



NATURAL HISTORY FIELD NOTE

The Search for Champion Lianas: The Largest Lianas on Six Continents

¹Department of Biological Sciences, Marquette University, Milwaukee, Wisconsin, USA | ²Smithsonian Tropical Research Institute, Balboa, Panama | ³AMAP, Univ. Montpellier, IRD, CNRS, CIRAD, INRAE, Montpellier, France | ⁴Cirad, UPR Forêts et Sociétés, Montpellier, France | ⁵Olam Agri, Ouesso, Republic of the Congo | 6Manipal Centre for Natural Sciences, Centre of Excellence, Manipal Academy of Higher Education, Manipal, Karnataka, India | 7Department of Theoretical and Applied Biology, College of Science, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana | 8Yunnan Key Laboratory of Forest Ecosystem Stability and Global Change, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, China | 9Department of Agriculture and Forest Science (DAFNE), Università degli Studi della Tuscia, Viterbo, Italy | 10 Department of Environmental Technology and Management, Faculty of Environment, Kasetsart University, Bangkok, Thailand | 11 National Biobank of Thailand, National Science and Technology Development Agency, Pathum Thani, Thailand | 12 Department of Biological Sciences, Tarleton State University, Stephenville, Texas, USA | 13Forest and People Research Centre, University of the Sunshine Coast, Sippy Downs, Queensland, Australia | 14School of Geography, University of Nottingham, Nottingham, UK | 15Forestry and Forest Products Research Institute, Tsukuba, $Ibaraki, Japan + {}^{16}Department of \ Biological \ Sciences, \ University \ of \ Pittsburgh, \ Pittsburgh, \ Pennsylvania, \ USA + {}^{17}The \ Forest \ School, \ Yale \ School \ Pannsylvania, \ USA + {}^{17}The \ Forest \ School, \ Yale \ School \ Pannsylvania, \ USA + {}^{17}The \ Forest \ School, \ Yale \ School, \ Yale \ School \ Pannsylvania, \ USA + {}^{18}Department \ OSA + {}^{18}Department \ Pittsburgh, \ Pennsylvania, \ Pennsylv$ of the Environment, New Haven, Connecticut, USA | 18School of Biological Sciences, Universiti Sains Malaysia, Penang, Malaysia | 19Insituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, México | 20 Nigerian Montane Forest Project, Ngel Nyaki, Taraba State, Nigeria | 21 Department of Biology, University of Florida, Gainesville, Florida, USA | 22 Reforest Africa, Mang'ula, Tanzania | ²³Flamingo Land, Kirby Misperton, Yorkshire, UK | ²⁴Association Francis Hallé, Metz, France | ²⁵Ligue pour la Protection de Oiseaux, Rochefort, France | ²⁶Department of Ecology and Environmental Sciences, School of Life Sciences, Pondicherry University, Puducherry, India | 27Department of Ecology, French Institute of Pondicherry, Puducherry, India | 28Department of Forest Resources and Environmental Conservation, Virginia Tech, Blacksburg, Virginia, USA

Correspondence: Stefan A. Schnitzer (s1@mu.edu)

Received: 29 November 2024 | Revised: 6 September 2025 | Accepted: 29 September 2025

Associate Editor: Rhett D. Harrison | Handling Editor: Margaret Metz

Funding: Financial support for liana censuses in Panama was provided by the US National Science Foundation through grants DEB 06-13666, 08-45071, 10-19436, 12-58070, 18-22473, 20-01799, and IOS 15-58093. An Anne McLaren Fellowship from the University of Nottingham and Centre National de la Recherche Scientifique (CNRS) funding supported G.H. H.P.T.D.D. was funded by the Carbon Mitigation Initiative at Princeton University. The ForestGEO Research Grant Program sponsored the Ngel Nyaki Liana Census, supporting G.A.D. E.M. was supported by Australian Research Council grant FT17010027.

Keywords: climbing plants | maximum size | temperate forests | tropical forests | woody vines

ABSTRACT

Determining species' maximum sizes provides valuable insights into their ecology, natural history, and potential ecosystem contributions. Using both plot-based and forest-wide surveys on six continents, we document the largest "Champion" liana ever recorded (866 mm diameter) from an African forest, as well as continental Champions Lianas from around the world.

© 2025 Association for Tropical Biology and Conservation.

1 | Introduction

The largest individuals in a community play a critical role in ecosystem structure and function. In forests, for example, the largest trees contribute disproportionately to ecosystem processes such as carbon sequestration and storage (Luyssaert et al. 2008; Mildrexler et al. 2020) and they provide complex heterogeneous environments that maintain animal diversity and abundance (Lindenmayer and Laurance 2017; Dudinszky et al. 2021; Mildrexler et al. 2023). Differences in maximum size among species may reveal predictable variation in functional traits and biomass allocation patterns (Kacamak et al. 2022), demography and natural history strategies (Savage et al. 2004; Schnitzer et al. 2023), and physiological constraints on maximum size and growth rate (Koch et al. 2004). Determining the sizes of the largest individuals also provides valuable insights for estimating forest age, disturbance history, and the ideal conditions for optimal plant growth or longevity (Lee et al. 2023).

For trees, the largest individuals have been studied and documented for decades, providing extensive knowledge of species-specific maximum diameter, height, and crown breadth (e.g., Sillett et al. 2010; Shenkin et al. 2019). For example, the "Champion Trees" program, which was established in 1940 in the USA to identify and track the largest individuals of select tree species (https://www.americanforests.org/champion-trees/), is now an international effort (Hemp et al. 2017). With their immense trunks and crown dimensions, the largest trees sequester and store a disproportionate amount of forest carbon (Stephenson et al. 2014; Ali et al. 2019). Large trees are also notable for the visceral reactions that they evoke, engaging public interest and promoting environmental awareness and forest conservation (e.g., Preston 2008; Gilhen-Baker et al. 2022).

Apart from trees, however, there is little information on the maximum sizes of other plant growth forms. For example, there are no systematic records of maximum liana size, even though lianas are commonly second only to trees in biomass, and they can have substantial effects on forest diversity, development, and dynamics (Kusakabe et al. 2023; Ngute et al. 2024). Lianas compete intensely with trees (Toledo-Aceves 2015; Schnitzer 2018; Medina-Vega et al. 2022) and thus can strongly influence forest carbon dynamics (van der Heijden et al. 2013, 2015; Centre National de la Recherche Scientifique Durán et al. 2015; Estrada-Villegas et al. 2020; Peters et al. 2023). Large lianas may have particularly outsized effects on forest processes due to their ability to compete with many trees simultaneously (Putz 1984; Mori et al. 2018). Furthermore, by connecting multiple tree canopies, large lianas increase forest canopy complexity and thereby enhance animal diversity (Adams et al. 2019; Odell et al. 2019). Given that lianas are common in many forests (Schnitzer and Bongers 2002; Ngute et al. 2024), where their density appears to be increasing (Phillips et al. 2002; Schnitzer and Bongers 2011; Rueda-Trujillo et al. 2024), determining maximum liana size may provide a more complete understanding of forest ecology.

Few studies have reported maximum liana sizes or focused exclusively on the largest individuals (Schnitzer et al. 2023, 2024). The search for Champion Lianas has been further impeded by the rarity of these forest giants, since most liana stems are narrow and large lianas are exceedingly uncommon. For

example, there are only ~10 lianas with a diameter≥100mm per hectare in tropical forests, and far fewer lianas in larger size classes (Phillips et al. 2002; Schnitzer et al. 2021; Ek-Rodríguez et al. 2022). Lianas larger than 400mm diameter are rarely found in even the largest plot-based studies (e.g., Parthasarathy, Vivek, et al. 2015; Addo-Fordjour et al. 2017), leading to uncertainties about the maximum size that lianas can attain.

We created the Champion Liana competition at (www.Liana EcologyProject.com) with the goal of determining the maximum sizes and identities of the world's largest lianas and how they vary among continents. We used our published and unpublished datasets, as well as "extra-plot" field surveys designed to discover the largest naturally occurring lianas. Here, we present the first list of naturally growing Champion Lianas, with the anticipation that even larger candidates will be discovered and reported.

2 | Methods

We searched for Champion Lianas using two distinct strategies. First, we examined our records from plot-based censuses from tropical regions in Africa, Australia, Central America, South America, South Asia, and Southeast Asia and from temperate regions in North America, South America, Europe, and East Asia (Japan). Because even the largest plot-based studies cover relatively little forest area, our second strategy was to use targeted searches to find and measure both undiscovered and previously reported but undocumented naturally growing large lianas. We used these "extra-plot" surveys to systematically search large expanses of forest to increase the probability of finding a Champion Liana. All Champion Lianas were climbing plants with true secondary (woody) growth, remained rooted in the ground (as opposed to hemi-epiphytes), and relied on external support to climb toward the canopy (Schnitzer and Bongers 2002). We standardized measurements among individuals by measuring liana diameter 130 cm along the stem from the final rooting point following established liana census protocols (Gerwing et al. 2006; Schnitzer et al. 2008).

3 | Results

The Champion Lianas presented in this study had enormous maximum diameters and were significantly larger than previously reported lianas. The world Champion Liana was an 866 mm diameter Entada gigas (Fabaceae) found in an "extraplot" survey along a forest-dynamics transect in Loundoungou, an old-growth lowland tropical moist forest in northern Republic of Congo, Africa (Figure 1A; Table 1). In tropical Asia, there were two Champion Lianas: a 640 mm diameter Spatholobus harmandii (Fabaceae) from the seasonal evergreen tropical forest of the Mo Singto Forest Dynamics Plot located in Khao Yai National Park, Thailand (Figure 1B), and a 640 mm Spatholobus suberectus growing in a subtropical monsoon evergreen broadleaved forest in Yunnan, southwest China. In South Asia, the Champion was a 503 mm Entada rheedei from a rainforest fragment of Agumbe, Western Ghats, southern India. The American Champion liana was a 580 mm diameter Entada gigas, in the Mamoni Valley Preserve (Reserva valle del Mamoni) in eastern

2 of 8 Biotropica, 2025



FIGURE 1 | Champion lianas: (A) the largest liana recorded to date—866 mm diameter *Entada gigas*, Fabaceae (Republic of Congo). The inset shows the diameter measurement. (B) A 640 mm diameter *Spatholobus harmandii*, Fabaceae (Thailand). (C) A 580 mm diameter *Entada gigas*, Fabaceae (Panama). (D) The temperate Champion Liana—430 mm diameter *Hedera helix*, Araliaceae (France); (E) A 404 mm diameter *Wisteria floribunda*, Fabaceae (Japan); (F) A 375 mm diameter *Hydrangea serratifolia*, Hydrangeaceae (Chile). The diameters of champion liana stems were measured 1.3 m from the most distal rooting point, as indicated by the arrow in the final panel (F). Photo credits: (A) B. Kaçamak, (B) W.Y. Brockelman, (C) S.A. Schnitzer, (D) A. Schnitzler, (E) H. Mori, and (F) E. Gianoli.

Panama (Figure 1C). The Australian Champion was a 244mm *Entada phaseoloides* from lowland tropical moist forest in Mission Beach, northeast Queensland (Mackintosh et al. 2024). There were other notably large lianas growing in forests throughout the tropics (Table 1), as well as a 541 mm diameter cultivated *Entada pursaetha* (synonymous with *Entada rheedei*) on a university campus in Bengaluru, India (Maheshwari et al. 2009).

Temperate lianas were smaller than their tropical counterparts, yet still able to reach extremely large sizes. The temperate Champion was a 430 mm diameter *Hedera helix* (Araliaceae) in Regalon Gorges, southeastern France (Figure 1D; Table 1). The next largest temperate liana was a 404 mm diameter *Wisteria floribunda* (Fabaceae) found in a 6-ha sampling plot in the broadleaved deciduous old-growth forest of the Ogawa Forest Reserve,

Biotropica, 2025 3 of 8

(Continues)

TABLE 1 | The list of the current tropical and temperate Champion Lianas, as well as notably large naturally growing lianas found in forests around the world. Species names and authorities were confirmed using the Plants of the World Online resource supplied by the Kew Royal Botanic Gardens. Data were derived from the authors' datasets and relevant citations were reported when available (footnoted at the bottom of the table). Data for the North American temperate Champion Liana were found in Allen et al. (1997).

		,		
Continent (country)	Diameter (mm)	Species (family)	Forest	Discoverer/Reporter
Tropical champions				
Africa (Republic of Congo)	998	Entada gigas (L) Fawc. & Rendle (Fabaceae)	Loundoungou; Old-growth lowland tropical moist forest	$I. Zombo^1$
Southeast Asia (Thailand)	640	Spatholobus harmandii Gagnep. (Fabaceae)	Khao Yai National Park; Seasonal tropical evergreen forest	W.Y. Brockelman
Central Asia (Southwest China)	640	Spatholobus suberectus Dunn (Fabaceae)	Yunnan; Monsoon evergreen tropical broad-leaved forest	W.F. Zhang
Central America (Panama)	580	Entada gigas (L) Fawc. & Rendle (Fabaceae)	Mamoni Valley Preserve (Reserva Valle del Mamoni); Late secondary tropical rainforest	Mamoni Guardians; measured by B. Bernal
South America (French Guiana)	551	Unidentified	Nouragues; Lowland terra-firme equatorial tropical evergreen forest	G. van der Heijden
South Asia (India)	503	Entada rheedei Spreng. (Fabaceae)	Agumbe, Western Ghats; Southern tropical wet evergreen forest	V. Pandi
Australia	244	Entada phaseoloides (L.) Merr. (Fabaceae)	Mission Beach; Lowland tropical rainforest	E. Mackintosh
Temperate champions				
Europe (France)	430	Hedera helix L. (Araliaceae)	Rhine River; temperate hardwood forest	A. Schnitzler, C. Dronneau
East Asia (Japan)	404	Wisteria floribunda (Willd.) DC (Fabaceae)	Ogawa Forest Reserve; Broad-leaved deciduous old-growth temperate forest	$ m H.~Mori^2$
North America (USA)	400	Campsis radicans (L.) Bureau (Bignoniaceae)	Congaree Swamp National Monument, South Carolina; Mature bottomland hardwood temperate forest	B.P. Allen and colleagues³
South America (Chile)	375	Hydrangea serratifolia (Hook. & Arn.) F.Phil. (Hydrangeaceae)	Puyehue National Park; Evergreen temperate rainforest	E. Gianoli ⁴
Europe (Italy)	265	Hedera helix L. (Araliaceae)	Foresta Umbra; Beech-dominated old-growth temperate forest	A. Di Filippo

q)
ä
=
Ξ.
Ξ
Ξ
Ş
<u>.</u>
_
_
E1
LE1
I
ABLE 1

Continent (country)	Diameter (mm)	Species (family)	Forest	Discoverer/Reporter
Notable large lianas				
Central America (Panama)	515	Combretum laxum Jacq. (Combretaceae)	Barro Colorado Island; Seasonally moist tropical forest ⁴	S.A. Schnitzer ⁵
Africa (Tanzania)	452 and 397	Entada rheedei Spreng. (Fabaceae)	Magombera Nature Reserve; Lowland tropical swamp forest	A. Marshall
Africa (Ghana)	450	Combretum sordidum Exell (Combretaceae)	Ankara Conservation Area; Evergreen tropical rainforest	P. Addo Fordjour
Asia (India)	449	Combretum albidum G. Don (Combretaceae)	Coromandel coast; Seasonally dry tropical forest	V. Pandi
North America (Mexico)	440	Machaerium floribundum Benth. (Fabaceae)	Los Tuxtlas Tropical Biology Station; Tropical rainforest	G. Ibarra-Manríquez, S. Sinaca-Colin
Asia (Malaysia)	327	Dalbergia rostrata Hassk. (Fabaceae)	Penang National Park; Rainforest	P. Addo Fordjour and colleagues ⁶
North America (Mexico)	227	Vitis tillifolia Humb. & Bonpl. ex Schult. (Vitaceae)	Michoacán state; Temperate forest	G. Ibarra-Manríquez
North America (USA)	225	Vitis sp. (Vitaceae)	Wallace Woods, Pennsylvania; Old-growth hemlock-northern hardwood forest	C.J. Davis

Note: 1. Kaçamak et al. (2025); 2. Mori et al. (2016); 3. Allen et al. (1997); 4. Gianoli et al. (2010); 5. Schnitzer et al. (2012); 6. Addo-Fordjour et al. (2017).

Biotropica, 2025 5 of 8

Japan (Figure 1E; Mori et al. 2016). Allen et al. (1997) reported a 400 mm *Campsis radicans* in the old-growth Congaree swamp forest in southeastern USA. A 375 mm *Hydrangea serratifolia* (Hydrangeaceae) was reported from evergreen rainforest of Puyehue National Park, southern Chile (Figure 1F; see also Jiménez-Castillo and Lusk 2009). In a warm temperate old-growth beech-dominated forest in Foresta Umbra, Italy, where large-diameter *Hedera* (200–230 mm) were common, A. Di Filippo found a 265 mm *Hedera helix*. In temperate forests of North America, large-diameter *Vitis* species (Vitaceae) were reported from Michoacán, Mexico (227 mm) and Pennsylvania, USA (225 mm; Table 1).

4 | Discussion

The Champion Lianas of the tropical continents were all legumes (Fabaceae) in the genera Entada and Spatholobus. Three of the six next largest lianas were also legumes (Machaerium, Entada, and Dalbergia; Table 1), indicating that leguminous tropical lianas tend to be the largest in tropical forests. By contrast, temperate Champion Liana species and families varied by continent (Table 1). Why the largest lianas are all legumes in the tropics but not the temperate zone is not known. For most liana species, little is known about the limits of stem size and how maximum stem size varies with anatomy, physiology, and life-history strategy (Schnitzer et al. 2023). Further research on how liana species vary in maximum size, the limitations of maximum size, and the tradeoffs between maximum size and performance may provide insights into key functional differences among species and whether these differences are important for species coexistence (Mello et al. 2020).

Champion Lianas were exceedingly uncommon in our datasets, and even stems reaching 200 mm diameter constituted only a small fraction (0.03%–0.08%) of the liana stems in any forest. For example, of the 6206 liana stems \geq 10 mm diameter in 5.76 ha of Congolese forest at Loundoungou, only two were 200 mm diameter or larger (Kaçamak et al. 2025). Of the 86,723 total liana stems \geq 10 mm diameter rooted in the BCI 50-ha plot, Panama, only 27 were \geq 200 mm diameter (Schnitzer et al. 2023). Similarly low proportions of large (\geq 200 mm) lianas were found in Australia (Mackintosh et al. 2024), peninsular India (Parthasarathy, Muthuramkumar, et al. 2015), Thailand (W. Y. Brockelman, unpublished), and Ghana and Malaysia (Addo-Fordjour et al. 2017). Stems reaching 400 mm diameter and larger were vanishingly rare in all forests.

Maximum stem diameter likely varies with the level of forest disturbance; forests that experience periodic natural disturbance from strong storms likely have smaller maximum stem sizes. For instance, the relatively small size of the Australian Champion liana may be due to frequent cyclone damage in Australian wet forests (Mackintosh et al. 2024), which limits both maximum tree and liana stem sizes. Anthropogenic disturbance can also limit maximum size. Many forests are managed by local communities, which may selectively harvest lianas or prioritize tree growth over liana survival, resulting in the loss of large liana stems.

Large lianas may have an extensive influence on the surrounding forest by colonizing dozens of tree crowns and competing for light over large swaths of forest. For example, in an old-growth forest on BCI, Putz (1984) tracked a 510 mm diameter Entada gigas liana through the crowns of 47 canopy trees and estimated that it covered ~0.5 ha of forest (see also Mori et al. 2018). These large lianas compete for light and reduce tree growth (Estrada-Villegas et al. 2022; Finlayson et al. 2022), thereby limiting tree and whole-forest carbon uptake and storage (van der Heijden et al. 2013; Peters et al. 2023). Because large lianas have extensive root systems and highly conductive vascular systems to supply their vast crowns of leaves (Ewers et al. 1991), they may compete intensely with trees for belowground resources (Schnitzer et al. 2005; Putz 2023) and influence forest water dynamics (Zhu and Cao 2009; Chen et al. 2015; Reid et al. 2015). Large lianas may severely reduce canopy tree reproduction (Kainer et al. 2014; Garcia-Leon et al. 2018), possibly influencing tree population demography.

Large lianas also have positive effects on forest ecosystems. By connecting many tree crowns together, large lianas provide habitat and enhance forest connectivity, which benefits animal species and thus increases wildlife diversity (Montgomery and Sunquist 1978; Adams et al. 2019, Marshall et al. 2020). Lianas themselves add enormous species diversity to the forest canopy (Schnitzer and DeFilippis 2025), which increases the diversity of specialist invertebrates (Ødegaard 2001; Odell et al. 2019). Leguminous lianas may contribute significantly to forest nitrogen fixation; in a Brazilian Atlantic Forest, lianas fixed a considerable proportion of total forest nitrogen (Winbourne et al. 2025), and all tropical Champion Lianas were legumes.

The search for Champion Lianas has only begun and, to date, relatively little forest area has been explored. With motivation to discover and publish large liana data, we are confident that new Champion Lianas will be documented—possibly even individuals exceeding 1 m diameter. To find the next generation of Champion Lianas, we recommend forest-wide searches that are not restricted by plot or political boundaries. Because of the rarity of large lianas, these extra-plot surveys are necessary to increase the probability of finding the largest forest lianas. We challenge ecologists, botanists, naturalists, and nature enthusiasts to submit their large liana records with photographic evidence of the stem diameter measurement 1.3 m above the roots (Gerwing et al. 2006; Schnitzer et al. 2008) at LianaEcologyProject.com, where we host the Champion Liana competition.

Acknowledgments

We thank the many field technicians for their essential contributions to these global liana censuses. Thanks also to Policarpio Acosta, Nelson Mogoruza, Daniel Pareja, Karol Herrera, and the Mamoni Valley Preserve (Reserva Valle del Mamoni), Panama. We thank Jennifer Powers for encouraging us to submit this work to *Biotropica* and three anonymous reviewers for their constructive comments. Financial support for liana censuses in Panama was provided by the US National Science Foundation through grants DEB 06-13666, 08-45071, 10-19436, 12-58070, 18-22473, 20-01799, and IOS 15-58093. An Anne McLaren Fellowship from the University of Nottingham and CNRS funding supported G.H. H.P.T.D.D. was funded by the Carbon Mitigation Initiative

6 of 8 Biotropica, 2025

at Princeton University. The ForestGEO Research Grant Program sponsored the Ngel Nyaki Liana Census, supporting G.A.D. E.M. was supported by Australian Research Council grant FT17010027. The idea for this project was conceived and launched at the 2024 annual meeting of the Association for Tropical Biology and Conservation in Kigali, Rwanda. All authors contributed to the manuscript by providing original data, insights into the Champion Liana idea, or both.

Conflicts of Interest

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

Data Availability Statement

Data sharing is not applicable to this article as no data were created or analyzed in this study.

References

Adams, B. J., S. A. Schnitzer, and S. P. Yanoviak. 2019. "Connectivity Explains Local Ant Community Structure in a Neotropical Forest Canopy: A Large-Scale Experimental Approach." *Ecology* 100: e02673.

Addo-Fordjour, P., Z. B. Rahmad, and R. J. Burnham. 2017. "Intercontinental Comparison of Liana Community Assemblages in Tropical Forests of Ghana and Malaysia." *Journal of Plant Ecology* 10: 883–894.

Ali, A., S. L. Lin, J. K. He, F. M. Kong, J. H. Yu, and H. S. Jiang. 2019. "Big-Sized Trees Overrule Remaining Trees' Attributes and Species Richness as Determinants of Aboveground Biomass in Tropical Forests." *Global Change Biology* 25: 2810–2824.

Allen, B. P., E. F. Pauley, and R. R. Sharitz. 1997. "Hurricane Impacts on Liana Populations in an Old-Growth Southeastern Bottomland Forest." *Journal of the Torrey Botanical Society* 124: 34–42.

Chen, Y.-J., K.-F. Cao, S. A. Schnitzer, Z.-X. Fan, J.-L. Zhang, and F. Bongers. 2015. "Water-Use Advantage of Lianas Over Trees in Seasonal Tropical Forests." *New Phytologist* 205: 128–136.

Dudinszky, N., S. Ippi, T. Kitzberger, G. Cerón, and V. Ojeda. 2021. "Tree Size and Crown Structure Explain the Presence of Cavities Required by Wildlife in Cool-Temperate Forests of South America." *Forest Ecology and Management* 494: 1–13.

Durán, S. M., G. A. Sánchez-Azofeifa, R. S. Rios, and E. Gianoli. 2015. "The Relative Importance of Climate, Stand Variables and Liana Abundance for Carbon Storage in Tropical Forests." *Global Ecology and Biogeography* 24: 939–949.

Ek-Rodríguez, I. L., R. Coates, S. Sinaca-Colín, and G. Ibarra-Manríquez. 2022. "Liana Community Attributes in One of the Northernmost Neotropical Rainforests." *Botanical Sciences* 100: 353–369.

Estrada-Villegas, S., J. S. Hall, M. van Breugel, and S. A. Schnitzer. 2020. "Lianas Reduce Biomass Accumulation in Early Successional Tropical Forests." *Ecology* 101: e02989.

Estrada-Villegas, S., S. S. Pedraza-Narvaez, A. Sánchez-Andrade, and S. A. Schnitzer. 2022. "Lianas Significantly Reduce Tree Performance and Biomass Accumulation Across Tropical Forests: A Global Meta-Analysis." Frontiers in Forests and Global Change 4: 812066. https://doi.org/10.3389/ffgc.2021.812066.

Ewers, F. W., J. B. Fisher, and K. Richtner. 1991. "Water Flux and Xylem Structure in Vines." In *Biology of Vines*, edited by F. E. Putz and H. Mooney, 119–152. Cambridge University Press.

Finlayson, C., A. Roopsind, B. W. Griscom, D. P. Edwards, and R. P. Freckleton. 2022. "Removing Climbers More Than Doubles Tree Growth and Biomass in Degraded Tropical Forests." *Ecology and Evolution* 12: e8758.

Garcia-Leon, M. M., L. Martinez-Izquierdo, F. N. A. Mello, J. S. Powers, and S. A. Schnitzer. 2018. "Lianas Reduce Community-Level Canopy Tree Reproduction in a Panamanian Forest." *Journal of Ecology* 106: 737–745.

Gerwing, J. J., S. A. Schnitzer, R. J. Burnham, et al. 2006. "A Standard Protocol for Liana Censuses." *Biotropica* 38: 256–261.

Gianoli, E., A. Saldaña, M. Jiménez-Castillo, and F. Valladares. 2010. "Distribution and Abundance of Vines Along the Light Gradient in a Southern Temperate Rainforest." *Journal of Vegetation Science* 21: 66–73.

Gilhen-Baker, M., V. Roviello, D. Beresford-Kroeger, and G. Roviello. 2022. "Old Growth Forests and Loarge Old Trees as Critical Organisms Connecting Ecosystems and Human Health. A Review." *Environmental Chemistry Letters* 20: 1529–1538.

Hemp, A., R. Zimmermann, S. Remmele, et al. 2017. "Africa's Highest Mountain Harbours Africa's Tallest Trees." *Biodiversity and Conservation* 26: 103–113.

Jiménez-Castillo, M., and C. H. Lusk. 2009. "Host Infestation Patterns of the Massive Liana Hydrangea Serratifolia (Hydrangeaceae) in a Chilean Temperate Rainforest." *Austral Ecology* 34: 829–834.

Kaçamak, B., N. Barbier, M. Aubry-Kientz, et al. 2022. "Linking Drone and Ground-Based Liana Measurements in a Congolese Forest." *Frontiers in Forests and Global Change* 5: 803194.

Kaçamak, B., M. Réjou-Méchain, N. Rowe, et al. 2025. "Local Forest Structure and Host Specificity Influence Liana Community Composition in a Moist Central African Forest." *Ecology and Evolution* 15: e71075.

Kainer, K. A., L. H. O. Wadt, and C. L. Staushammer. 2014. "Testing a Silvicultural Recommendation: Brazul Nut Responses 10 Years After Liana Cutting." *Journal of Applied Ecology* 51: 655–663.

Koch, G. W., S. C. Sillett, G. M. Jennings, and S. D. Davis. 2004. "The Limits to Tree Height." *Nature* 428: 851–854.

Kusakabe, G., H. Mori, and T. Hiura. 2023. "Distribution Patterns of Lianas From Subtropical to Subboreal Zones of the Japanese Archipelago and the Difference Between Climbing Types." *Basic and Applied Ecology* 72: 1–9.

Lee, Y. J., C. B. Lee, and M. K. Lee. 2023. "Tree Size Variation Induced by Stand Age Mainly Regulates Aboveground Biomass Across Three Major Stands of Temperate Forests in South Korea." *Frontiers in Forests and Global Change* 6: 1–11.

Lindenmayer, D. B., and W. F. Laurance. 2017. "The Ecology, Distribution, Conservation and Management of Large Old Trees." *Biological Reviews* 92: 1434–1458.

Luyssaert, S., E.-D. Schulze, A. Börner, et al. 2008. "Old-Growth Forests as Global Carbon Sinks." *Nature* 455: 213–215.

Mackintosh, E. J., C. E. Waite, F. E. Putz, S. Brennan, M. Pfeifer, and A. R. Marshall. 2024. "Lianas Associated With Continued Forest Biomass Losses Following Large-Scale Disturbances." *Biotropica* 56: e13348.

Maheshwari, R., K. Rao, and T. Ramachandra. 2009. "Structural Characteristics of a Giant Tropical Liana and Its Mode of Canopy Spread in an Alien Environment." *Current Science* 96: 58–64.

Marshall, A. R., P. J. Platts, R. J. Chazdon, et al. 2020. "Conceptualising the Global Forest Response to Liana Proliferation." *Frontiers in Forests and Global Change* 3: 35. https://doi.org/10.3389/ffgc.2020.00035.

Medina-Vega, J., G. M. F. van der Heijden, and S. A. Schnitzer. 2022. "Lianas Decelerate the Pattern of Tree Self-Thinning During Tropical Forest Succession." *Ecology Letters* 25: 1432–1441.

Mello, F. N. A., S. Estrada-Villegas, D. M. Defilippis, and S. A. Schnitzer. 2020. "Can Functional Traits Explain Plant Coexistence? A Case Study with Tropical Lianas and Trees." *Diversity* 12: 397. https://doi.org/10.3390/d12100397.

Biotropica, 2025 7 of 8

Mildrexler, D. J., L. T. Berner, B. E. Law, R. A. Birdey, and W. R. Moonaw. 2023. "Protect Large Trees for Climate Mitigation, Biodiversity, and Forest Resilience." *Conservation Science and Practice* 5: e12944.

Mildrexler, D. J., L. T. Berner, B. E. Law, R. A. Birdsey, and W. R. Moomaw. 2020. "Large Trees Dominate Carbon Storage in Forests East of the Cascade Crest in the United States Pacific Northwest." *Frontiers in Forests and Global Change* 3. https://doi.org/10.3389/ffgc.2020.594274.

Montgomery, G. G., and M. E. Sunquist. 1978. "Habitat Selection and Use by Two-Toed and Three-Toed Sloths." In *The Ecology of Arboreal Folivores*, edited by G. G. Montgomery, 329–359. Smithsonian Institution Press.

Mori, H., T. Kamijo, and T. Masaki. 2016. "Liana Distribution and Community Structure in an Old-Growth Temperate Forest: The Relative Importance of Past Disturbances, Host Trees, and Microsite Characteristics." *Plant Ecology* 217: 1171–1182.

Mori, H., S. Ueno, A. Matsumoto, T. Kamijo, Y. Tsumura, and T. Masaki. 2018. "Large Contribution of Clonal Reproduction to the Distribution of Deciduous Liana Species (*Wisteria floribunda*) in an Old-Growth Cool Temperate Forest: Evidence From Genetic Analysis." *Annals of Botany* 121: 359–365.

Ngute, A. S. K., D. S. Schoeman, M. Pfeifer, et al. 2024. "Global Dominance of Lianas Over Trees Is Driven by Forest Disturbance, Climate, and Topography." *Global Change Biology* 30: e17140.

Ødegaard, F. 2001. "The Relative Importance of Trees Versus Lianas as Hosts for Phytophagous Beetles (Coleoptera) in Tropical Forests." *Journal of Biogeography* 27: 283–296.

Odell, E. H., N. E. Stork, and R. L. Kitching. 2019. "Lianas as a Food Resource for Herbivorous Insects: A Comparison With Trees." *Biological Reviews* 94: 1416–1429.

Parthasarathy, N., S. Muthuramkumar, C. Muthumperumal, P. Vivek, N. Ayyappan, and M. S. Reddy. 2015. "Liana Composition and Diversity Among Tropical Forest Types of Peninsular India." In *Ecology of Lianas*, edited by S. A. Schnitzer, F. Bongers, R. J. Burnham, and F. E. Putz, 36–49. Wiley Blackwell.

Parthasarathy, N., P. Vivek, C. Muthumperumal, S. Muthuramkumar, and N. Ayyappan. 2015. "Biodiversity of Lianas and Their Functional Traits in Tropical Forests of Peninsular India." In *Biodiversity of Lianas*, edited by N. Parthasarathy, 123–148. Springer.

Peters, J. D. J., J. M. Portmann, and B. W. Griscom. 2023. "Lianas (*Vitis* spp.) Reduce Growth and Carbon Sequestration of Light-Demanding Tree Species in a Temperate Forest." *Restoration Ecology* 31: e13886.

Phillips, O. L., R. Vásquez Martinez, L. Arroyo, et al. 2002. "Increasing Dominance of Large Lianas in Amazonian Forests." *Nature* 418: 770–774.

Preston, R. 2008. *The Wild Trees: A Story of Passion and Daring*. 294 pp. Random House.

Putz, F. E. 1984. "The Natural History of Lianas on Barro Colorado Island, Panama." *Ecology* 65: 1713–1724.

Putz, F. E. 2023. "Climbing Plants Beat Trees to Soil Nutrient Patches." Current Biology 33: R659–R676.

Reid, J. P., S. A. Schnitzer, and J. S. Powers. 2015. "Soil Moisture Variation After Liana Removal in a Seasonally Moist, Lowland Tropical Forest." *PLoS One* 10: e0141891.

Rueda-Trujillo, M. A., M. P. Veldhuis, P. M. van Bodegom, H. P. T. De Deurwaeder, and M. Visser. 2024. "Global Increases of Lianas in Tropical Forests." *Global Change Biology* 30: e17485.

Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. "Effect of Body Size and Temperature on Population Growth." *American Naturalist* 163: E429–E441.

Schnitzer, S. A. 2018. "Testing Ecological Theory With Lianas." *New Phytologist* 220: 366–380.

Schnitzer, S. A., and F. Bongers. 2002. "The Ecology of Lianas and Their Role in Forests." *Trends in Ecology & Evolution* 17: 223–230.

Schnitzer, S. A., and F. Bongers. 2011. "Increasing Liana Abundance and Biomass in Tropical Forests: Emerging Patterns and Putative Mechanisms." *Ecology Letters* 14: 397–406.

Schnitzer, S. A., and D. M. DeFilippis. 2025. "Does Increasing Canopy Liana Density Decrease the Tropical Forest Carbon Sink?" *Ecology* 106: e70196.

Schnitzer, S. A., D. M. DeFilippis, A. Aguilar, et al. 2023. "Maximum Stem Diameter Predicts Liana Population Demography." *Ecology* 104: 1–7

Schnitzer, S. A., D. M. DeFilippis, F. N. A. Mello, et al. 2024. "The BCI Liana Oligarchy: Dominance, Distribution, and Traits of the Ten Most Common Liana Species." In *The First 100 Years of Research on Barro Colorado: Plant and Ecosystem Science*, edited by H. C. Muller-Landau and S. J. Wright. Smithsonian Institution Scholarly Press.

Schnitzer, S. A., D. M. DeFilippis, M. Visser, et al. 2021. "Local Canopy Disturbance as an Explanation for Long-Term Increases in Liana Abundance." *Ecology Letters* 24: 2635–2647.

Schnitzer, S. A., M. Kuzee, and F. Bongers. 2005. "Disentangling Aboveand Below-Ground Competition Between Lianas and Trees in a Tropical Forest." *Journal of Ecology* 93: 1115–1125.

Schnitzer, S. A., S. A. Mangan, J. W. Dalling, et al. 2012. "Liana Abundance, Diversity, and Distribution on Barro Colorado Island, Panama." *PLoS One* 7: e52114.

Schnitzer, S. A., S. Rutishauser, and S. Aguilar. 2008. "Supplemental Protocol for Liana Censuses." *Forest Ecology and Management* 255: 1044–1049.

Shenkin, A., C. J. Chandler, D. S. Boyd, et al. 2019. "The World's Tallest Tropical Tree in Three Dimensions." *Frontiers in Forests and Global Change* 2: 32. https://doi.org/10.3389/ffgc.2019.00032.

Sillett, S. C., R. Van Pelt, G. W. Kock, et al. 2010. "Increasing Wood Production Through Old Age in Tall Trees." *Forest Ecology and Management* 259: 976–994.

Stephenson, N., A. Das, R. Condit, et al. 2014. "Rate of Tree Carbon Accumulation Increases Continuously With Tree Size." *Nature* 507: 90–93.

Toledo-Aceves, T. 2015. "Above- and Belowground Competition Between Lianas and Trees." In *Ecology of Lianas*, edited by S. A. Schnitzer, F. Bongers, R. J. Burnham, and F. E. Putz, 147–163. Wiley-Blackwell Publishing.

van der Heijden, G. M., J. S. Powers, and S. A. Schnitzer. 2015. "Lianas Reduce Carbon Accumulation in Tropical Forests." *Proceedings of the National Academy of Sciences of the United States of America* 112: 13267–13271.

van der Heijden, G. M., S. Am . Schnitzer, J. S. Powers, and O. L. Phillips. 2013. "Liana Impacts on Carbon Cycling, Storage and Sequestration in Tropical Forests." *Biotropica* 45: 682–692.

Winbourne, J. B., K. E. Hasenstab-Lehman, A. N. Egan, D. Piotto, W. J. Kress, and S. Porder. 2025. "Inga and Lianas Are Key Players in the Tropical Nitrogen Cycle of Brazilian Atlantic Forest: Insights From Linking Rates of Nitrogen Fixation With DNA Barcoding Root Identification." *Biotropica* 57: e70021.

Zhu, S.-D., and K.-F. Cao. 2009. "Hydraulic Properties and Photsynthetic Rates in Co-Occurring Lianas and Trees in a Seasonal Tropical Rainforest in Southwestern China." *Plant Ecology* 204: 295–304.

8 of 8 Biotropica, 2025