conducted a systematic literature review and meta-analysis. This approach allowed us to synthesize data from published longitudinal studies examining liana trends across the tropics. We calculated standardized effect sizes and standard errors, and applied a Bayesian hierarchical meta-analytic model to adjust for publication bias. Our analysis reveals an overall pan-tropical increase in lianas abundance, occurring at an average rate of 1.7 ± 0.7 SE% per year (~10% to 24% per decade). This upward trend, confirmed to be robust against publication bias, extends beyond Neotropical regions, indicating a widespread phenomenon. Although a global trend of increasing liana abundance is evident, significant local variation exist, attributable to differences in life cycle stages, abundance metrics, forest successional stages, and biogeographical realms. Notably, increases in stem density of saplings and biomass of canopy lianas, especially in old-growth forests, point to global climatic drivers and heightened turnover rates in tropical forests as factors promoting sustained liana growth in the canopy and clonal colonization in the understory. These trends suggest that the rise in liana abundance may not only persist but could also intensify under climate change. Considering both previous and current research on lianas, our findings confirm growing concerns about lianas' expanding impact on pan-tropical carbon storage, highlighting their significant potential effect on global carbon dynamics.

KEYWORDS
carbon cycle, climbers, clonal growth, disturbance, environmental drivers, lianas dominance, temporal trends, woody vines

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1 | INTRODUCTION

Lianas are an essential component of tropical forests in terms of abundance, biomass, and diversity (Chave et al., 2001; Gentry, 1992; Gerwing & Lopes Farias, 2000), bearing the potential to significantly influence forest community composition and the dynamics of carbon, water, and energy fluxes. At the community level, lianas lower tree recruitment, growth, and survival by means of competition for light and belowground resources (Santiago et al., 2015; Schnitzer & Bongers, 2011), while affecting tree community composition through numerous detrimental effects that vary across tree species (Schnitzer & Carson, 2010; van der Heijden et al., 2008; Visser et al., 2018). At the ecosystem level, lianas decrease primary productivity, reduce available soil moisture during seasonal droughts, and increase forest albedo (Andrade et al., 2005; Meunier et al., 2021, 2022; Schnitzer, 2005). The negative impacts of lianas on carbon storage by trees, which cannot be compensated for by lianas themselves, raise significant concerns about their influence on the global carbon cycle (van der Heijden et al., 2013, 2015).

A considerable amount of research, and previous reviews, have focused on the potential drivers of changes in liana abundance (Schnitzer, 2015; Schnitzer & Bongers, 2011). As a result, several mechanisms have been proposed to explain liana trends: increased natural gap formation caused by increased turnover in old-growth forests (Phillips et al., 2002), leading to increased light availability; anthropogenic disturbances affecting both light availability and forest structure (Addo-Fordjour et al., 2021; Chandler et al., 2021; Pandian & Parthasarathy, 2016; Yorke et al., 2013); rising atmospheric CO_2 concentrations and nitrogen deposition potentially benefiting lianas through a fertilization effect (Phillips et al., 2002; Schnitzer, 2015); declining precipitation giving lianas enhanced performance during dry periods (Swaine & Grace, 2007); ENSO climatic oscillations and higher temperatures which increase tree mortality and hence create suitable gaps for liana propagation (Vogado et al., 2022; Wright et al., 2004; Yorke et al., 2013); and shifts in plant–animal interactions determining the dispersion success, establishment, and survival of trees and lianas (Bongers et al., 2020; Itoh & Nakamura, 2015; Scott Luskin et al., 2019; Souza et al., 2022; Wright et al., 2015).

However, a focus on the drivers of the increase may have been premature. While there are indications of increases in lianas abundance (e.g., Chave et al., 2008; Enquist & Enquist, 2011; Ingwell et al., 2010; Laurance et al., 2014; Phillips et al., 2002; Yorke et al., 2013), there are concerns about the overrepresentation of the Neotropics in these assessments (Wright et al., 2015). Moreover, more recent studies show no evidence for directional changes in lianas density, biomass, and fruit production (Mendoza et al., 2018; Souza Gerolamo et al., 2018). These might indicate possible publication biases such as geographic, selective reporting (Csada et al., 1996), and time-lag bias (Koricheva & Kulinskaya, 2019). These factors raise questions about whether the increases in lianas are more localized, rather than a widespread pan-tropical phenomenon. Consequently, it is prudent to first determine the robustness of this increasing liana trend—globally and in the Neotropics—through an objective systematic analysis before delving into its causes.

Most longitudinal studies measuring lianas so far focused on a single life stage, and reproduction metrics (e.g., number of flowers and seeds) were reported in isolation from metrics in vegetative life stages (Wright & Calderón, 2006; Zimmerman et al., 2018). Given that forest dynamics is driven by the combined effects of growth, survival, and reproduction across the full life cycle (Visser et al., 2016), positive liana trends on a single life stage may be offset by opposite trends at other life stages, precluding the identification of the potential drivers of change. Moreover, most studies have been conducted in old-growth or largely undisturbed forests (Schnitzer, 2015). In younger forests, forest structure and light environment have a strong influence on liana and tree communities (Dewalt et al., 2000; Letcher & Chazdon, 2012), an effect that might be overlooked in longitudinal studies focusing on old-growth forests.

To tackle these challenges, a systematic, evidence-based approach must evaluate and quantify longitudinal global liana trends within a unified framework. Such an approach enables a comprehensive synthesis, allowing for the comparison of liana trends using relevant and consistent metrics. This is a prerequisite to accurately linking observed trends with their hypothesized drivers, and gaining insights which cannot be gained from static or space-for-time substitution approaches (Damgaard, 2019; Detto et al., 2019; Johnson & Miyanishi, 2008). Our goal is to consolidate existing knowledge from longitudinal studies that document temporal changes in liana metrics. We achieved this through a systematic literature review and meta-analysis spanning the pantropical region. We address the following research questions:

1. Does the existing body of scientific literature suggest an average global increase of lianas across tropical forests?
2. Are lianas increasing at different rates at different life stages, metrics, biogeographical realms, or forest successional stages?

2 | METHODS

2.1 | Overview

Our review builds on the PICO (population, intervention, control, outcome) framework for systematic reviews, which included a systematic search and an initial screening of abstracts by three independent reviewers. The statistical approach starts with the calculation of effect sizes and standard errors based on the slope of the linear regression liana metric versus time. It then builds upon a conceptual population model in which trends are grouped according to life stages and liana metrics. This structure is also used for imputation of missing standard errors and to fit the subsequent hierarchical meta-analytic model with effect sizes nested within studies. Potential effects of publication bias were considered through sensitivity analyses, and by adding standard error and year of publication as predictors to the hierarchical model. Our analysis aims to synthesize the wide range of studies done on lianas, allowing for identification of potential biases that may have influenced the reported trends.

2.2 | Systematic literature review

We defined eligibility criteria based on the PICO framework (Counsell, 1997; Stewart et al., 2013). We treat tropical forests as the population (P), time as the intervention (I), and liana metrics as the outcome (O). Due to the observational nature of studying trends, there was no comparator or control (C). We included studies in tropical forests without restrictions on precipitation and altitude (i.e., dry to wet, lowland to montane), and under varying successional stages and phenology types (i.e., secondary to old-growth, deciduous to evergreen). We selected studies reporting lianas trends during a time span greater or equal to 1 year to obtain trends beyond the seasonal behavior. We considered liana metrics including stem density, basal area, above-ground biomass (AGB), number of seeds, flowering and fruiting activity, infested trees, among others, and included both remote sensing approaches and measurements in plots on the ground. We focused on studies directly observing temporal trends and did not include those using space-for-time substitution such as chronosequences due to potential biases (Damgaard, 2019; Detto et al., 2019; Johnson & Miyanishi, 2008). We also excluded experiments involving the removal of lianas (unless a control plot was present).

We conducted searches for eligible studies on September 16th, 2022, in Web of Science, covering studies published since 1900, and in Scopus, covering studies published since 1788. The keywords were formulated according to the PICO approach, allowing for synonyms and related terms. The following query was used for both databases: forest* AND tropic* AND (climber* OR liana* OR vine*) AND (trend* OR change*). The searches were restricted to the Title or Abstract fields with no filters applied to publication year. We deduplicated records using the online app Rayyan (Ouzzani et al., 2016). Then 30 random abstracts were screened by three independent reviewers in three rounds to further refine the eligibility criteria before screening all records. After three screening rounds, disagreements were discussed, and the eligibility criteria were adjusted. The PICO components and the detailed eligibility criteria are listed in Supplementary Appendix A.

A total of 553 records were found through Web of Science and Scopus. After duplicates removal, we screened 303 records and subsequently selected 93 studies for full-text reading. 35 studies met all the eligibility criteria for meta-analysis. The main reasons for exclusion were the lack of longitudinal measurements and the use of lianas only as a grouping factor for analyzing variables not related to our research questions. In addition, we included studies covered by the previous non-systematic reviews in Schnitzer and Bongers (2011) and Schnitzer (2015) satisfying all our eligibility criteria. This process led to the selection of 39 studies for the meta-analysis, encompassing 505 unique effect sizes, as several studies reported effects from various sites and/or metrics. A sensitivity analysis was carried out to verify that including the latter studies did not introduce any bias to the calculated overall trend. Detailed information about the excluded studies, the reasons for exclusion, and the PRISMA flow diagram can be found in Supplementary Appendix B.

2.3 | Preprocessing of effect sizes and standard errors

2.3.1 | Database

We extracted temporal data of liana metrics from each study selected for meta-analysis from the text and available tables, figures, appendices, supplementary material, and online repositories. We used the Engauge Digitizer tool (Mitchell et al., 2020) to extract the data points from figures. Besides liana metrics, we added the following relevant information for each study to our database: authors, publication year, biogeographical realm (Neotropical, Afrotropical, Australian, Indomalayan), country, location (plot name), coordinates, forest type (i.e., secondary to old-growth), approach (remote sensing/plots on the ground), time span and resolution, surveyed area, life stage of lianas, life form for studies reporting results for both lianas and trees, taxa, disturbance type, reported uncertainty, sample size, and initial stock values. A list of the studies included in the meta-analysis is provided in Supplementary Appendix C. The database is archived at https://zenodo.org/records/10787951.

2.3.2 | Effect sizes (ES) and standard errors (SE)

Only 17 ES with their respective SE were provided directly in primary studies. For the other studies, the statistical approach starts with the calculation of the ES as the slope of the linear regression liana metric versus time. ES and SE were calculated based on the number of temporal measurements and the reported uncertainty. Separate ES and SE were calculated per plot, metric, and life stage. Since only a handful of studies (5/39) provided data at the species level, taxa were aggregated to estimate a single effect including all species per plot, metric, and life stage. For metrics not comparable among different species (e.g., seed counts and flower presence), we fitted a mixed-effects model taking species as a random effect. The other studies were processed following one of the approaches explained below.

> *Case* 1. >2 temporal measurements with reported uncertainty (SD): to consider the uncertainty reported by the authors for each temporal measurement in their primary study, the Ordinary Least Significance (OLS) slope coefficient and its SE were estimated with a parametric bootstrapping with 10,000 iterations

assuming metrics were normally distributed. 6 out of 155 ES fall in Case 1.

Case 2. >2 temporal measurements without reported uncertainty: the slope coefficient and its SE were estimated by fitting a Bayesian linear regression to the raw temporal measurements with a gaussian error model and flat priors. 56 out of 155 ES fall in Case 2.

Case 3. Two temporal measurements with reported uncertainty (based on a normal distribution): the ES were calculated as the difference between the two temporal measurements and the individual uncertainties were propagated using the general formula for error propagation, that is, $\delta_{\mathrm{ES}} = \left(\delta_{\mathrm{ip}}^2 + \delta_{\mathrm{fp}}^2\right)^{1/2}$, where δ_{ES} is the uncertainty of the ES, δ_{ip} is the uncertainty of the initial measurement, and δ_{fp} is the uncertainty of the last measurement. 10 out of 155 ES fall in Case 3.

Case 4. Two temporal measurements without reported uncertainty: the ES were calculated as the difference between the two temporal measurements. The SE were estimated using multiple imputation by chained equations (MICE algorithm) which creates multiple datasets where missing values are imputed with values based on regression models (van Buuren & Groothuis-Oudshoorn, 2011). The Bayesian linear regression imputation method, defined by Rubin (1987), was used to fit an imputation model with life stage and liana metric as categorical predictors. The imputation method follows an iterative process for robust meta-analysis, as recommended by Schafer (1997), which is summarized below. For details, please see Supplementary Appendix D. The process follows three stages:

1. Initialization: Missing Standard Errors (SE) are imputed using predictive mean matching as a preliminary step. This involves a linear regression, of the form SE ~ Life stage + Liana metric on observed data from Cases 1 to 3 to predict missing values multiple times, and then randomly selecting among these predictions to build a complete dataset. The imputed SE were constrained to be equal or greater than the lowest observed SE, causing imputed SE to be relatively conservative.
2. Bayesian linear regression: first a regression is fitted using the now-complete dataset, with coefficients modeled as a multivariate normal distribution. Next, missing SE are re-imputed from a multivariate normal distribution, based on updated estimates, and constrained to avoid overly optimistic imputations.
3. Meta-analytic model: the two steps above are iterated over 30 cycles or until estimates converge. Next, the entire procedure is repeated five times to create multiple imputed datasets each to which a meta-analytic model is fit. All models are then combined through posterior pooling of the results as explained below in Section 2.4.2 to create a final model from which inference is made. A total of 66 out of 155 ES fall in Case 4.

Our method for assessing uncertainty, and accounting for missing standard errors in primary studies, particularly through the process of multiple imputation, introduces increased variability into our estimates. As a result, trend estimates in our meta-analysis tend to become more conservative. For diagnostic graphs illustrating the imputation process and its convergence, refer to the Supplementary Appendix D.

2.3.3 | Standardization of ES and SE

To address the issue of comparability among different liana metrics, we standardized the ES and SE with respect to initial stock values, that is, dividing by the liana metric measured at the first census (I_s). If no uncertainty was provided, I_s was assumed to be certain, and both the ES and the SE were divided by I_s. If uncertainty was provided, the general formula for error propagation was used to calculate the SE of the standardized ES with Equation (1).

$$\text{SE of the standardized ES} = \frac{1}{I_s}\sqrt{\mathrm{SE}_{\mathrm{ES}}^2 + \frac{\mathrm{ES}^2\mathrm{SE}_{I_s}^2}{I_s^2}} \qquad (1)$$

where: $\mathrm{SE}_{\mathrm{ES}}$ = Standard error of the effect size before standardization. SE_{I_s} = Standard error of the initial stock value.

Henceforth, ES and SE will refer to the standardized values.

2.4 | Meta-analysis

2.4.1 | Conceptual model

To synthesize the myriad of metrics being used as proxies to measure liana population growth rates, liana life stages and metrics were organized following a conceptual model based on principles of population ecology. This model groups the ES according to distinct life stages and elucidates how liana metrics relate to the overall pattern of interest: population growth rates (Figure 1). Inconsistencies in defining diameter classes among various studies presented a challenge and necessitated grouping all lianas ≥1 cm dbh into a single category, as it was the only uniform classification facilitating a fair analysis. For the detailed equivalences among liana life stages and metrics extracted from studies and the broader categories used in our conceptual model, see Supplementary Appendix E.

2.4.2 | Statistical model

We developed a Bayesian regression model to quantify the overall trend in lianas. Data were structured hierarchically in the model with

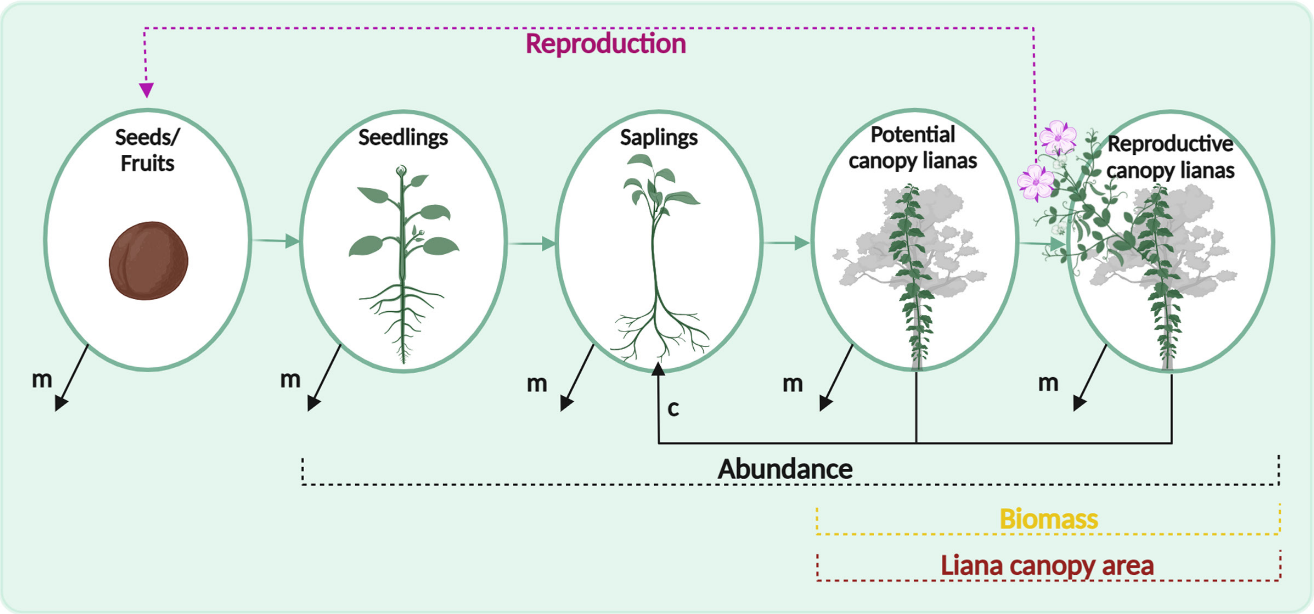


FIGURE 1 Conceptual model of the different life stages and liana metrics considered in this study. Seedlings and saplings were defined in each study based on height limits; in our analyses, we kept the classification used by each author based on their respective study site. Potential canopy lianas were taken as individuals with a diameter at breast height (dbh) ≥1 cm as the probability of these stems being in the canopy is already substantial ranging between 10% and 50% among sites at 1 cm dbh (Kurzel et al., 2006). Reproductive stage lianas refer to lianas for which flowering metrics were reported or lianas infesting tree crowns detected through remote sensing approaches or field observations. Mortality = m. Clonal reproduction = c. Liana metrics are represented with dashed lines. This diagram is a simplification of liana ontogeny since seedlings and saplings might or might not be freestanding depending on the species (Letcher, 2015). Created with BioRender.com.

ES nested within studies by introducing a study-specific random intercept. We analyzed the influence of life stage, liana metric, biogeographical realm, and forest successional stage in the mean slope by adding a categorical predictor to the regression in each case. For each categorical predictor, we fitted the model in Equation (2).

$$\begin{aligned} y_{ij} &\sim N\left(\alpha_j + \beta x_{ij}, \sigma_y^2\right), \quad \text{for } i = 1, \dots, n_j, j = 1, \dots, J, \\ \alpha_j &\sim N\left(\gamma_0, \sigma_\alpha^2\right), \quad \text{for } j = 1, \dots, J, \end{aligned} \tag{2}$$

where: y_{ij} = Estimate of the ith effect size in the jth study. α_j = random intercept for study j. β = main effect of the moderator. x_{ij} = Moderator for which y_{ij} was measured (be it life stage, liana metric, biogeographical realm, or forest successional stage). σ_y^2 = Within-study variance, including measurement error and variation between y_{ij}'s (beyond what is explained by the moderator). γ_0 = Global effect size. σ_α^2 = Between-study variance. n_j = Number of effect sizes in the jth study. J = Number of studies.

Analyses were performed using the R package brms version 2.19.0 (Bürkner, 2017), using Hamiltonian Monte Carlo and the No-U-Turn Sampler (NUTS) (Duane et al., 1987; Hoffman & Gelman, 2014; Neal, 2011). We used uninformative priors for the overall trend and the variation between studies. Specifically, the prior distribution for the overall effect and the random intercepts was the standard normal, with $\mu = 0$ and $\sigma^2 = 1$. The standard deviations for random-effect intercepts and between-study variation were modeled with a half-Cauchy prior with location parameter $x_0 = 0$ and scaling parameter $s = 0.5$. This constrains variances to positive values (van Erp et al., 2017) while still allowing large values in the tail regions (Williams et al., 2018). For β coefficients in Equation (2), we used the default flat priors set in the brm() function of the brms R package.

The meta-analytic model was fitted to each imputed dataset (see Section 2.3.2. Case 4) separately and results were pooled across models afterwards. Pooling was achieved by combining the posterior draws of the models (Bürkner, 2017). Posterior pooling is conceptually similar to model averaging (Burnham & Anderson, 2002; Grueber et al., 2011) though with more robust estimates of uncertainty. From the pooled posteriors, mean parameters as well as confidence intervals can be calculated. As we were a priori explicitly interested in assessing the existing evidence of liana increases in tropical forests, we considered any effect with a 5% lower credible interval greater than zero to be a statistically significant effect.

2.5 | Publication and related biases

To address potential biases affecting reported liana trends, we fitted additional meta-analytic models that incorporated SE and publication year as predictors. These additions help to correct for two key biases: publication bias, characterized by selective reporting of outcomes in the literature (Csada et al., 1996), and time-lag bias, where positive results tend to be published sooner than negative ones (Koricheva & Kulinskaya, 2019). We followed the approach proposed by Nakagawa et al. (2022) in which a multilevel meta-regression is used to extend existing regression-based methods (i.e., Egger's regression) and residual funnel plots are used as visual supplements to the analysis. This method can both detect and correct for funnel asymmetry or small-study effects, while modelling heterogeneity and non-independence of data. To test if the effect in the main analysis (Section 2.4.2) was robust to publication bias, we extended the model towards:

$$\begin{aligned} y_{ij} &\sim N\left(\alpha_j + \beta x_{ij} + \beta_1 \mathrm{SE}_{ij} + \beta_2 c(\mathrm{year}_{ij}), \sigma_y^2\right), && \text{for } i = 1, \dots, n_j, j = 1, \dots, J, \\ \alpha_j &\sim N\left(\gamma_0, \sigma_\alpha^2\right), && \text{for } j = 1, \dots, J, \end{aligned} \tag{3}$$

where: β_1 = measures the reporting bias as predicted by the SE. SE_{ij} = standard error of the ith effect size in the jth study. β_2 = measures the time-lag bias as a function of publication year. $c(\mathrm{year}_j)$ = centered publication year of the jth study.

The other parameters are as above.

In the context of the model in Equation (3), γ_0 can be interpreted as an adjusted overall effect after accounting for potential publication and time-lag biases. The adjusted estimates are reported in Section 3. Residual funnel plots and unadjusted estimates can be found in Supplementary Appendix F.

3 | RESULTS

Our meta-analysis resulted in 505 effect sizes (ES) extracted from 39 unique studies (Figure 2). An initial exploratory analysis following the vote counting approach showed a general trend of increasing liana prevalence throughout the tropics is evinced by 333 positive ES (66%) compared to 172 ES (34%) with decreasing or stable trends. After grouping ES per life stage and aggregating the results reported at the species level, 155 ES and their respective standard errors (SE) were obtained. The general increasing pattern and its geographical coverage hold for the reduced dataset, with 112 ES (72%) showing an increasing trend.

Based on the hierarchical meta-analytic model, the overall increase of lianas in tropical forests as a percentage of initial stock values was on average 1.7±0.7 SE % per year (Figure 3; 5% LCI: 0.6) during the period covered by all the primary studies included in the meta-analysis (1976–2022). The additional moderator analyses revealed statistically significant increases (5% LCI>0) for saplings and potential canopy lianas, and for the biomass metric. Increases were also significant in Neotropical and Indomalayan forests, and particularly in old-growth forests. Decreasing trends were obtained only for the seeds life stage ($n=3$) and for the Australian region ($n=3$), but none of them had statistical significance. Most significant trends were robust to publication and related biases, except for the estimated trend for the abundance metric which was not statistically significant after adjusting for small-study effects and time-lag bias. Sensitivity analyses excluding studies found in previous non-systematic reviews, and nesting studies within countries (to account for the effect of multiple studies from single sites), support the main results (see Supplementary Appendixes G and H). The main result was also robust to excluding all studies from Barro Colorado Island (BCI).

4 | DISCUSSION

Through synthesizing available data from published longitudinal studies reporting trends of lianas in tropical forests, we show that an overall liana increase in tropical forests is underway. Moreover, our systematic literature review with meta-analysis shows that this result is robust to publication bias. The strength of our synthesis lies in employing a Bayesian approach to fit the hierarchical meta-analytic model, enabling us to quantify the uncertainty of effect sizes and correct for publication bias. Complementing this, our focus on longitudinal data offers a direct and more reliable understanding of liana dynamics and their driving factors, free from the common biases associated with static or chronosequence-based analyses (Damgaard, 2019; Detto et al., 2019; Johnson & Miyanishi, 2008). Building on these foundations, our findings reveal that liana proliferation is taking place at varying rates, influenced by metrics, life stages, forest successional stages, and biogeographical realms (Figure 3). We discuss below how these differences may be informative and help in disentangling the drivers of temporal trends in liana abundance. We do so by focusing on four questions that arise

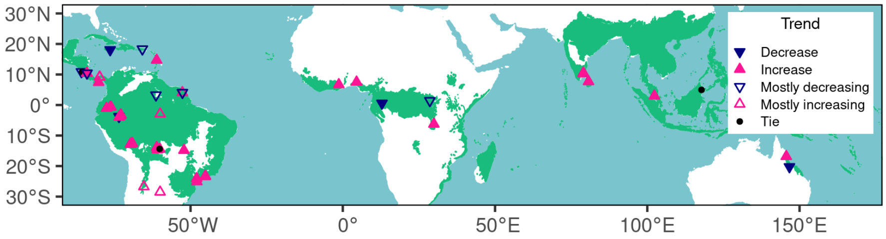
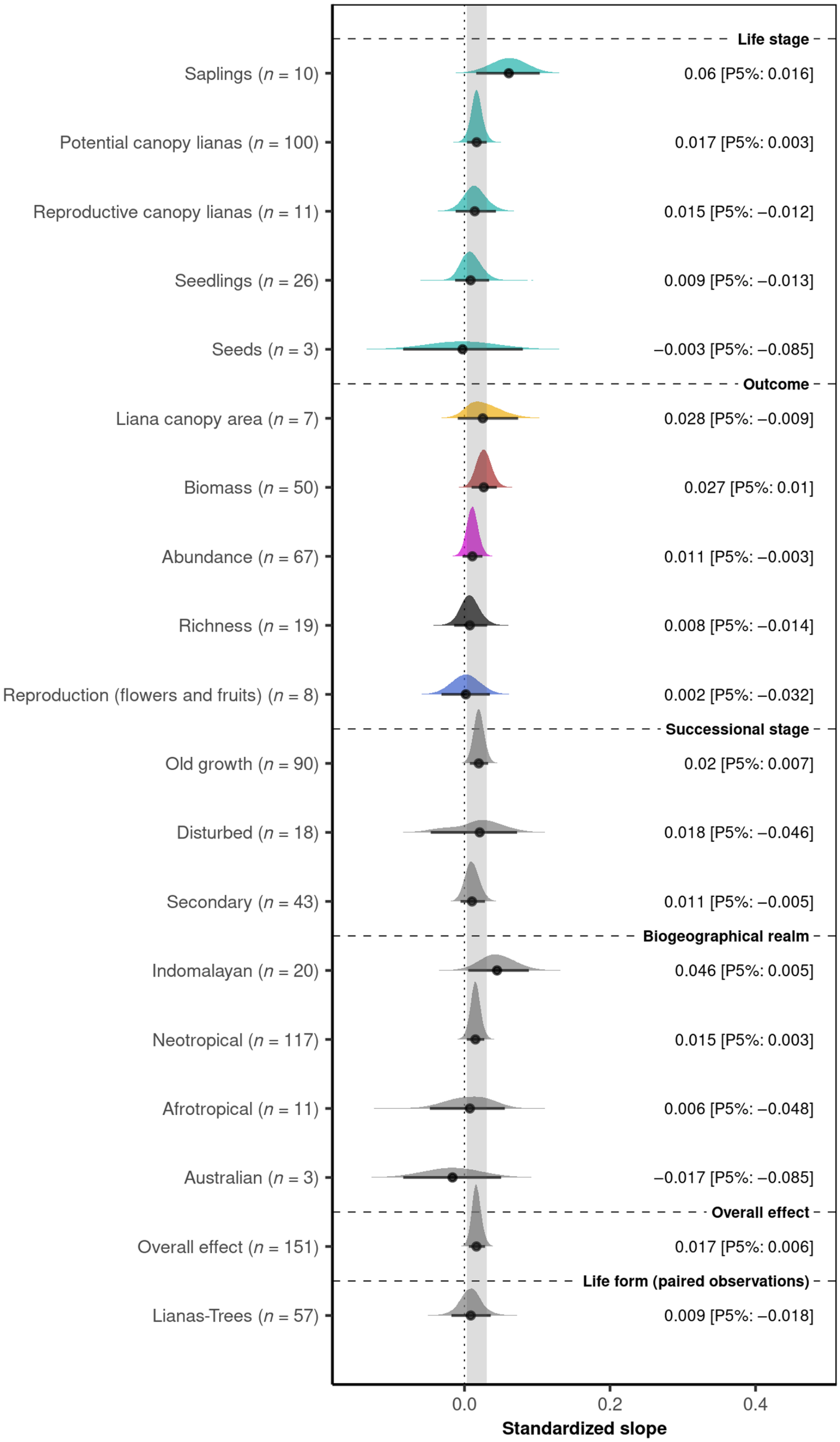


FIGURE 2 Geographical coverage of the studies selected for meta-analysis. Filled triangles represent consistent increasing (all effect sizes positive) or decreasing (all effect sizes negative) trends across outcomes and life stages. Open triangles represent contrasting results evincing mostly increasing (>50% of effect sizes positive) or mostly decreasing (>50% of effect sizes negative) trends. Dots represent sites where there is an equal number of positive and negative effect sizes. Green areas correspond to the ecoregions for tropical and subtropical broadleaf forests (Olson et al., 2001).

FIGURE 3 Posterior distributions for the overall increase of lianas in tropical forests and for the moderators of interest (life stage, outcome/liana metric, biogeographical realm, and successional stage). Points and intervals are posterior means and 90% Credible Intervals (CI), with the lower 5% CI labeled as P5%. Mean effect sizes and CI were calculated with 10,000 samples from the model posterior distribution after convergence. Richness refers to temporal trends in liana species richness reported in some studies. Secondary forests refer to forests with reported disturbances prior to the census period. Disturbed forests refer to forests suffering natural disturbances or logging in between the census period. The model for the difference between lianas and trees (see bottom section) was applied to a condensed dataset of 18 studies featuring simultaneous paired observations of trees and lianas at identical life stages within the same study. For a forest plot at the study level see Supplementary Appendix I.



from our results: (1) What causes the contrasting liana trends in saplings versus seeds and seedlings? (2) Why is biomass increasing when no significant changes can be detected in abundance? (3) What reasons could explain the significant versus non-significant increasing trends in old-growth versus secondary and disturbed forests? (4) Do our results support the pattern of increasing lianas in the Neotropics versus decreasing lianas in the Afrotropics?

4.1 | Saplings versus seeds and seedlings

Lianas are increasing with an average trend of 1.7% per year, although at different rates throughout their life cycle with four out of five life stages showing positive trends. The large increase in saplings compared with non-significant changes in seeds and seedlings (6.0% vs. −0.3% and 0.9% per year) may indicate that the overall increasing trend depends—in part—on recruitment method. Saplings increase in abundance due to the influx of new individuals from seeds, seedlings, and clonal stems (Figure 1). As both seeds and seedlings showed no increasing trends, increased clonal growth is the remaining logical explanation for the overall observed increase. Clonal reproduction is effective (e.g., Schnitzer et al., 2021; Yorke et al., 2013) due to the secure supply of resources from the parent stem, which allows clonal stems to rapidly increase in height and to be more resistant to species-specific enemies compared to seedlings (Ledo & Schnitzer, 2014). It is possible that large lianas in the canopy acting as parent stems are investing more in clonal reproduction because of CO_2 fertilization effects or that they are enforced to create new rooting points to maintain hydraulic integrity as they get bigger. In contrast, influx into the seedling size-class via sexual reproduction should be more variable as seed production is notoriously high in variability (Wright et al., 2004; Zimmerman et al., 2018), and seedlings, with limited storage, are more vulnerable to availability of resources (Khurana & Singh, 2001; Vázquez-Yanes & Orozco-Segovia, 1993). The fact that these stages are more variable also means that it is statistically more challenging to find an effect here.

4.2 | Lianas in the canopy

An increase in prevalence of lianas in the forest canopy is reflected by the positive and significant trend in biomass (2.7% per year) and the increase in liana canopy area (2.8% per year). The non-significant effect in total abundance (increasing 1.1% per year on average), does not necessarily contrast these trends, as the total abundance metric consist of all life stages including seedlings which adds uncertainty. Particularly, we expect that the stronger increase in lianas biomass could be explained given the relative stability of old growth forests, with communities of large trees with greater wood density and low mortality rates even when heavily infested, resulting in stable enduring structural support and access to high light conditions for canopy lianas (Poulsen et al., 2017; Visser et al., 2018). Such conditions may allow existing lianas in the canopy to become thicker and longer than before, boosting up their biomass and covered canopy area.

4.3 | Increases in old growth forests and the role of disturbance

Our findings of a significant increase in liana populations in old-growth forests suggest that, when free from anthropogenic activities or widespread natural disturbances, lianas appear to be increasing due to long-term shifts in global environmental factors. These factors encompass rising atmospheric CO_2 levels, more frequent or severe droughts, and elevated temperatures. For example, results from Costa Rica indicate that lianas have increased as a consequence of less rainfall and higher temperatures during the dry season in La Selva Biological Station, while in the San Emilio Forest Dynamics Plot, the relative abundance of lianas has increased along with the abundance of deciduous, compound-leaved and canopy tree species driven by changes in precipitation (Enquist & Enquist, 2011; Yorke et al., 2013). Similarly, static spatial analyses have found that lianas dominance over trees is enhanced by increased temperature and decreased precipitation (DeWalt et al., 2010, 2015; Ngute et al., 2024). Yet, the large increase in lianas in these undisturbed forests, are not directly expected from such spatial pattern analyses.

Our research showed an increasing trend of liana metrics in old-growth, secondary and disturbed forests (2.0%, 1.1%, and 1.8% per year, respectively)—with only old-growth forests showing an effect size that did not overlap with zero—This is surprising as previous work correlating liana abundance with disturbance using static data have found strong positive and significant correlations (Dewalt et al., 2000; Mumbanza et al., 2022; Ngute et al., 2024; Silva Magnago et al., 2017). While it is well known that static and dynamic analyses may not always align (Damgaard, 2019; Detto et al., 2019; Johnson & Miyanishi, 2008), the discrepancies could also be attributed to the variety and intensity of the disturbances evaluated in different studies included here, each having distinct effects. For instance, intense anthropogenic disturbance such as cattle grazing and the extraction of forest resources for construction, fuel, or medicinal purposes, has been found to affect lianas negatively in the smallest diameter classes given the lack of suitable supports (Pandian & Parthasarathy, 2016), while recurrent natural disturbances such as hurricanes can affect the recruitment and survival of trees and lianas post-hurricane due to uprooted trees and complete defoliation of remaining vegetation, leading to increased mortality (Luke et al., 2016). Hence, we may expect different types of disturbances to create significantly different biotic and abiotic stress factors for the survival and growth of lianas. In some cases, disturbances may even surpass the optimum disturbance threshold beyond which lianas are negatively impacted (e.g., Catford et al., 2012). Therefore, a more compelling explanation for the non-significant temporal trend for lianas in secondary and disturbed forests would require longitudinal studies along the disturbance's frequency and intensity gradients as well as information about the species dominating the temporal changes, which is beyond the scope of our analysis.

4.4 | Liana increases not restricted to neotropical sites

Our results clearly illustrate a strong geographic bias in research focus, with 28 of the 39 studies originating from the Neotropics. However, despite the lower number of sites outside the Neotropics, the reported trends in the Paleo-tropics support the notion of an average global increase of lianas with 3/5 sites in Africa and 4/6 sites in the Indomalayan region showing consistently increasing trends (Figure 2). Our systematic analysis' results are thus not in line with the idea that liana increases are restricted to Neotropical forests (Wright et al., 2015). It therefore also suggests that biogeographical factors—for example, the dominance of Dipterocarpoids (less susceptible to liana proliferation) in forests of Southeastern Asia, and the loss of frugivores favoring wind-dispersed lianas in Neotropical forests through the reduced dispersion of tree seeds (see Smith et al., 2017; Wright et al., 2015)—are not supported as drivers of lianas trends at the pantropical scale. We note, however, that an overall average net increase in liana abundance does not preclude the existence of varying local trends. Across all regions, we observed a spectrum of trends, from decreasing to stable and increasing. This simply shows that local factors can override the hypothesized global drivers of liana change, and often play a significant role in determining liana abundance. Such local factors could plausibly account for the decreasing or stable liana trends observed in certain tropical regions (e.g., Bongers et al., 2020; but see Coverdale et al., 2021).

4.5 | Perspectives

Our findings show that there are increasing liana trends in forests across the pan-tropics. However, it is important to clarify that our estimates of increase should be considered an average rate of increase observed between 1976 and 2022—rather than a projection for future increase—as many of the liana metrics considered here should saturate over time (e.g., liana canopy area). In addition, some topics are worth further exploration and would help to disentangle the causal mechanisms behind lianas temporal trends. First, incorporating variables like liana functional types (e.g., light-demanding vs. shade-tolerant traits) and climbing mechanisms into primary studies would significantly enhance our understanding of whether specific liana species are behind the observed changes in abundance. Moreover, comprehensive studies covering the full life cycle of lianas, from their establishment on the forest floor to their ascent into the canopy (i.e., Figure 1), are essential. Such research would, for instance, help elucidate the point at which global influences outweigh local successional dynamics as determinants of temporal changes in liana populations, given the critical role these variables play in liana successional trends (Bongers et al., 2020; Caballé & Martin, 2001; Ceballos & Malizia, 2017; Gerwing, 2004). Second, quantifying trends in metrics related to lianas sexual and asexual reproduction (i.e., seeds and flowers vs. clonal tillers) would allow to confirm if clonal colonization is indeed the driver of increasing liana trends as has been hypothesized previously (Ledo & Schnitzer, 2014; Yorke et al., 2013). Third, a better estimation of lianas trends relative to trees would further improve the quantification of long-term liana impacts on carbon storage. Our preliminary estimate with a condensed dataset of 18 studies featuring simultaneous paired observations of trees and lianas at identical life stages suggest opposite trends between lianas and trees (see Figure 3), but the fact that most of the studies included in this review reported measurements exclusively for lianas precluded a better estimation of the relative trend. Finally, conclusions regarding Afrotropical sites unsurprisingly remain highly dependent on individual studies as shown by the change from an increasing to a decreasing (but still non-significant) liana trend in the Afrotropical region when excluding the study by Caballé and Martin (2001) (Supplementary Appendix G). Clearly, additional long-term research in paleo-tropical sites should be encouraged as it is necessary to comprehensively assess the extent, geographic patterns, and drivers of liana change.

5 | CONCLUSION

This study is the first evidence-based systematic approach demonstrating that lianas are increasing globally in tropical forests documented through a wide variety of metrics that can be unified within a cohesive population ecological framework. Our results reveal that lianas are increasing in old-growth tropical forests where local successional dynamics appear to favor sustained liana increase, notably biomass accruement of potential canopy lianas and clonal reproduction in the understory. The quantified global increase in lianas presented in this analysis suggests that their proliferation is driven by global factors modified by local conditions.

Given the ongoing sustained change in global factors linked to liana proliferation—such as increasing atmospheric CO_2 levels, more frequent and severe droughts, and higher turnover rates in tropical forests—it's reasonable to anticipate a continuation of the liana proliferation trend rather than a halt in the near future. The documented effects of this shift in forest composition on biodiversity and carbon storage further underscore that earlier concerns regarding lianas' impact on the global carbon cycle are significant and valid.

AUTHOR CONTRIBUTIONS

Manuela A. Rueda-Trujillo: Data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Michiel P. Veldhuis:** Conceptualization; methodology; supervision; writing – original draft; writing – review and editing. **Peter M. van Bodegom:** Methodology; supervision; writing – original draft; writing – review and editing. **Hannes P. T. de Deurwaerder:** Writing – review and editing. **Marco Visser:** Conceptualization; methodology; supervision; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at http://doi.org/10.5281/zenodo.10787951.

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