Meeting report

Lianas from lives to afterlives

1st International workshop on liana forest ecology, Xishuangbanna, China, 12–16 October 2023

Tropical forests constitute the world's largest biomass carbon pool and are important global reservoirs of biodiversity, yet they are being increasingly degraded by anthropogenic activities. Evidence from American tropical forests suggests that forest disturbance and climate change result in increased liana abundance and biomass, but data are still lacking from African and Asian forests. An increasing abundance of lianas may affect forest ecosystem services, which is concerning as these services are poorly understood.

Recognizing the urgent need to evaluate how increases in lianas could affect local and regional carbon, nutrient, and water cycles, 35 scientists (Fig. 1), at different career stages, from 14 countries working across Africa, America, and Asia, convened at the 1st International Workshop on Liana Forest Ecology held at Xishuangbanna Tropical Botanical Garden (XTBG), China, 12–16 October 2023. With the focus 'From life to afterlife: liana proliferation and its consequences for carbon and water cycling', the workshop discussed how carbon, nutrient, and water cycles are affected by: (1) drivers of liana distribution and demography; (2) hydraulics of lianas vs trees; (3) lives of lianas; (4) afterlives of lianas (Fig. 2). Here, we provide a summary of our discussions.

Drivers of liana distribution and demography

S.A. Schnitzer (Marquette University, USA), R. T. Corlett (Xishuangbanna Tropical Botanical Garden, China), and B. Ofosu-Bamfo (Kwame Nkrumah University of Science and Technology, Ghana) provided overviews of liana research in

Fig. 1 Participants of the workshop at Xishuangbanna Tropical Botanical Garden research center, Yunnan, China.

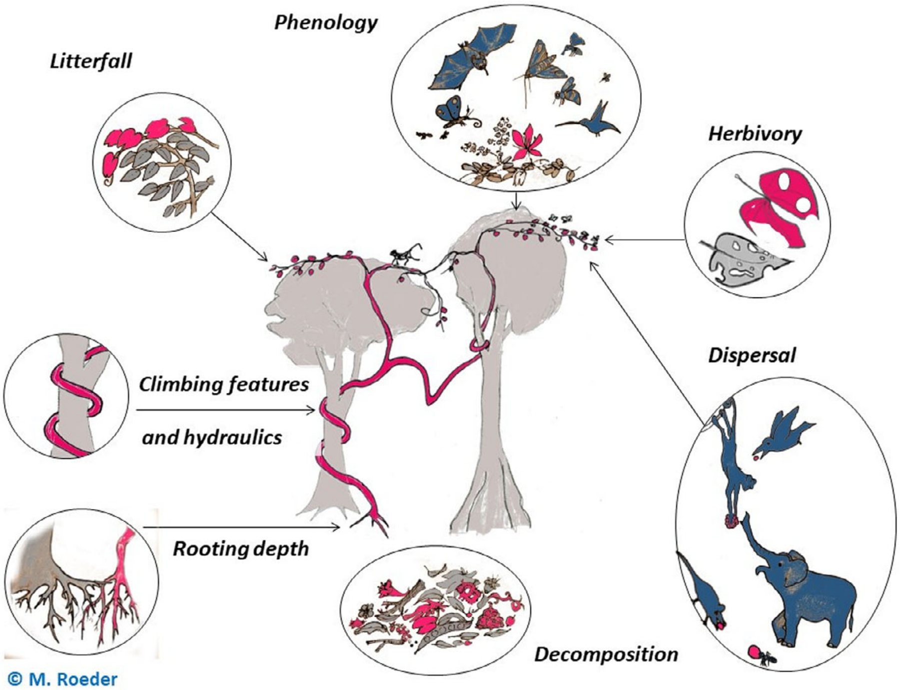

Fig. 2 Overview of topics covered during the workshop.

the Americas, Asia, and Africa respectively. Most quantitative research has occurred in the Americas, but there is increasing effort in other continents. S.A. Schnitzer highlighted recent work, which shows that lianas reach high density and diversity in tree fall gaps in the tropics and can suppress trees and other growth forms. He noted that information on liana demography using established sampling protocols is critical to reveal the age and size classes where lianas are thriving, and provides a way to compare the potential causes of liana increases among sites. Such censuses must be further expanded to sites in Africa, Australia, and Asia. In the latter region, a combination of such censuses with in-depth studies will also contribute to better insights into the ecology of rattans, a diverse and commercially important group of climbing palms (R. T. Corlett).

Hydraulics of lianas vs trees

Understanding hydraulic differences between trees and lianas is critical to explaining both their competitive interactions and their impacts on soil–water resources. Lianas have, on average, wider vessel diameters and greater lengths than trees, resulting in more efficient hydraulic transport and potentially greater vulnerability to embolism (Smith-Martin *et al.*, 2022). However, studies with refined methods, including X-ray micro-computed tomography, optical vulnerability techniques, and improved bench-top dehydration methods to assess dehydration-induced embolism, have shown that lianas are more resistant to embolisms than previously thought (Chen *et al.*, 2021; Smith-Martin *et al.*, 2022; K. Cao, Guangxi University, China). This may be because of the wider distribution of xylem vessel diameters in lianas compared with trees: Small vessels can continue to transport water even after larger vessels have been embolized (Smith-Martin *et al.*, 2022; Zhang *et al.*, 2023). There was debate during the workshop about the possible mechanisms, leading to the conclusion that the refilling of embolized vessels is not supported by concrete evidence. C.M. Smith-Martin (University of Minnesota, USA) suggested that more comparative studies on xylem anatomy, examining pit membrane thickness and xylem vessel connectivity, are needed to establish whether large vessels are isolated from the smaller vessels in lianas, as this would prevent the propagation of embolisms, with implications for water cycling.

Lianas perform better than trees during seasonal drought, with higher photosynthetic rates, fewer negative predawn leaf water potentials, and higher growth rates than trees (Schnitzer & van der Heijden, 2019; Smith-Martin *et al.*, 2019). C.M. Smith-Martin pointed out that, although this difference was previously ascribed to lianas having deeper roots than trees, stable isotopic studies revealed deep or shallow water use by lianas relative to trees. Meanwhile, excavation studies reported no difference in rooting depth among juvenile lianas and trees, but a greater depth of mature trees than lianas (Smith-Martin *et al.*, 2019, 2020). C.M. Smith-Martin also noted that rooting depth is likely species- and site-specific, so further root excavation studies are needed. If lianas are not accessing deeper sources of water, then they must rely on other mechanisms to outperform trees during seasonal drought. Potential explanations include that lianas lower their leaf turgor loss point during the dry season to increase drought resistance (S.A. Schnitzer, Marquette University, USA), and/or have peak photosynthetic rates early in the morning when vapor pressure deficit is low (Chen *et al.*, 2017). K. Tomlinson (Xishuangbanna Tropical Botanical Garden, China) suggested that controlled dry-down experiments would yield critical data on leaf physiological responses of lianas and trees to soil drying.

Lives of lianas

A diversity of life histories

Talks on seed, seedling, and adult liana diversity emphasized that studies to date typically focused on few species, whereas the rare examples of community assessment show the great diversity of liana life forms. Those analyses suggest that lianas should not be treated as a single functional type when understanding forest community dynamics. M. Roeder (Karlsruhe Institute of Technology, Germany) reported a large range of seed traits and germination requirements in an Amazonian forest community. She also reported on seedling traits, which were related to remarkable differences in the life histories of lianas from different forest types. Under a closed canopy primary forest, lianas can form free-standing seedling or sapling banks (often by clonal vegetative reproduction). In secondary forests, with increased light availability, liana vegetative regeneration increases in importance and growth. Associated traits were more heterogenous than in primary forests. M. Roeder advocated expanding trait-based liana community analyses to generate a deeper understanding of the functional ecology of lianas across forest types, further pointing out that biometric analyses of seeds can provide a large amount of information without the need for resource-intensive germination tests. G. Zotz (Carl von Ossietzky University, Germany) advocated a more holistic approach to growth forms. He noted that herbaceous vines are understudied, and further concluded that ecologists should avoid treating 'woody lianas', 'herbaceous vines', and 'epiphytes' as homogenous functional groups, a sentiment that has been put forward elsewhere (e.g. Meunier *et al.*, 2021; Schnitzer & Carson, 2023).

Liana reproductive phenology

Liana reproductive phenology is important for plant and animal community dynamics, as flowers and fruits are important animal food resources. Liana reproductive phenology ranges from seasonal to aseasonal depending on dry season length; in seasonal environments with asynchrony in reproductive phenology between trees and lianas, lianas may provide critical fallback resources for animals. Unfortunately, there are few studies on liana phenology and they are mostly from the American tropics; most do not quantify flower and fruit resources over time, which is critical to understanding their contribution to ecosystem functions and services. At the meeting, two recent studies from Asia and Africa were reported. In an Asian seasonal forest, peak flowering coincided in the late dry season between trees and lianas, but lianas produced more flowers earlier in the dry season (T.C. Ling, Chiang Mai University, Thailand), which contrasts with asynchrony between the growth forms in seasonal forests in Mexico (Cortés-Flores *et al.*, 2017). In two African seasonal forests, liana flowering peaked twice per year in the wetter forest and only once in the drier forest, corresponding with the rainfall patterns of each forest (B. Ofosu-Bamfo). Remote sensing and on-site cameras may rapidly increase the spatial and temporal coverage of phenological studies (e.g. Kaçamak *et al.*, 2022), allowing future research to establish how abiotic (e.g. rainfall, seasonality) and biotic factors (e.g. phylogeny and pollinator guilds) influence liana phenology.

Afterlives of lianas

The contributions to carbon and nutrient cycling of litter generated from lianas vs trees remain poorly documented. M. Roeder highlighted the lack of community-level studies on litterfall and decomposition of lianas vs trees and presented evidence (including higher leaf nitrogen content) that leaves of lianas consistently decompose faster than trees in a multi-community study (Roeder *et al.*, 2022). This corresponded with experimental evidence from temperate species reported by H. Cornelissen (Vrije Universiteit Amsterdam, the Netherlands), J. Zuo (Wuhan Botanical Garden, China) suggested that differences in litter quality sourced from lianas and trees offer an opportunity to test some ecological hypotheses such as mixture effect mechanisms. D. Schaefer (Kunming Institute of Botany, China) pointed out that wood and leaf decomposition studies, in general, have been performed separately, and that future decomposition studies should include leaf and wood litter mixtures.

Liana wood decomposition is thought to be enhanced by its low wood density, and large-diameter and long xylem vessels allowing fungal hyphae to proliferate and invertebrates to invade. Due to differences in liana woody debris nutrient content compared with trees, the two growth forms could host different communities of invertebrate decomposers. G.G.O. Dossa (Xishuangbanna Tropical Botanical Garden, China) expected invertebrate contribution to liana woody debris decomposition to be higher in magnitude compared with tree woody debris, and H. Cornelissen proposed that the role of termites should be considered in future studies. Termites are quite selective for food quality; thus, deadwood studies will provide more insights if they include anti-termite cages. Furthermore, since some of the decaying material remains suspended in the forest canopy, studies should quantify this suspended portion of decaying litter and compare ground vs suspended woody debris for (abiotic and biotic contributions to) decomposition (G.G.O. Dossa).

Conclusions

The increase in liana density and basal area is one of the major changes now occurring in many tropical forests and was a central theme of the workshop. The potential ramifications of increasing liana density illuminated the need for a deeper understanding of the fundamental ecology of lianas.

A more complete understanding of liana hydraulics and underlying traits may be critical to understanding their ability to efficiently move more water from the soil to their sun-exposed leaves. Resolving where lianas access water in the soil profile, the amount of water they take up, and how these vary with climate and soils, remains a priority area of research.

Leaf phenology and the afterlives of lianas are clear gaps in our general understanding of the contribution of lianas to ecosystem services and nutrient cycling in forests. Liana stem and leaf properties differ from those of trees, making unique contributions to forest soil dynamics. Thus, the contribution of lianas to decay rates of dead plant matter and their interactions therein with tree-derived deadwood and litter are understudied but potentially important to understanding forest ecology.

One key outcome of this workshop is the acknowledgement that insight can be gained by merging analyses of species-level functional traits of wide-ranging lianas and trees, with those of community-level plant and decomposer composition, demography, and matter cycling. This will likely be a key theme to be addressed in a follow-up workshop (potentially in Beijing in 2025).

Acknowledgements

The participants of the workshop are grateful for financial support from the Chinese Academy of Sciences and Xishuangbanna Tropical Botanical Garden. In addition, G.G.O.D. was supported by the Yunnan provincial government talents program (E1YN101B01). G.G.O.D. and J.Z. were supported by Open Funding from CAS Key Laboratory of Tropical Forest Ecology (22-CAS-TFE-06).

ORCID

Kun-Fang Cao https://orcid.org/0000-0002-2253-7189
Ya-Jun Chen https://orcid.org/0000-0001-5753-5565
Jean Evans Israel Codjia https://orcid.org/0000-0002-6385-3268
Richard T. Corlett https://orcid.org/0000-0002-2508-9465
Johannes H. C. Cornelissen https://orcid.org/0000-0002-2346-1585
Jinlong Dong https://orcid.org/0009-0006-2731-3551
Gbadamassi G. O. Dossa https://orcid.org/0000-0001-9767-7306
Ze-Xin Fan https://orcid.org/0000-0003-4623-6783
Pratibha Khatri https://orcid.org/0009-0008-5075-1933
Tial C. Ling https://orcid.org/0000-0002-6360-4106
Bartosz Marek Majcher https://orcid.org/0000-0002-5679-3340
Denis M. Njoroge https://orcid.org/0000-0002-6556-2843
Bismark Ofosu-Bamfo https://orcid.org/0000-0001-9716-5212
Mareike Roeder https://orcid.org/0000-0002-8312-4118
Douglas A. Schaefer https://orcid.org/0000-0003-0760-8599
Stefan A. Schnitzer https://orcid.org/0000-0002-2715-9455
Chris M. Smith-Martin https://orcid.org/0000-0002-6557-1432
Kyle W. Tomlinson https://orcid.org/0000-0003-3039-6766
Sissou Zakari https://orcid.org/0000-0002-0062-5997
Jiao-Lin Zhang https://orcid.org/0000-0003-3693-7965
Yun-Bing Zhang https://orcid.org/0000-0002-2739-4324
Gerhard Zotz https://orcid.org/0000-0002-6823-2268
Juan Zuo https://orcid.org/0000-0001-6670-392X

Gbadamassi G. O. Dossa[1]*, Shambhu Adhikari[1], Kun-Fang Cao[2], Ya-Jun Chen[1], Jean Evans Israel Codjia[1,3], Richard T. Corlett[4], Jinlong Dong[1,5], Ze-Xin Fan[1], Pratibha Khatri[6,7], Mathieu Kiki[1], Hong-Lin Li[1,8], Tial C. Ling[9], Guangyu Liu[1,10], Bartosz Marek Majcher[11], Nehrish Nisar[5], Denis M. Njoroge[1,12], Bismark Ofosu-Bamfo[13,14], Steven Pearce[15], Mareike Roeder[16], Douglas A. Schaefer[17], Stefan A. Schnitzer[18], Chris M. Smith-Martin[19], Wai Phyo Thu[1], Kyle W. Tomlinson[4], Shui-Yuan Xu[8], Sissou Zakari[20], Jiao-Lin Zhang[1], Yun-Bing Zhang[1], Gerhard Zotz[21,22], Juan Zuo[12] and Johannes H. C. Cornelissen[23]

[1]CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan, 666303, China;
[2]Ecophysiology and Evolution Group, State Key Laboratory for Conservation and Utilization of Subtropical Agro-Bioresources, Guangxi Key Laboratory of Forest Ecology and Conservation, and College of Forestry, Guangxi University, Nanning, 530004, China;
[3]Research Unit Tropical Mycology and Plants-Soil Fungi Interactions, Faculty of Agronomy, University of Parakou, Parakou, BP 123, Benin;
[4]Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan, 666303, China;
[5]University of Chinese Academy of Sciences, Beijing, 100049, China;
[6]Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences & Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, 666303, China;
[7]Yunnan International Joint Laboratory of Southeast Asia Biodiversity Conservation & Yunnan Key Laboratory for Conservation of Tropical Rainforests and Asian Elephants, Menglun, Mengla, Yunnan, 666303, China;
[8]College of Biological and Chemical Science, Puer University, Puer, Yunnan, 665000, China;
[9]Bee Protection Laboratory, Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai, 50200, Thailand;
[10]Environmental education department, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan, 666303, China;
[11]School of Biological Sciences, The University of Hong Kong, Hong Kong SAR, China;
[12]CAS Key Laboratory of Aquatic and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, 430074, China;
[13]Department of Biological Science, University of Energy and Natural Resources, Sunyani, P.O. Box 214, Ghana;
[14]Department of Theoretical and Applied Biology, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana;
[15]The Tree Projects Lead Tree Climber, Big Tree State Pty. Ltd., Hobart, TAS, Australia;
[16]Department of Wetland Ecology, Institute of Geography and Geoecology, Karlsruhe Institute of Technology – KIT, Josefstr.1, Rastatt, D-76437, Germany;

[17]Centre for Mountain Futures, Kunming Institute of Botany, Chinese Academy of Science, Kunming, 650201, Yunnan, China;
[18]Department of Biological Sciences, Marquette University, Milwaukee, P.O. Box 1881,WI, USA;
[19]Department of Plant and Microbial Biology, University of Minnesota, St Paul, MN 55108, USA;
[20]Laboratory of Hydraulics and Environmental Modeling (HydroModE-Lab), Faculté d'Agronomie, Université de Parakou, 03 BP 351, Parakou, Benin;
[21]Functional Ecology of Plants, Carl von Ossietzky University, Carl-von-Ossietzky-Str. 9-11, 26111, Oldenburg, Germany;
[22]Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Panama City, Panama;
[23]Systems Ecology, Amsterdam Institute for Life and Environment (A-LIFE), Faculty of Science, Vrije Universiteit, De Boelelaan 1085, 1081 HV, Amsterdam, the Netherlands
(*Author for correspondence: email dgbadamassi@gmail.com)

References

Chen YJ, Maenpuen P, Zhang YJ, Barai K, Katabuchi M, Gao H, Kaewkamol S, Tao LB, Zhang JL. 2021. Quantifying vulnerability to embolism in tropical trees and lianas using five methods: can discrepancies be explained by xylem structural traits? *New Phytologist* **229**: 805–819.

Chen Y-J, Schnitzer SA, Zhang Y-J, Fan Z-X, Goldstein G, Tomlinson KW, Lin H, Zhang J-L, Cao K-F. 2017. Physiological regulation and efficient xylem water transport regulate diurnal water and carbon balances of tropical lianas. *Functional Ecology* **31**: 306–317.

Cortés-Flores J, Hernández-Esquivel K, González-Rodríguez A, Ibarra-Manríquez G. 2017. Flowering phenology, growth forms, and pollination syndromes in tropical dry forest species: influence of phylogeny and abiotic factors. *American Journal of Botany* **104**: 39–49.

Kaçamak B, Barbier N, Aubry-Kientz M, Forni E, Gourlet-Fleury S, Guibal D, Loumeto J-J, Pollet S, Rossi V, Rowe N *et al.* 2022. Linking drone and ground-based liana measurements in a congolese forest. *Frontiers in Forests and Global Change* **5**: 803194.

Meunier F, Verbeeck H, Cowdery B, Schnitzer SA, Smith-Martin CM, Powers JS, Xu XT, Slot M, De Deurwaerder HPT, Detto M *et al.* 2021. Unraveling the relative role of light and water competition between lianas and trees in tropical forests: a vegetation model analysis. *Journal of Ecology* **109**: 519–540.

Roeder M, Dossa GGO, Cornelissen JHC, Yang X, Nakamura A, Tomlinson KW. 2022. Liana litter decomposes faster than tree litter in a multispecies and multisite experiment. *Journal of Ecology* **110**: 2433–2447.

Schnitzer SA, Carson WP. 2023. Ecology of Lianas on Barro Colorado Nature Monument. In: Muller-Landau HC, Wright SJ, eds. *The first 100 years of research on Barro Colorado: plant and ecosystem science.* Washington, DC, USA: Smithsonian Institution Scholarly Press.

Schnitzer SA, van der Heijden GMF. 2019. Lianas have a seasonal growth advantage over co-occurring trees. *Ecology* **100**: e02655.

Smith-Martin CM, Bastos CL, Lopez OR, Powers JS, Schnitzer SA. 2019. Effects of dry-season irrigation on leaf physiology and biomass allocation in tropical lianas and trees. *Ecology* **100**: e02827.

Smith-Martin CM, Jansen S, Brodribb TJ, Medina-Vega JA, Lucani C, Huppenberger A, Powers JS. 2022. Lianas and trees from a seasonally dry and a wet tropical forest did not differ in embolism resistance but did differ in xylem anatomical traits in the dry forest. *Frontiers in Forests and Global Change* **5**: 834891.

Smith-Martin CM, Xu X, Medvigy D, Schnitzer SA, Powers JS. 2020. Allometric scaling laws linking biomass and rooting depth vary across ontogeny and functional groups in tropical dry forest lianas and trees. *New Phytologist* **226**: 714–726.

Zhang KY, Yang D, Zhang YB, Liu Q, Wang YSD, Ke Y, Xiao Y, Wang Q, Dossa GGO, Schnitzer SA *et al.* 2023. Vessel dimorphism and wood traits in lianas and trees among three contrasting environments. *American Journal of Botany* **110**: e16154.

Key words: 1st International Workshop on Lianas Forest Ecology, afterlife, carbon cycle, disturbance, liana biogeochemistry, liana phenology, liana roots, meeting report.