Mechanisms and Ecological Effects of Excessive Liana Increases in Forests: Postprint

Authors: Song Shuling, Yi Lingli, Zhang Lilong, Chen Lin, Yu Zeping, Song Qingni, Luan Fenggang, Fang Xiong, Liu Jun

Date: 2022-06-29T00:00:00+00:00

Abstract

Woody lianas constitute an integral component of forest species diversity maintenance; however, the recent excessive increase in liana abundance within tropical and subtropical forests, particularly secondary forests, has emerged as a threat to forest recovery and healthy development, a phenomenon that has received inadequate attention. To date, no domestic research has provided a comprehensive synthesis of the phenomenon of excessive liana abundance in forests, its increasing mechanisms, and ecological effects. This paper reviews relevant literature from China and abroad, analyzing and summarizing the mechanisms underlying liana abundance increase and its ecological consequences, with the aim of providing a scientific basis for macro-level decision-making in forest management and restoration. Synthesizing relevant research indicates that: (1) The increase in liana abundance is associated with meteorological drought, rising atmospheric CO_2 concentrations, natural disturbances, and forest fragmentation. Under changing environmental conditions, lianas possess competitive advantages over trees in morphology, behavior, and physiology, manifested as faster growth rates, stronger reproductive capacity, plasticity, and efficient resource acquisition. (2) Lianas primarily affect trees through shading stress, resource competition, and mechanical pressure and damage. (3) Excessive liana increase impedes tree growth and reproduction and induces tree mortality at the individual level; at the community level, it alters species composition and reduces diversity; at the ecosystem level, it decreases forest carbon storage and modifies carbon, mineral nutrient, and water cycling processes. Based on these findings, we recommend integrating long-term field monitoring with controlled experiments to investigate the relationships between liana population dynamics and environmental changes, the effects of forest disturbance on liana growth, liana responses and adaptation mechanisms to environmental changes, and ecological effect assessments of excessive liana abundance. Simultaneously, reasonable

methods for liana management and control in forests should be actively explored.

Full Text

Preamble

Mechanisms and Ecological Consequences of the Over-increase of Lianas in Forests

SONG Shuling[1,2], YI Lingli[3], ZHANG Lilong[3], CHEN Lin[3], YU Zeping[3], SONG Qingni[1,2], LUAN Fenggang[1], FANG Xiong[4], LIU Jun[1*]

[1]College of Forestry, Jiangxi Agricultural University, Nanchang 330045, China
[2]Jiangxi Provincial Key Laboratory for Bamboo Germplasm Resources and Utilization, Jiangxi Agricultural University, Nanchang 330045, China
[3]Administration of Jiangxi Guanshan National Nature Reserve, Yichun 336300, Jiangxi, China
[4]College of Land Resources and Environment, Jiangxi Agricultural University, Nanchang 330045, China

Abstract: Lianas are essential components of forest species diversity, yet their recent over-increase in tropical and subtropical forests—particularly secondary forests—threatens forest restoration and healthy development, a phenomenon that has received insufficient attention. To date, no domestic study has comprehensively examined the phenomenon of excessive liana abundance, its underlying mechanisms, and ecological consequences. This paper reviews relevant literature to analyze and synthesize current understanding of liana increase mechanisms and ecological effects, aiming to provide scientific guidance for forest management and restoration. Based on existing research, we conclude that: (1) Liana proliferation correlates with meteorological drought, rising atmospheric CO_2 concentrations, natural disturbances, and forest fragmentation. Under changing environmental conditions, lianas possess competitive advantages over trees in morphology, behavior, and physiology, manifested as faster growth rates, stronger reproductive capacity, greater phenotypic plasticity, and efficient resource acquisition. (2) Lianas impact trees primarily through shading stress, resource competition, and mechanical pressure or damage. (3) At the individual level, excessive liana increase hinders tree growth, reproduction, and survival; at the community level, it alters species composition and reduces diversity; and at the ecosystem level, it decreases forest carbon storage and modifies carbon, mineral nutrient, and water cycling processes. Based on these findings, we recommend future research combining long-term field monitoring with controlled experiments to investigate liana population dynamics in relation to environmental change, forest disturbance effects on liana growth, liana responses and adaptive mechanisms to environmental change, and ecological consequence assessments. Simultaneously, we should actively explore rational management strategies for controlling excessive liana proliferation.

Keywords: disturbance, global change, forest health, forest management, Guanshan Nature Reserve

Funding: National Natural Science Foundation of China (42067050, 32060319); Jiangxi Provincial "Thousand Talents Program" for Young Innovative Leading Talents (jxsq2020101079); Jiangxi Provincial Graduate Innovation Program (YC2017-S199)

Corresponding Author: LIU Jun, Ph.D., Associate Professor, Research Interests: Forest Ecology, E-mail: ljaim99@163.com

---

Lianas are plant groups that cannot stand upright independently and grow by using their main stems or climbing organs, characterized by a higher length-to-diameter ratio compared to trees (Schnitzer & Bongers, 2002). As common components of forest communities, lianas play important roles in maintaining community structure and function (Schnitzer & Bongers, 2002). However, when forests experience severe disturbance, excessive liana proliferation threatens forest health by suppressing tree growth, simplifying community structure, and reducing species diversity, thereby severely impacting forest ecosystem function (Schnitzer & Bongers, 2011). This issue has attracted widespread attention from international scholars.

International researchers have long recognized the increasing abundance of lianas and their negative impacts, conducting extensive studies on liana distribution patterns (Schnitzer, 2005), population dynamics (Addo-Fordjour et al., 2021), monitoring methods (van der Heijden et al., 2022), liana-tree interactions (Leonor et al., 2015), and the mechanisms and ecological consequences of liana increase (Schnitzer & Bongers, 2011; de Azevedo Amorim et al., 2018; Marshall et al., 2020; Reis et al., 2020; Meunier et al., 2021a). In contrast, Chinese researchers have primarily focused on the positive aspects of lianas, such as forest diversity (Hu et al., 2010; Wang et al., 2014), economic value (Ji et al., 2008), and ecological functions (Zhang et al., 2007). Due to difficulties in field identification and survey, lianas are often overlooked in many studies. In reality, excessive liana proliferation is common in many forests across southern China, particularly in secondary forests. For instance, in some nature reserve secondary forests, lianas form blanket-like coverage that severely hinders forest restoration, turning forest protection policies into "liana protection policies" [Figure 1: see original paper].

Domestic research on liana impacts remains limited. Guan (1980) early reported on vine damage in plantations and its control, but this received little response. Chen et al. (2007) reviewed liana ecological functions in tropical forests, while others evaluated specific liana species impacts (Wang et al., 2009). Subsequent studies examined liana effects on forest species diversity, community structure, and regeneration (Hao et al., 2011; Wang et al., 2020), liana-tree relationships (Lu et al., 2021), and trait comparisons between lianas and trees (Chen et al., 2021). However, no comprehensive domestic study has yet integrated the phenomenon, mechanisms, and ecological effects of excessive liana abundance.

Therefore, to raise awareness of liana over-increase and its impacts, this paper synthesizes international and domestic research progress, focusing on analyzing the mechanisms of liana proliferation, elaborating on its potential ecological consequences, and proposing new research directions to inform management strategies and policy development.

[Figure 1: see original paper] Liana *Uncaria rhynchophylla* blanketing trees in Guanshan National Nature Reserve, Jiangxi province (Photos from Song Shuling, 2019)

1 Over-increase of Lianas in Forests

Although lianas contribute to forest species diversity maintenance (Schnitzer & Bongers, 2002) and provide economic, medicinal, and ecological functions (Zhang et al., 2007; Liu et al., 2021), as well as serving as habitat, corridors, and important food sources for many animals (Adams et al., 2016, 2019; Odell et al., 2019), their positive roles transform into negative impacts when the liana-to-tree ratio exceeds critical thresholds. In secondary or fragmented forests, excessive liana proliferation impedes forest succession and regeneration (Marshall et al., 2020). We define "liana over-increase" as the relative or absolute increase in liana abundance caused by environmental changes that negatively impacts local forest ecosystems.

Liana increase manifests through rising abundance (density), basal area, biomass, richness, and degree of tree infestation (Wright et al., 2004; Ingwell et al., 2010; Laurance et al., 2014; Wright et al., 2016). Phillips et al. (2002a) first documented this phenomenon in Amazonian forests, analyzing 47 non-fragmented tropical rainforest plots across four regions and finding significant increases in large liana (DBH $ $10 cm) relative basal area, relative abundance, and tree mortality risk over 20 years. Subsequent studies have reported similar trends. For example, in a fire-disturbed lowland rainforest in Nigeria, climbing plant species increased from 49 to 61 between 2005-2014, with density rising from 448-1,152 to 1,712-4,492 individuals per hectare (Uwalaka & Muoghalu, 2017). Temperate forests have also experienced liana increases, with understory liana frequency rising nearly 39% in European temperate forests between 1967-2007 (Perring et al., 2020). While some studies report different findings (Smith et al., 2017; Bongers et al., 2020; Umaña et al., 2020), most evidence indicates increasing liana trends. In China' s tropical and subtropical secondary forests, lianas such as *Merremia boisiana* in tropical forests and *Uncaria rhynchophylla* and *Pueraria lobata* in subtropical forests form extensive coverage, severely affecting local forest health (field observations, [Figure 1: see original paper]).

2 Mechanisms of Liana Over-increase

Research suggests that increasing liana dominance in forest communities relates to environmental changes, primarily global climate change, natural disturbances (e.g., gap formation), and anthropogenic disturbances such as deforestation that cause forest fragmentation and secondary succession [Figure 3: see original paper]. Lianas can adjust and adapt to these changes, possessing superior physiological, structural, and behavioral traits compared to trees.

2.1 Meteorological Drought

Studies demonstrate strong relationships between liana populations and precipitation-evaporation dynamics. Liana abundance, richness, and biomass decrease with increasing rainfall and soil moisture, while increasing with drought severity and duration (Schnitzer, 2005; Swaine & Grace, 2007). In Panama' s dry forests, liana density and richness are absolutely and relatively higher than in wet forests (Parolari et al., 2020).

Under drought conditions, lianas exhibit superior growth and physiological performance compared to trees. Liana growth exceeds tree growth by 2-fold during rainy seasons and up to 7-fold during dry seasons (Schnitzer & van der Heijden, 2019), with greater carbon accumulation in dry seasons (van der Heijden et al., 2019). Liana seedlings also show higher survival than tree seedlings under reduced rainfall (Umaña et al., 2019). Furthermore, lianas demonstrate superior water use efficiency, hydraulic conductivity, and resource acquisition strategies (Cai et al., 2009; Zhu & Cao, 2009; Medina-Vega et al., 2021a; Medina-Vega et al., 2021b). While tropical rainforest trees exhibit a trade-off between hydraulic safety and efficiency, lianas do not, suggesting greater drought tolerance through strong conductive capacity and embolism resistance (van der Sande et al., 2019).

Liana components also show strong plasticity and adaptability under drought. During dry seasons, lianas exhibit stronger leaf osmotic adjustment than trees, conferring growth advantages under intensifying drought (Maréchaux et al., 2017). Smith-Martin et al. (2019) found that dry-season irrigation significantly increased tree diameter and biomass but did not affect lianas, indicating stronger liana adaptability to drought. Additionally, lianas possess well-developed root vascular systems for efficient nutrient transport and allocation. Their long, complex root systems can extend up to 10 m deep (Restom & Nepstad, 2004), accessing water from various sources to effectively mitigate drought stress (Chen et al., 2015). Thus, under global drought intensification, liana morphological, physiological, and behavioral advantages can drive their relative and absolute abundance increases.

2.2 Rising Atmospheric CO_2 Concentration

Continuously increasing atmospheric CO_2 concentration represents a potential driver of liana proliferation. Elevated CO_2 benefits liana growth (Granados &

Korner, 2002). When CO_2 concentration increased, *Hedera helix* showed nearly 60% increases in shoot length and biomass (Zotz et al., 2006). CO_2 enrichment experiments also revealed that temperate forest liana *Toxicodendron radicans* exhibited significantly higher growth rates, photosynthesis, and water use efficiency compared to ambient conditions (Mohan et al., 2006). Lianas respond more rapidly to CO_2 increases than trees (Belote et al., 2004), with higher leaf-to-stem ratios and lower leaf construction costs per unit area, providing advantages in CO_2 absorption and fixation (Zhu & Cao, 2010).

2.3 Natural Disturbances

Natural disturbances such as ice storms, fires, and tree mortality promote liana proliferation in forest gaps. Liana abundance and richness are typically significantly higher in gaps than non-gap areas (Schnitzer & Carson, 2001). Gaps provide fertile soil, enhanced light, and increased niche availability, creating favorable conditions for liana growth. Many lianas exhibit rapid growth and strong reproductive capacity in gaps, enhancing their dominance. By reducing investment in support structures, lianas allocate most resources to rapid stem growth and leaf accumulation (Putz, 1984). Besides seed germination, lianas can reproduce clonally in gaps through underground and stoloniferous stems that continuously produce new shoots, increasing individual numbers (Schnitzer et al., 2021). Even when host trees collapse, many lianas can resprout and reclimb to the canopy, increasing absolute or relative abundance (Rocha et al., 2020).

2.4 Forest Fragmentation

Anthropogenic disturbances such as deforestation and hunting cause forest fragmentation and secondary succession, increasing lianas along forest edges and in secondary forests. Fragmentation creates drier conditions, fertile soil, increased light, and shorter vegetation, all facilitating liana climbing and rapid growth. Consequently, liana growth rates and individual numbers are faster and greater at forest edges and in secondary forests (Ladwig & Meiners, 2010; Roeder et al., 2019), with higher liana richness and carbon storage at edges compared to interiors (Londré & Schnitzer, 2006; Magnago et al., 2017; Campbell et al., 2018). Forest fragmentation also creates conditions for clonal growth; in a selectively logged tropical rainforest in La Selva, long-distance clonal reproduction contributed 7.5% to liana abundance increase and 60% to basal area increment (Yorke et al., 2013).

3 Liana Competition Mechanisms with Trees

3.1 Shading Stress

Lianas climb into tree canopies using stems, branches, and leaves, causing extensive shading that reduces light availability for trees, impeding photosynthesis and affecting growth and development, potentially causing tree death [Figure

2A: see original paper]. Liana canopy coverage increases stand density, hindering understory seedling regeneration. In Panama' s tropical forests, severe liana canopy coverage doubled tree mortality (Ingwell et al., 2010) and reduced gap tree regeneration by 46% (Schnitzer & Carson, 2010). With longer leaf phenology and many species remaining evergreen year-round (Putz & Windsor, 1987), persistent shading can cause understory seedling death due to insufficient light.

3.2 Resource Competition

Lianas and trees compete intensely for light, water, and nutrients (Meunier et al., 2021b). After liana removal, tree sap flow rates increased by 60% (Leonor et al., 2015). Liana-tree competition for mineral nutrients and water can be even stronger than tree-tree competition. Tree sap flow rates increased approximately 8% after liana removal but showed no response to tree removal (Tobin et al., 2012). Lianas possess higher resource absorption, transport, and use efficiency, with higher leaf-level carbon assimilation rates and light absorption/utilization than trees (Cai et al., 2009; Asner & Martin, 2012), and have well-developed root systems (Collins et al., 2016). When soil nutrients increase, liana leaf area ratio and photosynthetic capacity are significantly higher than those of trees (Cai et al., 2008; Pasquini et al., 2015).

3.3 Mechanical Pressure and Damage

Liana climbing exerts mechanical pressure and damage on trees (Vleut & Pérez-Salicrup, 2005). Extensive canopy coverage creates substantial loading, making tree tops or branches prone to breakage while hindering new shoot emergence, resulting in "topped" or "stilted" trees. Twining lianas can cause trunk distortion and indentation, increasing breakage and pest/disease risks, impairing water and nutrient transport, and ultimately causing tree death [Figure 2B: see original paper].

[Figure 2: see original paper] A. Liana *U. rhynchophylla* climbing *Cunninghamia lanceolata* crowns with 90% coverage; B. Liana causing tree death by twining tree stem.

4 Ecological Consequences of Liana Over-increase

4.1 Impeding Tree Growth and Development

At the individual level, liana over-increase: (1) impedes tree growth, reducing tree growth by 156% and biomass accumulation by 209% (Finlayson et al., 2022). Song (2019) found that *Cunninghamia lanceolata* climbed by lianas showed 29% and 40% reductions in annual radial and basal area growth, respectively. (2) Increases tree mortality—large trees in Amazonian lowland rainforest showed >2-fold mortality increase after liana infestation (Phillips et al., 2005). (3) Reduces fruiting rate and quantity—tree fruiting correlates negatively with liana coverage in tropical forests (Nabe-Nielsen et al., 2009), with lianas reducing nut-producing tree fruit yield by 2-fold (Kainer et al., 2014).

Lianas also negatively affect seedlings and saplings. For example, lianas reduced tree seedling leaf area by 5-fold. Martínez-Izquierdo et al. (2016) planted 14 tree species in liana-cleared and control plots, finding lianas reduced seedling survival and height growth by 75% and 300%, respectively. Schnitzer et al. (2005) planted three shade-tolerance sapling types in liana-dense lowland rainforest, finding lianas altered biomass allocation patterns and tree architecture after two years. Thus, liana impacts extend throughout the entire tree life cycle.

4.2 Altering Community Composition and Structure

At the community level: (1) Liana over-increase alters species composition. Differential impacts among tree species can shift community composition (Visser et al., 2018b; Reis et al., 2020). In Ghana' s tropical evergreen-deciduous mixed forest, lianas reduced pioneer species *Nauclea diderichii* and *Khaya anthotheca* biomass to 32% and 50%, respectively, while not affecting shade-tolerant non-pioneer *Garcinia kola* (Toledo-Aceves & Swaine, 2008). (2) Liana over-increase hinders community regeneration, reduces species diversity, and alters community structure. Lianas reduce tree reproductive capacity, decreasing flowering and fruiting individuals, flower quantity, and fruit yield (García León et al., 2018). Schnitzer & Carson (2010) found lianas reduced gap tree regeneration and diversity by 46% and 65%, respectively. Differential impacts on trees of different DBH classes also alter community structure (Estrada-Villegas et al., 2020).

4.3 Affecting Ecosystem Functions

At the ecosystem level, liana over-increase affects forest carbon sink function. In Panama' s tropical forest, liana interference reduced tree biomass increment by 22% over five years, with model predictions suggesting 32% and 47% reductions after 30 and 60 years, respectively (Lai et al., 2017). Liana removal experiments validated these models—in a 60-year-old tropical forest, lianas reduced aboveground net biomass accumulation by 76%, with tree biomass increment decreasing by 48% (van der Heijden et al., 2015). Similar results emerged from other monitoring, modeling, and removal studies (di Porcia e Brugnera et al., 2019; van der Heijden et al., 2019; Estrada-Villegas et al., 2020; Meunier et al., 2021a). Although liana biomass increased, this increment compensated for <30% of tree biomass loss (Schnitzer et al., 2016; Lai et al., 2017).

Liana over-increase also alters forest water dynamics. Despite comprising only 5% of tropical forest basal area, lianas account for 12% of total forest leaf transpiration (Restom & Nepstad, 2001). Lianas exhibit advantages in water uptake, transport, and use (Andrade et al., 2005; Cai et al., 2009; Zhu & Cao, 2010; Chen et al., 2015) and affect tree water balance, reducing tree sap flow rates by nearly half (Campanello et al., 2016).

Furthermore, liana over-increase modifies mineral nutrient dynamics. High leaf production ratios (Schnitzer & Bongers, 2002; Kusumoto & Enoki, 2008) and distinct leaf properties alter forest nutrient dynamics and soil physicochemical properties. Tropical forest liana leaf biomass comprises up to 36% of aboveground biomass (Gerwing & Farias, 2000), with litter production and leaf area accounting for 40% of totals (Schnitzer & Bongers, 2002). Liana nutrient content (e.g., nitrogen, phosphorus) significantly exceeds that of tree leaves (Asner & Martin, 2012). Thus, liana over-increase may accelerate leaf litter decomposition and nutrient release, alter soil nutrient status and respiration rates, and increase soil nutrient heterogeneity and leaching risks (Putz, 1984; Kusumoto & Enoki, 2008; Liu et al., 2017).

[Figure 3: see original paper] Mechanisms and ecological consequences of liana over-increase

5 Research Prospects

Although increasing research focuses on liana impacts, current understanding of proliferation mechanisms and evaluation remains incomplete, with many unresolved questions. Based on the above synthesis, we propose future research directions.

5.1 Emphasize Liana Mapping in Forest Dynamics Monitoring Plots

Long-term monitoring is crucial for understanding population and community dynamics. Overall, liana mapping studies started late, cover limited regions, and operate at small scales. Many forest dynamics monitoring networks have not incorporated lianas (Schnitzer & Bongers, 2011), with major studies concentrated in Central and South American tropical forests (Brazil, Panama, Mexico), few in Africa, and minimal participation from other continents. Subtropical and temperate forest liana studies are particularly lacking (Schnitzer et al., 2015). Future forest dynamics monitoring should include lianas, especially expanding Asian and African sites to understand global distribution patterns and dynamics. Given field identification and data collection difficulties, we recommend remote sensing information technology applications (Waite et al., 2019; Chandler et al., 2021).

5.2 Strengthen Research on Environmental Change and Liana Population Dynamics

Existing research preliminarily explores climate change and disturbance effects on liana increase, but studies remain fragmented and independent, with unclear mechanisms. Recommended research includes: (1) Individual and synergistic effects of factors on liana dynamics, particularly large-scale relationships between atmospheric CO_2 changes and liana abundance (Schnitzer & Bongers, 2011). (2) Mechanisms of liana increase following forest disturbance, integrating disturbance regimes, ecological factors, and liana biological/physiological characteristics to analyze regeneration and diversity maintenance mechanisms, with comparative studies across disturbance types. (3) Liana responses to environmental change—adaptation to changing environments is key to competitive advantage, requiring investigation of physiological, behavioral, and functional trait adaptations (Liu et al., 2021), combined with controlled experiments simulating multiple environmental factors (light, CO_2, water) effects on liana growth, physiology, and behavior.

5.3 Construct Evaluation Systems for Liana Increase Ecological Effects

Evaluating liana impacts forms the basis for management policy. While liana over-increase negatively affects individual, population, community, and ecosystem levels, research remains insufficient. Key gaps include: (1) Limited large-scale, long-term studies. Liana impacts relate closely to forest type and age (Lai et al., 2017; Estrada-Villegas et al., 2021), with most studies in tropical forests, insufficient research in other regions, and few long-term studies. Future work should evaluate liana impacts across multiple regions and forest types at large spatiotemporal scales. (2) Incomplete ecological effect evaluation, focusing mainly on individual-level impacts with single indicators (e.g., DBH growth), while lacking studies on forest biomass, ecosystem material cycling, and productivity. Model-based approaches are recommended for comprehensive ecosystem impact assessment (di Porcia e Brugnera et al., 2019; Meunier et al., 2022). In southern China' s nature reserve secondary forests, excessive liana proliferation severely hinders restoration, warranting studies on potential ecosystem function impacts. (3) Liana-tree relationship studies typically treat both as uniform groups, yet different tree species show varying susceptibility (Visser et al., 2018b) and different lianas exert species-specific pressures (Muller-Landau et al., 2018), making accurate impact quantification difficult. Research on tree responses to liana infestation and environmental effects on liana-tree interactions remains limited. (4) Liana-forest animal relationships receive insufficient attention. Animals are crucial ecosystem components—lianas provide important food resources (Odell et al., 2019) and increase animal diversity (Schnitzer et al., 2020), but negative liana effects on trees reduce animal food sources (Adams et al., 2016; García León et al., 2018). Key questions include: What is the net impact of lianas on animals? How does liana increase affect different animal species/types? How does animal herbivory influence liana population dynamics? Do these interactions vary by forest type and region? Future research should systematically and quantitatively evaluate these questions (Schnitzer, 2018; Coverdale et al., 2021).

5.4 Integrate Liana Conservation with Over-increase Management

While excessive liana proliferation causes negative impacts, lianas are components of forest biodiversity, include rare and endangered species, possess economic and ornamental value, and can form mutualistic relationships with trees that aid forest restoration under certain conditions. Large liana abundance also serves as an indicator of primary forest health. Future research should balance liana conservation and control based on forest restoration and protection goals. Lianas should be protected in ecologically sound areas but appropriately removed in severely affected forests. However, developing new management technologies presents a major challenge—current approaches are often one-size-fits-all, labor-intensive, costly, and ineffective (Pérez-Salicrup et al., 2001). Questions of where, how, and how effectively to remove lianas require in-depth study to develop rational management methods that provide scientific guidance for forest management and ecological restoration decisions.

References

ADAMS BJ, SCHNITZER SA, YANOVIAK SP. 2016. Trees as islands: canopy ant species richness increases with the size of liana-free trees in a neotropical forest[J]. *Ecography*, 40(9): 001-010.

ADAMS BJ, SCHNITZER SA, YANOVIAK SP. 2019. Connectivity explains local ant community structure in a neotropical forest canopy: a large-scale experimental approach[J]. *Ecology*, 100(6): e02673.

ADDO-FORDJOUR P, L, OFOSU-BAMFO B, et al., 2021. Temporal dynamics of liana communities in moist semi-deciduous forest stands with different management histories in Ghana[J]. *For Ecol Manag*, 489, 119042.

ANDRADE JL, MEINZER FC, GOLDSTEIN G, et al., 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest[J]. *Trees*, 19(3): 282-289.

ASNER GP, MARTIN RE. 2012. Contrasting leaf chemical traits in tropical lianas and trees: implications for future forest composition[J]. *Ecol Lett*, 15(9): 1001-1007.

BELOTE RT, WELTZIN JF, NORBY RJ. 2004. Response of an understory plant community to elevated [CO_2] depends on differential responses of dominant invasive species and is mediated by soil water availability[J]. *New Phytol*, 161(3): 827-835.

BONGERS F, EWANGO CEN, VAN DER SANDE MT, et al., 2020. Liana species decline in Congo basin contrasts with global patterns[J]. *Ecology*, 101(5): e03004.

CAI ZQ, BONGERS F. 2007. Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China[J]. *J Trop Ecol*, 23(1): 115-118.

CAI ZQ, POORTER L, HAN Q, et al., 2008. Effects of light and nutrients on seedlings of tropical *Bauhinia* lianas and trees[J]. *Tree physiol*, 28(8): 1277-1285.

CAI ZQ, SCHNITZER SA, BONGERS F. 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest[J]. *Oecologia*, 161(1): 001-010.

CAMPBELL MJ, EDWARDS W, MAGRACH A, et al., 2018. Edge disturbance drives liana abundance increase and alteration of liana-host tree interactions in tropical forest fragments[J]. *Ecol Evol*, 8(8): 4237-4251.

CHANDLER CJ, VAN DER HEIJDEN GMF, BOYD DS, et al., 2021. Remote sensing liana infestation in an aseasonal tropical forest: addressing mismatch in spatial units of analyses[J]. *Remote Sens Ecol Con*, 7(3): 397-410.

CHEN YJ, CHOAT B, STERCK F, et al., 2021. Hydraulic prediction of drought-induced plant dieback and top-kill depends on leaf habit and growth form[J]. *Ecol Lett*, 24(11): 2350-2363.

CHEN YJ, CAO KF, SCHNITZER SA, et al., 2015. Water-use advantage for lianas over trees in tropical seasonal forests[J]. *New Phytol*, 205(1): 128-136.

COLLINS CG, WRIGHT SJ, WURZBURGER N. 2016. Root and leaf traits reflect distinct resource acquisition strategies in tropical lianas and trees[J]. *Oecologia*, 180(4): 1037-1047.

COVERDALE TC, O' CONNELL RD, HUTCHINSON MC, et al., 2021. Large herbivores suppress liana infestation in an African savanna[J]. *Proc Natl Acad Sci USA*, 118(41): 001-010.

DE AZEVEDO AMORIM T, NUNES-FREITAS AF, ROSADO BHP. 2018. Revisiting the hypothesis for increasing liana abundance in seasonal forests: a theoretical review[J]. *Plant Soil*, 430(1): 1-6.

DI PORCIA E BRUGNERA M, MEUNIER F, LONGO M, et al., 2019. Modeling the impact of liana infestation on the demography and carbon cycle of tropical forests[J]. *Global Change Biol*, 25(11): 3767-3780.

ESTRADA-VILLEGAS S, HALL JS, VAN BREUGEL M, et al., 2020. Lianas reduce biomass accumulation in early successional tropical forests[J]. *Ecology*, 101(5): e02989.

ESTRADA-VILLEGAS S, HALL JS, VAN BREUGEL M, et al., 2021. Lianas do not reduce tree biomass accumulation in young successional tropical dry forests[J]. *Oecologia*, 195(4): 001-010.

FINLAYSON C, ROOPSIND A, GRISCOM BW, et al., 2022. Removing climbers more than doubles tree growth and biomass in degraded tropical forests[J]. *Ecol Evol*, 12(3): e8758.

GARCíA LEóN MM, MARTíNEZ IZQUIERDO L, MELLO FNA, et al., 2018. Lianas reduce community-level canopy tree reproduction in a Panamanian forest[J]. *J Ecol*, 106(2): 737-745.

GERWING JJ, FARIAS DL. 2000. Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest[J]. *J Trop Ecol*, 16(3): 327-335.

GRANADOS J, KORNER C. 2002. In deep shade, elevated CO_2 increases the vigor of tropical climbing plants[J]. *Global Change Biol*, 8(11): 1109-1117.

GUAN L. 1980. Damage of vines in forest plantations and of their control and management[J]. *J Jilin Fore Sci Tech*, (4): 120-121.

GOLDSTEIN G, SANTIAGO LS. 2016. Carbon allocation and water relations of lianas versus trees[M]// *Tropical Tree Physiology*. Switzerland: Springer: 103-124.

HAO JH, TAO JP, ZHAO K, et al., 2011. The effects of lianas on community structure and regeneration of *Vatica astrotricha* plantations in Bawangling Nature Reserve, Hainan province, China[J]. *J SW Univ (Nat Sci)*, 33(2): 34-39.

HU L, LI MG, LI Z. 2010. Geographical and environmental gradients of lianas and vines in China[J]. *Global Ecol Biogeogr*, 19(4): 554-561.

INGWELL LL, WRIGHT SJ, BECKLUND KK, et al., 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama[J]. *J Ecol*, 98(4): 879-887.

JI MC, ZHEN G, YU SG. 2008. Resources and landscape application of wild vine in Longwangshan national nature reserve, Zhejiang province[J]. *Sci Silv Sin*, 44(9): 165-169.

KAINER KA, WADT LHO, STAUDHAMMER CL. 2014. Testing a silvicultural recommendation: Brazil nut responses 10 years after liana cutting[J]. *J Appl Ecol*, 51(3): 655-663.

KUSUMOTO B, ENOKI T. 2008. Contribution of a liana species, *Mucuna macrocarpa* Wall., to litterfall production and nitrogen input in a subtropical evergreen broad-leaved forest[J]. *J For Res*, 13(1): 35-42.

LADWIG LM, MEINERS SJ. 2010. Spatiotemporal dynamics of lianas during 50 years of succession to temperate forest[J]. *Ecology*, 91(3): 671-680.

LAI HR, HALL JS, TURNER BL, et al., 2017. Liana effects on biomass dynamics strengthen during secondary forest succession[J]. *Ecology*, 98(4): 1062-1070.

LAURANCE WF, ANDRADE AS, AINHOA M, et al., 2014. Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian forests[J]. *Ecology*, 95(6): 001-010.

LEONOR AC, SCHNITZER SA, REID JP, et al., 2015. Liana competition with tropical trees varies seasonally but not with tree species identity[J]. *Ecology*, 96(1): 39-45.

LIU Q, STERCK FJ, ZHANG J-L, et al., 2021. Traits, strategies, and niches of liana species in a tropical seasonal rainforest[J]. *Oecologia*, 196(2): 499-514.

LIU Y, ZHANG N, LUO J, et al., 2021. Chemical constituents of stems and leaves from *Uncaria rhynchophylla* in Guizhou and their antitumor activities[J]. *Guihaia*, 41(7): 1061-1069.

LIU YC, SHANG Q, ZHANG B, et al., 2017. Effects of understory liana *Trachelospermum jasminoides* on distributions of litterfall and soil organic carbon in an oak forest in central China[J]. *Sustainability*, 9(6): 1019.

LONDRé RA, SCHNITZER SA. 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years[J]. *Ecology*, 87(12): 2973-2978.

LU F, LI X K, WANG B, et al., 2021. Spatial pattern of lianas of *Litsea dilleniifolia* community and its relationship with main tree species in Nonggang, Guangxi[J]. *Acta Ecol Sin*, 41(15): 6191-6202.

MAGNAGO LFS, MAGRACH A, BARLOW J, et al., 2017. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests?[J]. *Funct Ecol*, 31(2): 542-552.

MARéCHAUX I, BARTLETT MK, IRIBAR A, et al., 2017. Stronger seasonal adjustment in leaf turgor loss point in lianas than trees in an Amazonian forest[J]. *Biol Lett*, 13(1): 20160819.

MARSHALL AR, PLATTS PJ, CHAZDON RL, et al., 2020. Conceptualising the global forest response to liana proliferation[J]. *Front For Glob Change*, 3(35).

MARTíNEZ-IZQUIERDO L, GARCíA MM, POWERS JS, et al., 2016. Lianas suppress seedling growth and survival of 14 tree species in a Panamanian tropical forest[J]. *Ecology*, 97(1): 001-010.

MEDINA-VEGA JA, BONGERS F, POORTER L, et al., 2021a. Lianas have more acquisitive traits than trees in a dry but not in a wet forest[J]. *J Ecol*, 109(6): 2367-2384.

MEDINA-VEGA JA, BONGERS F, SCHNITZER SA, et al., 2021b. Lianas explore the forest canopy more effectively than trees under drier conditions[J]. *Funct Ecol*, 35(2): 318-329.

MEUNIER F, VAN DER HEIJDEN GMF, SCHNITZER SA, et al., 2021a. Lianas significantly reduce aboveground and belowground carbon storage: a virtual removal experiment[J]. *Front For Glob Change*, 4(75).

MEUNIER F, VERBEECK H, COWDERY B, et al., 2021b. Unraveling the relative role of light and water competition between lianas and trees in tropical forests: a vegetation model analysis[J]. *J Ecol*, 109(1): 519-540.

MEUNIER F, VISSER MD, SHIKLOMANOV A, et al., 2022. Liana optical traits increase tropical forest albedo and reduce ecosystem productivity[J]. *Global Change Biol*, 28(1): 001-010.

MOHAN JE, ZISKA LH, SCHLESINGER WH, et al., 2006. Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO_2[J]. *Proc Natl Acad Sci USA*, 103(24): 9086-9089.

MULLER-LANDAU HC, VISSER MD, GODOY O. 2018. How do lianas and vines influence competitive differences and niche differences among tree species? Concepts and a case study in a tropical forest[J]. *J Ecol*, 107(3): 1469-1481.

NABE-NIELSEN J, KOLLMANN J, PEñA-CLAROS M. 2009. Effects of liana load, diameter and distances between conspecifics on seed production in tropical timber trees[J]. *For Ecol Manag*, 257(3): 987-993.

ODELL EH, STORK NE, KITCHING RL. 2019. Lianas as a food resource for herbivorous insects: a comparison with trees[J]. *Biol Rev*, 94(4): 1416-1429.

PAROLARI AJ, PAUL K, GRIFFING A, et al., 2020. Liana abundance and diversity increase with rainfall seasonality along a precipitation gradient in Panama[J]. *Ecography*, 43(1): 25-33.

PASQUINI SC, WRIGHT SJ, SANTIAGO LS. 2015. Lianas always outperform tree seedlings regardless of soil nutrients: results from a long-term fertilization experiment[J]. *Ecology*, 96(7): 001-010.

PéREZ-SALICRUP DR, CLAROS A, GUZMáN R, et al., 2001. Cost and efficiency of cutting lianas in a lowland liana forest of Bolivia[J]. *Biotropica*, 33(2): 324-329.

PERRING MP, DE FRENNE P, HERTZOG LR, et al., 2020. Increasing liana frequency in temperate European forest understories is driven by ivy[J]. *Front Ecol Evol*, 18(10): 550-557.

PHILLIPS OL, VáSQUEZ MARTíNEZ R, ARROYO L, et al., 2002a. Increasing dominance of large lianas in Amazonian forests[J]. *Nature*, 418(15): 770-774.

PHILLIPS OL, VáSQUEZ MARTíNEZ R, MONTEAGUDO MENDOZA A, et al., 2005. Large lianas as hyperdynamic elements of the tropical forest canopy[J]. *Ecology*, 86(5): 1250-1258.

PUTZ FE. 1984. The natural history of lianas on Barro Colorado Island, Panama[J]. *Ecology*, 65(6): 1713-1724.

PUTZ FE, WINDSOR DM. 1987. Liana phenology on Barro Colorado Island, Panama[J]. *Biotropica*, 19(4): 334-341.

REIS SM, MARIMON BS, MORANDI PS, et al., 2020. Causes and consequences of liana infestation in southern Amazonia[J]. *J Ecol*, 108(6): 2184-2197.

RESTOM TG, NEPSTAD DC. 2001. Contribution of vines to the evapotranspiration of a secondary forest in eastern Amazonia[J]. *Plant Soil*, 236(2): 155-163.

RESTOM TG, NEPSTAD DC. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia[J]. *For Ecol Manag*, 190(1): 109-118.

ROCHA EX, SCHIETTI J, GEROLAMO CS, et al., 2020. Higher rates of liana regeneration after canopy fall drives species abundance patterns in central Amazonia[J]. *J Ecol*, 108(4): 001-010.

ROEDER M, LIU J, PASION B, et al., 2019. Wood density, growth and mortality relationships of lianas on environmental gradients in fragmented forests of montane landscapes[J]. *J Veg Sci*, 30(6): 1143-1152.

SCHNITZER SA. 2005. A mechanistic explanation for global patterns of liana abundance and distribution[J]. *Am Nat*, 166(2): 262-276.

SCHNITZER SA. 2018. Testing ecological theory with lianas[J]. *New Phytol*, 220(2): 366-380.

SCHNITZER SA, BONGERS F. 2002. The ecology of lianas and their role in forests[J]. *Trends Ecol Evol*, 17(5): 223-230.

SCHNITZER SA, BONGERS F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms[J]. *Ecol Lett*, 14(4): 397-406.

SCHNITZER SA, BONGERS F, BURNHAM RJ, et al., 2015. Ecology of Lianas[M]// DeWalt SJ, SCHNITZER SA, Alves LF et al., Biogeographical pattern of liana abundance and diversity. Oxford: Wiley-Blackwell: 132-143.

SCHNITZER SA, CARSON WP. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest[J]. *Ecology*, 82(4): 913-919.

SCHNITZER SA, CARSON WP. 2010. Lianas suppress tree regeneration and diversity in treefall gaps[J]. *Ecol Lett*, 13(7): 849-857.

SCHNITZER SA, DEFILIPPIS DM, VISSER M, et al., 2021. Local canopy disturbance as an explanation for long-term increases in liana abundance[J]. *Ecol Lett*, 24(12): 2635-2647.

SCHNITZER SA, GEERTJE VDH, MASCARO J, et al., 2016. Lianas in gaps reduce carbon accumulation in a tropical forest[J]. *Ecology*, 95(11): 3008-3017.

SCHNITZER SA, MICHEL NL, POWERS JS, et al., 2020. Lianas maintain insectivorous bird abundance and diversity in a neotropical forest[J]. *Ecology*, 101(12): e03176.

SCHNITZER SA, MIRJAME.KUZEE, BONGERS F. 2005. Disentangling above-and below-ground competition between lianas and trees in a tropical forest[J]. *J Ecol*, 93(6): 001-010.

SCHNITZER SA, VAN DER HEIJDEN GMF. 2019. Lianas have a seasonal growth advantage over co-occurring trees[J]. *Ecology*, 100(5): e02655.

SMITH-MARTIN CM, BASTOS CL, LOPEZ OR, et al., 2019. Effects of dry-season irrigation on leaf physiology and biomass allocation in tropical lianas and trees[J]. *Ecology*, 100(11): e02827.

SMITH JR, QUEENBOROUGH SA, ALVIA P, et al., 2017. No strong evidence for increasing liana abundance in the Myristicaceae of a neotropical aseasonal rain forest[J]. *Ecology*, 98(2): 001-010.

SONG SL. 2019. Liana diversity and its effects on tree growth and community structure in Guanshan evergreen broad-leaved forest[D]. Nanchang: Jiangxi Agricultural University.

SWAINE MD, GRACE J. 2007. Lianas may be favoured by low rainfall: evidence from Ghana[J]. *Plant Ecol*, 192(2): 271-276.

TOBIN MF, WRIGHT AJ, MANGAN SA, et al., 2012. Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees[J]. *Ecosphere*, 3(2): 1-11.

TOLEDO-ACEVES T, SWAINE M. 2008. Effect of lianas on tree regeneration in gaps and forest understorey in a tropical forest in Ghana[J]. *J Veg Sci*, 19(5): 717-728.

UMAñA MN, FORERO-MONTAñA J, NYTCH CJ, et al., 2019. Dry conditions and disturbance promote liana seedling survival and abundance[J]. *Ecology*, 100(1): e02556.

UMAñA MN, MANZANé-PINZóN E, COMITA LS. 2020. Long-term dynamics of liana seedlings suggest decelerating increases in liana relative abundance over time[J]. *J Ecol*, 108(2): 001-010.

UWALAKA NO, MUOGHALU JI. 2017. Nine years of climber community dynamics in a Nigerian lowland rain forest 31 years after a ground fire[J]. *Biodivers Conserv*, 26(4): 001-010.

VAN DER HEIJDEN GMF, POWERS JS, SCHNITZER SA. 2015. Lianas reduce carbon accumulation and storage in tropical forests[J]. *Proc Natl Acad Sci USA*, 112(43): 001-010.

VAN DER HEIJDEN GMF, POWERS JS, SCHNITZER SA. 2019. Effect of lianas on forest-level tree carbon accumulation does not differ between seasons: results from a liana removal experiment in Panama[J]. *J Ecol*, 107(4): 1890-1900.

VAN DER HEIJDEN GMF, PROCTOR ADC, CALDERS K, et al., 2022. Making (remote) sense of lianas[J]. *J Ecol*, 110(3): 498-513.

VAN DER SANDE MT, POORTER L, SCHNITZER SA, et al., 2019. The hydraulic efficiency–safety trade-off differs between lianas and trees[J]. *Ecology*, 100(5): e02666.

VISSER MD, MULLER-LANDAU HC, SCHNITZER SA, et al., 2018b. A host-parasite model explains variation in liana infestation among co-occurring tree species[J]. *J Ecol*, 106(6): 001-010.

VLEUT I, PéREZ-SALICRUP DR. 2005. Lianas and their supporting plants in the understorey at Los Tuxtlas, Mexico[J]. *J Trop Ecol*, 21(5): 577-580.

WAITE CE, VAN DER HEIJDEN GMF, FIELD R, et al., 2019. A view from above: unmanned aerial vehicles (UAVs) provide a new tool for assessing liana infestation in tropical forest canopies[J]. *J Appl Ecol*, 56(4): 902-912.

WANG YS, YANG XJ, CHEN LJ, et al., 2014. Biodiversity of wild woody vine resources in Yunshan, Hunan[J]. *Acta Bot Bor-Occid Sin*, 34(3): 604-613.

WANG ZW, ZGANG KM, WU N, et al., 2020. Effect of liana on the understory species richness in deciduous broadleaf forest of Jigong Mountain in Henan[J]. *J Yunnan Agric Univ (Nat Sci)*, 35(3): 476-482.

WANG BS, PENG SL, LI DJ, et al., 2009. Research progress on *Merremia boisiana*[J]. *Chinese J Ecol*, 28(11): 2360-2365.

WRIGHT SJ, CALDERóN O, HERNANDéZ A, et al., 2004. Are lianas increasing in importance in tropical forest? A 17-year record from Panama[J]. *Ecology*, 85(2): 484-489.

WRIGHT SJ, SUN IF, PICKERING M, et al., 2016. Long-term changes in liana loads and tree dynamics in a Malaysian forest[J]. *Ecology*, 96(10): 2748-2757.

ZHANG ZY, ZHOU FX, XU GF. 2007. Application of liana in ecological restoration of side slope[J]. *Res Soil Water Conserv*, 16(4): 462-464.

ZHU SD, CAO KF. 2009. Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China[J]. *Plant Ecol*, 204(2): 295-304.

ZHU SD, CAO KF. 2010. Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern China[J]. *Oecologia*, 163(3): 591-599.

ZOTZ G, CUENI N, KOERNER C. 2006. In situ growth stimulation of a temperate zone liana (*Hedera helix*) in elevated CO_2[J]. *Funct Ecol*, 20(5): 763-769.

Note: Figure translations are in progress. See original paper for figures.