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Asli-Begüm Kaçamak. Stratégies écologiques des lianes d’Afrique centrale : de la diversité macro-anatomique aux structures des communautés. Génétique des plantes. Université de Montpellier, 2023. Français. NNT : 2023UMONG034 . tel-04629906v2

**HAL Id: tel-04629906**

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Submitted on 1 Jul 2024

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# THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Ecologie et Biodiversité

École doctorale GAIA

Unité mixte de recherche AMAP

## ECOLOGICAL STRATEGIES OF CENTRAL AFRICAN LIANAS: FROM MACRO-ANATOMICAL DIVERSITY TO COMMUNITY PATTERNS

Présentée par Begüm KAÇAMAK

Le 14/12/2023

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UNIVERSITÉ  
DE MONTPELLIER



*« Je m'attache à toi, lierre de rien » La Dactylo*

*« Tout cela me plonge dans la perplexité » Tarzan*





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## Remerciements

Beaucoup de mal à commencer à rédiger mes remerciements depuis 1 mois. A chaque fois que je m'y mets, je veux commencer à remercier en premier les deux personnes qui m'ont suivi depuis le début, depuis mon stage en 2017 où je me tâtais à aller en recherche, et je commence à pleurer, et donc j'arrête. Sauf que là je dois rendre ma thèse dans quelques jours, et je n'arrive toujours pas à passer le stade des premières lignes...

J'ai commencé dans les couloirs de Baillarguet, remplie de questions sur le sens de la vie, hésitante sur toutes mes décisions, et aucune idée claire sur ce que je voulais faire concrètement. Quoique ça n'a pas forcément beaucoup évolué depuis ;) C'est là en tout cas, que j'ai commencé à embêter Sylvie, dans le bureau d'à côté, souvent avec des discussions logiques et civilisées, et parfois étalée sur son sol en désespérant sur les choix de vie que j'avais à faire. Merci Sylvie pour toutes ces discussions, toutes ces anecdotes incroyables, des voyages périlleux aux missions de terrain de rêves, qui m'ont d'autant plus donné envie de continuer là-dedans. Merci de m'avoir montré l'exemple de comment c'est possible de trouver sa place en tant que femme dans un domaine principalement constitué d'hommes, et surtout, de ne jamais se retenir d'affirmer son opinion. Plus que la science, tu étais toujours là pour savoir comment j'allais et prête à discuter des problèmes de la vie autour d'un café. Même si tu ne te rendais pas forcément compte de l'influence que tu avais sur les autres, et à quel point tu les touchais, je ne l'oublie pas. Donc promis, au moins pendant ma soutenance, quand je te remercierais, j'essayerais de pas pleurer. Je me dis que si j'ai réussi à l'écrire, j'arriverais peut-être à le dire.

Max, après m'avoir supporté tous les jeudis pendant 6 mois, qu'est ce qui t'as poussé à me faire revenir sur Montpellier, je ne sais pas ! Peut-être que c'est justement parce que tu ne m'avais pas encore supporté une semaine entière et que tu ne savais pas encore dans quoi tu t'embarquais :D. En tout cas, merci de ne pas m'avoir lâché et de m'avoir poussé à quitter un travail qui ne me plaisait dans aucun sens, et encouragé à revenir en recherche et à continuer en thèse. Honnêtement sans ce soutien je ne sais pas si aujourd'hui j'aurais réussi à finir en recherche, et dans le domaine qui me plait le plus, en forêt tropicale. Merci d'avoir été là pendant ces 6 dernières années, que ça soit pour me redescendre sur terre quand je plane avec mes habilités organisationnelles pourries, pour me remotiver quand je commence à papillonner, ou bien pour écouter mes histoires de cœur quand ça n'allait pas du tout. Merci de ne pas désespéré constamment de mes bourdes ou de mes codes mal tenus. Je te jure c'est un peu mieux, enfin, pour les codes du moins :D Merci pour ton humour toujours présent, grâce à toi j'ai appris à être moins naïve, enfin j'espère, à force de croire à toutes tes blagues, même les pourries :P J'ai même appris à reconnaître tes bruits de pas dans le couloir vers la fin :P. Last but not least, merci de m'avoir montré à éviter de me surcharger de travail comme toi, pour éviter de ne plus dormir ;). Non mais sans déconner, je me sens sincèrement beaucoup trop chanceuse d'avoir eu toi et Sylvie autour de moi, maintenant le problème c'est que la barre est trop haute pour la suite :D.

Merci Nick, d'avoir pris le risque de me prendre sous ton aile avant de me connaître. J'en suis très reconnaissante. Merci de m'avoir fait rêver à travers multiples discussions des possibilités que peuvent offrir les plantes et toutes les inspirations qu'on peut en tirer. J'ai toujours l'impression de faire partie de manière très brief d'un groupe qui fait de la science-fiction et invente des choses sorties tout droit d'un film. Merci de m'avoir poussé vers une certaine indépendance et une confiance en soi, qui n'est

pas toujours facile à avoir, pour toutes les anecdotes d'expérience que tu as partagées avec moi, et pour être passé presque tous les jours quelques minutes pour savoir comment j'allais ce dernier mois de rédaction. Ça m'a énormément touché.

Merci Vivien, d'avoir accepté de faire partie de ma thèse, même si ce n'était pas évident d'échanger et de se tenir au courant par distance. Malgré tout cela tu étais toujours là dans mes réunions de thèse quand tu le pouvais, toujours intéressé par ce que je faisais, et toujours prêt à contribuer. Si j'avais un problème de stat ou de modélisation, tu étais toujours là pour m'aider, malgré la difficulté à suivre mon travail de loin. Merci d'être même venu jusqu'au fond de la forêt sur le terrain avec moi pour voir ce que je faisais, malgré les abeilles et les mélipones !

Ma thèse ne s'est pas faite toute seule. J'ai eu de l'aide et du soutien dans tous ses aspects, que ça soit au labo, sur le terrain, ou bien dans ma vie perso. Beaucoup de personnes à remercier, auxquelles je suis tellement reconnaissante, mais aussi beaucoup que j'oublie, tellement la liste est longue. Je vais essayer de couvrir le plus de monde possible, mais si j'en oublie (c'est sûr !) je m'en excuse d'avance !

Merci tout d'abord à AMAP, le CNRS, le projet GrowBot, et le Cirad, pour m'avoir accueilli et financé pendant toute ma thèse, qui n'est clairement pas réalisable sans de la moulaga. Mais il ne faut clairement pas que ça ! En suit toute une ribambelle de problèmes administratif toujours plus complexes. Mille fois merci à Marie-Laure d'avoir été patiente et d'avoir su régler tous les problèmes, que ça soit lié à mon contrat hybride, à mon terrain difficile, ou bien à mes envies de donner des cours à la fac. Merci à Valérie et Miléna pour toujours m'accueillir dans votre bureau et prendre le temps de discuter, même si vous êtes tous le temps débordé de travail. Merci Valérie pour toujours m'ouvrir la porte quand j'oublie ma carte (au moins une fois par mois), mais j'attends toujours de découvrir le code du coffre-fort de AMAP ;) Merci Miléna pour toutes les histoires, pour tous les ragots, les bons plans de vacances, et aussi pour ton placard magique derrière toi :P Merci à Héroïse pour avoir été partante pour organiser des sorties canoë ! Merci à Thierry d'avoir été de manière si bienveillante en tête du labo, d'avoir des discours toujours aussi bien préparés, de m'avoir personnellement suivi dans ma thèse, que ce soit dès le début en nous poussant à faire des formations pour que celle-ci se passe bien compte tenu du grand nombre d'encadrants que j'avais, ou pour ta bienveillance pendant mes comités de suivi. Merci pour toutes tes blagues, et d'être toujours bon public aux miennes qui ne sont pas forcément meilleures :D Merci à vous tous.tes, à Nathalie, à Caroline, et tous.tes ceux et celles de l'administration qui permette au labo de tourner et nous soutien tous les jours dans la bonne réalisation de nos activités !

J'ai eu la chance pendant ma thèse de découvrir différents outils, différentes techniques de labo, et différents domaines, qui n'auraient pas été possible sans l'aide et la coopération de beaucoup de personne. Merci à Patrick Langbour et Daniel Guibal, de toujours m'avoir bien accueilli au labo du bois. Merci Daniel de toujours prendre le temps de me répondre quand je reviens chaque année pour des questions. Merci à Raphaëlle Leclerc du CEFÉ pour m'avoir montré et expliqué comment réaliser des analyses chimiques. Merci à Samantha pour toute son aide à l'herbier. Merci de m'avoir initié au travail d'herbier, montré toutes les ressources qui existent et où chercher. Merci à David Harris pour toute sa précieuse aide, particulièrement pour les identifications botaniques et tout ce qu'on prévoit par la suite, mais aussi pour toute son implication dans ma thèse et mon comité de suivi de thèse. J'espère qu'un jour je pourrais venir te visiter à Edinburgh et à l'herbier du Royal Botanic Garden. Merci Nico,

pour m'avoir patiemment aidé à manipuler des données LiDAR, mais aussi pour ton cynisme sans égard. Merci Hervé, pour avoir tenté de me brancher et de m'apprendre le deep learning (même si ça n'a pas trop marché :P). Merci Eric d'avoir pris le temps de m'expliquer toutes mes questions en rapport avec les analyses de diversité. Merci à Quentin, Merlin et Stéphane pour m'avoir aidé avec les mesures de traits. Merci aux stagiaires que j'ai encadrées, Carla et Maël, pour votre aide précieuse. Particulièrement Carla, de m'avoir suivi sur le terrain pendant 2 mois, tout en gardant la bonne humeur, d'avoir partagé ta chambre avec moi pendant tout ce temps, entre maladies, positions bizarres de dormance, tempêtes et chèvres, accompagner dans des envies de goûter à tout, d'être aussi exaltée que moi devant une grosse liane (Aaaaaaah, comme dirait Cyril), dans les frénésies pétage de câble avec les tissus africains, les petits plaisirs chez Glacy, et surtout dans le diplôme d'apprenti secouriste obligatoire dans l'avion. J'espère que notre courage et bravoure sont passés de bouches en oreilles dans tous les Air-France pour qu'on nous offre des couvertures en plus dans tous nos trajets.

Merci à tous.tes ceux et celles en plus qui ont aussi contribué à enrichir ma culture scientifique. Merci à Lourens Poorter pour les discussions très intéressantes, ainsi que d'avoir accepté d'être mon rapporteur de thèse. Merci aussi à Adeline Fayolle d'avoir accepté d'être ma rapportrice. Merci à tous.tes les deux d'avance de prendre le temps de lire et d'apprécier mon travail de thèse. Merci au reste de mon jury, Geertje van der Heijden et Sandrine Isnard, d'avoir accepté d'évaluer mon travail. J'espère qu'elle vous intéressera autant que moi :). Merci Geertje pour tous ces échanges intéressants sur les lianes et d'avoir accepté d'être la Keynote speaker à la session lianes à la conférence GTOE à Montpellier. Je remercie particulièrement tous les participants de la session, pour les échanges riches, la session de partage de retour d'expérience de « lianes extraordinaires », ainsi que les moments passés en dehors dans la ville de Montpellier. Merci à Patrick, et à Pierre-Olivier Cheptou pour avoir accepté de faire partie de mon comité de suivi de thèse et m'avoir suivi pendant 3 ans.

La bonne ambiance et l'environnement chaleureux dans lequel j'ai été tous les jours au labo est clairement une des raisons pour laquelle j'ai tant apprécié ma thèse. Merci à ma première colocation de bureaux, Brigitte et Isa, pour avoir eu la patience d'écouter et de répondre à toutes mes questions farfelues. Merci Brigitte, de m'avoir supporté pendant presque 2 ans, en assistant directement à toutes mes indécisions de vie et changement d'envies. Merci Guillaume pour tes conseils pour les cours à la fac ; Anne-Laure pour tes conseils pour m'expliquer comment fonctionne les concours dans le public ; Gilles pour toujours penser à passer à pile 11h45 pour la cantine même si je ne te suis pas toujours, et Phillipe pour avoir donné vie à mon compost avec tes bokashis. Merci au « Let's play : the thing », Juliette, Bruno, Paul, Housseem, Lily et Colin, pour tous ces gifs toujours aussi plus beaux les uns que les autres. Juliette, merci de me supporter presque tous les jours au bureau et de partager mon quotidien, entre les sessions de yoga qu'on n'a finalement fait qu'une seule fois en 2 ans, les recherches de motivation, les temps passé à rêver et rechercher des futures idées de vacances plutôt que nos thèses, la note quotidienne de « tu sais pas ce que Max m'a dit ? », les moments d'hypoglycémies, les souvenirs et le manque de Sylvie, la flemme de prendre le vélo les matins, tes conseils de défoulement d'énergie, et la responsabilité de Pénélope, Timothée, Luc et Dead Bouboule. Merci Colin pour ton côté pessimiste qui me fait souvent relativiser, les câlins d'urgence, ton amour des chats, et surtout pour Pout <3. Merci Housseem d'être ma go-girl avec Rihanna, toujours OP pour une journée improvisée à Marseille, les paillettes au cinéma et de partager avec-moi ton désarroi envers la France et la facilité de l'intégration dans ce pays qui nous fait un gros câlin. Merci Lily pour les moments de raviolis, les photos de rêves d'où tu es maintenant, et de nous avoir léguer (ou oublier plutôt) Bouboule aka Dead

Bouboule. Merci Paul d'avoir partagé ton canoë avec moi et aider à déplacer des gros bouts de bois le long de la rivière. Et merci Bruno, en étant même pas au labo, de nous nourrir constamment de bonnes choses, des choux, des macarons, des éclairs, des tartes, sans arrêts ! Merci à David, mon acolyte de la natation, de toujours « essayer » de me motiver à aller nager (une fois sur 2 ça marche !), d'être chaud pour le toboggan et de m'avoir aussi branché au body tonic les jeudis midi. Merci d'être toujours de bonne humeur et rempli d'humour, de me donner pleins de conseils de bien être mental pendant la thèse, parler du futur, de l'avenir, et de me rassurer. J'ai très hâte de vivre 10 jours au fond du Sarek à -20 degrés avec toi ! :D Merci Brunaõ d'avoir été si fou et de m'avoir fait découvrir tant de bonnes choses à travers tous vos repas et brunch brésilien avec Jannah. Pareil pour Erica, je me souviens encore des brigadeiros incroyable !!! Par contre, j'attends encore les lasagnes ;) Merci à Clément, qui n'a débarqué qu'à la fin mais m'a accompagné sur toutes les soirées longues à AMAP en plein écriture, à stresser pour sortir à temps et ne pas déclencher l'alarme de 20h, et tous les remonte-morals lié à la nourriture. Merci à Camille G., Camille S., Daniela, James, Jeanne, Laetitia, Alex, ose-Eva, Dim, Emilie, Vinciane, Hadrien, Jean-Baptiste, Jérôme, Fabien, Fred, Melaine, Raphael, François et tous.les les autres stagiaires, doctorants, post-doctorants et chercheurs que j'ai eu l'occasion de croiser et de côtoyer, et j'en oublie sûrement pleins, pour ces 4 années à AMAP. Merci à Sarah Cubaynes pour avoir été ma mentor dans le mentorat de Femmes & Sciences, et même si on n'était pas très assidues, merci d'avoir toujours eu quand on se voyait des discussions revigorantes et rassurantes sur la vie et les différentes tournures de carrière. Et petite mention spéciale à l'équipe du volley (#BLT) et en particulier Alex qui nous a longtemps porté ! On n'était pas forcément bons, mais on était là !

Mes phases préférées pendant ma thèse, c'était le terrain au Congo. Toutes ces missions, à chaque fois différentes et hyper riches en expérience, n'auraient jamais été possible sans l'appui de tout ceux au Congo qui m'ont accompagné. Merci Eric, pour ton humour et ta bienveillance, et d'avoir toujours été là pour aider dans l'organisation de chaque mission de terrain. Merci Yorick, pour toutes ses missions qu'on a passées ensemble, pour tous ses trajets en voiture où tu voyais tout pleins de panthères et moi jamais, pour tout ce que tu as fait pour la logistique et l'organisation des missions, et surtout mais surtout pour ses vacances incroyables de malade mental qui me fait encore baver aujourd'hui avec Juliette à Dzanga Sangha en RCA et à Nouabalé-Ndoki à voir de près les gorilles (#babyIpolo) et passer des heures à regarder des éléphants de forêts dans des salines. Merci à la CIB, Vincent Istace et Baptise, pour toujours nous accueillir et être intéressé par les lianes et ce que je fais avec elles. Merci Kleis pour les soirées déjantées à Pokola, à passer de bar en bar et de boîte en boîte, pour finir au petit matin dans la piscine. Merci pour tes histoires toujours plus folles, je ne m'en remets toujours pas pour certaines, et ta liberté de parole toujours plus facile ! Merci à toute l'équipe du camp, d'avoir toujours été là, Isaac pour les moments de réveil radio avec des chants religieux et tes conseils sur la vie, la botanique, la forêt et le lingala « Mboté ! Namoni ebobo, kasi namoni te nzoku, kaka tufi... Nakei kolala, lobi ! » ; Marien pour m'avoir initié en premier à la découverte des lianes, tes histoires de guerres, convictions philosophiques et discussions toujours intéressantes ; Pachtely pour ta bonne humeur et d'avoir été là pour toutes mes missions, tes bobos à chaque terrain que je retrouvais à soigner et ta mauvaise foi dans les jeux de cartes ; Ati pour être un fou furieux dans la forêt, une vrai machine de guerre, toujours motivé, toujours plein d'énergie ; Cyril d'avoir accepté de partager toute ta connaissance botanique sur les lianes avec moi, et de m'avoir aider à essayer de faire un premier jet de guide de terrain ; Dambilo pour nous avoir initié à la culture et danses pygmée, et Ibrahim pour ton calme et ta facilité à prendre en main la mission. Raoul, Fred, Ariel, merci pour tous les repas savoureux préparés au camp (#3pièces). Et merci à tous ceux et celles qui était aussi de passage sur le terrain,

avec qui j'ai pu partager des moments en forêt ou le soir au camp : Aimée, Alain, Latifa, Mara, Raphaël, Robin, Sasha, et encore d'autres que j'oublie sûrement ! Et pour finir avec le Congo, un énorme merci aux abeilles et aux mélipones, dans le t-shirt, dans le blanc des yeux, dans le fût, pour m'avoir permis de toujours être au taquet en forêt.

Forcément, je ne peux pas m'arrêter sans remercier toutes les personnes qui ont partagé ma vie pendant ces 3 dernières années, à Montpellier ou pendant des week-ends, ou des vacances, qui ont sûrement si bien m'aimer, si bien m'aider dans les moments durs, et si bien me faire rigoler pour me changer les idées. Merci Coralie et Laina, d'être toujours là depuis maintenant plus de 10 ans, et de toujours venir quand ça ne va pas, même si je ne vous le dis pas et ne vous le demande pas, même quand on est à des lieux et des lieux de l'une d'entre nous ! Merci pour toutes ces vacances ensemble qui perdurent, les piercings et les tatouages spontanées et j'en passe ! Merci Samy, de m'avoir supporté pendant toutes mes crises de larmes cette dernière année entre tout ce qui s'est passé, d'être toujours complètement fou et toujours mais toujours de bonne humeur. Merci Théo pour ton affection à laquelle je ne m'attendais pas, pour ta douceur, pour les bonnes bouffes, pour le linguo de jeunes que tu me réapprends, c'est incr, pour tous les messages que tu commences par « cc » comme si tu me mettais en copie, et pour tous les week-ends échappatoires qu'on ait pu faire. Merci Mariette, toujours là pour les ragots, et je ne m'en lasse jamais, pour avoir pris le temps de venir me faire à manger les week-ends quand je devais bosser, de partager avec moi la passion du puzzle pendant des heures et des jours entiers, pour tous les moments de la vie qu'on partage ensemble, du banal au plus incroyable, et toutes les discussions, du sérieux au plus débile et j'oublie encore tellement de choses que je pense que tu me connais limite mieux que moi-même. Je pense qu'avec nos mémoires de merde à deux on pourrait faire un cerveau commun. Merci à l'équipe « tape-tape canette C marseille BB » de Montpellier ; Val, Robin, Bière et Lucie, pour toutes les soirées de couvre-feu et de confinement qui nous permitâmes de tenir le coup socialement et mentalement. Merci à Dulce et Lucie d'avoir partagé votre amour de poterie avec moi. Merci à Mushu pour 6 mois de câlins et bavage intensif. A toutes mes colocs avec qui j'ai pu substanté depuis 3 ans, Rebecs, Noé, Emma, Auriane et Silouane, merci pour tous ces moments de bouffe, de jeux, de films, de rando, de baignade, de ragots et de plaisir. Mes ptits Q, Briac, Théo, Camilou, Coralay et Lélé, merci pour tous nos week ends de folie (#Charlène) et un trip aux USA incroyable ! Merci à Mel, avec qui j'ai partagé toutes les soirées du confinement une séance sport de Sisi par visio, pendant un moment où toutes les deux, ça nous a permis de survivre ensemble. Merci à Izel et Sel d'être venues me voir et déconner pendant ces moments pas drôles. Mes trois GO sûres, Mel, Izel et Sel, and mischieves pour toujours. Merci à Marion d'avoir partagé le même bateau que moi avec la thèse, les mêmes galères et les mêmes échéances. J'en retiendrais surtout les voicenotes pétage de plomb, ras le bol et être bored de son propre boredom et stress :D. On se retrouve en chômage-vacances bientôt ! Merci à Sisi, Sese et Ayse, pour avoir continué à faire des vacances ensemble, j'avoue parfois où je pète des plombs, mais qui font toujours autant de bien. Merci surtout d'être venus cet été, même si j'ai râlé, ça m'a fait beaucoup de bien. Merci à Janus, Fanny, Raph, Guigui, Katish, Flo, Loulou, Nak, Dilou, Perrouss', Valou, Soso, Gus, Sofia, Guibeurre, Robin, Steph', Théo et toutes celles et ceux qui ont partagé mon mariage avec la France et la Roumanie et toutes celles et ceux que j'oublie forcément, d'être là, d'être qui vous êtes, et de me compter dans vos amies !

P.S. N(merci)=81, ca fait beaucoup de choses to be thankfull for dis donc







## Abstract

Lianas develop some of the most complex vascular organizations in plants and are an emblematic growth form in the diversity and dynamics of tropical forests. However, their ecology and especially the links between traits, anatomy and community structure remain poorly known. The goal of this thesis is to deepen our understanding of the ecological strategies of lianas, from macroanatomical diversity to community-level patterns, using both ground- and drone-based field data. The study was carried out in Northern Congo, where trees and lianas are monitored in permanent plots through time. In three independent chapters, I explore (i) the link between commonly used ground-based liana measurements and drone-based measurements of liana leaf coverage over tree crowns; (ii) the influence of local topography, forest structure, and tree composition on liana community structure and floristic and functional composition; and (iii) the strategies associated with the macroanatomical diversity of lianas, their links to the leaf economic spectrum, and their patterns across a phylogeny and environmental gradients. Most ground-derived liana metrics were significantly related to drone-derived liana leaf coverage over tree crowns. This was best predicted by liana basal area and negatively mediated by liana wood density, with a higher leaf area-to-diameter ratio for light-wooded lianas (see [doi:10.3389/ffgc.2022.803194](https://doi.org/10.3389/ffgc.2022.803194)). Along environmental gradients, the liana community structure was mainly determined by local forest structure, with an increased abundance of small-sized lianas and basal area in open canopy areas where they competed with giant herbs. The floristic and functional composition of lianas varied marginally along these gradients. Faster acquisition strategies tended to occur in open canopy areas (low liana wood density, high specific leaf area, and %PO<sub>4</sub>). Lianas exhibited significant species-specific associations with the most common lianas and trees. Through the lens of functional ecology, liana species exhibited a large diversity of macroanatomical structures and cambial variants. These were associated with strategies ranging from hydraulic efficiency to hydraulic safety, and higher density stems in the self-supporting phase to resilience during climbing. Both leaf and wood strategies were significantly coupled and distributed throughout the phylogeny. However, only the trade-off between acquisitive and conservative leaf strategies was significantly affected by environmental gradients, while wood strategies appeared to remain neutral. I hope that this work will contribute to a better understanding of the temporal and spatial distribution of liana species and better predict shifts under large-scale and environmental conditions.

## Résumé

Les lianes développent des organisations vasculaires parmi les plus complexes chez les plantes et constituent une forme de croissance emblématique de la diversité et de la dynamique des forêts tropicales. Cependant, leur écologie et notamment les liens entre traits, anatomie et structure des communautés restent peu connus. L'objectif de cette thèse est d'approfondir notre compréhension des stratégies écologiques des lianes, de la diversité macro-anatomique à la structure des communautés, en utilisant des données de terrain au sol et par drone. L'étude a été menée dans le nord du Congo, où les arbres et les lianes sont suivis dans des parcelles permanentes au fil du temps. Dans trois chapitres indépendants, j'explore (i) le lien entre les mesures au sol des lianes couramment utilisées et les mesures par drone de la couverture foliaire des lianes sur les couronnes des arbres ; (ii) l'influence de la topographie locale, de la structure forestière et de la composition du peuplement d'arbres sur la structure des communautés de lianes et sur leur composition floristique et fonctionnelle ; et (iii) les stratégies associées à la diversité macro-anatomique des lianes, leurs liens avec le spectre économique des feuilles, et leurs distributions à travers une phylogénie et le long de gradients environnementaux. La plupart des mesures de lianes dérivées du sol étaient significativement liées à la couverture foliaire des lianes dérivée des drones sur les couronnes des arbres. C'est la surface terrière des lianes qui permettait le mieux de prédire la couverture foliaire des lianes, influencé négativement par la densité du bois des lianes, avec un rapport surface foliaire-diamètre plus élevé pour les lianes à faible densité de bois (voir doi:10.3389/ffgc.2022.803194). Le long des gradients environnementaux, la structure de la communauté de lianes était principalement déterminée par la structure forestière locale, avec une abondance plus importante de lianes de petite taille, et de surface terrière dans les zones de canopée ouverte où elles sont en concurrence avec les herbacées géantes. La composition floristique et fonctionnelle des lianes variait légèrement le long de ces gradients. Des stratégies plus acquiescentes de ressources tendent à se développer dans les zones à canopée ouverte (faible densité de bois de liane, surface foliaire spécifique et %PO<sub>4</sub> élevée). Les espèces de lianes communes étaient significativement associées avec les espèces d'arbres les plus communes. Du point de vue de fonctionnel, les espèces de lianes présentent une grande diversité de structures macro-anatomiques et de variantes cambiales. Celles-ci sont associées à des stratégies allant de l'efficacité hydraulique à la sécurité hydraulique, et à des tiges plus denses dans la phase d'autoportance à la résilience lors de leur ascension dans la canopée. Les stratégies relatives aux feuilles et au bois sont étroitement liées et réparties sur l'ensemble de la phylogénie significativement. Cependant, seul le compromis entre les stratégies foliaires acquiescentes et conservatrices est significativement affecté par les gradients environnementaux, tandis que les stratégies du bois semblent rester neutres. J'espère

que ce travail contribuera à une meilleure compréhension de la répartition temporelle et spatiale des espèces de lianes et permettra de mieux prévoir les changements dans des conditions environnementales et à grande échelle.



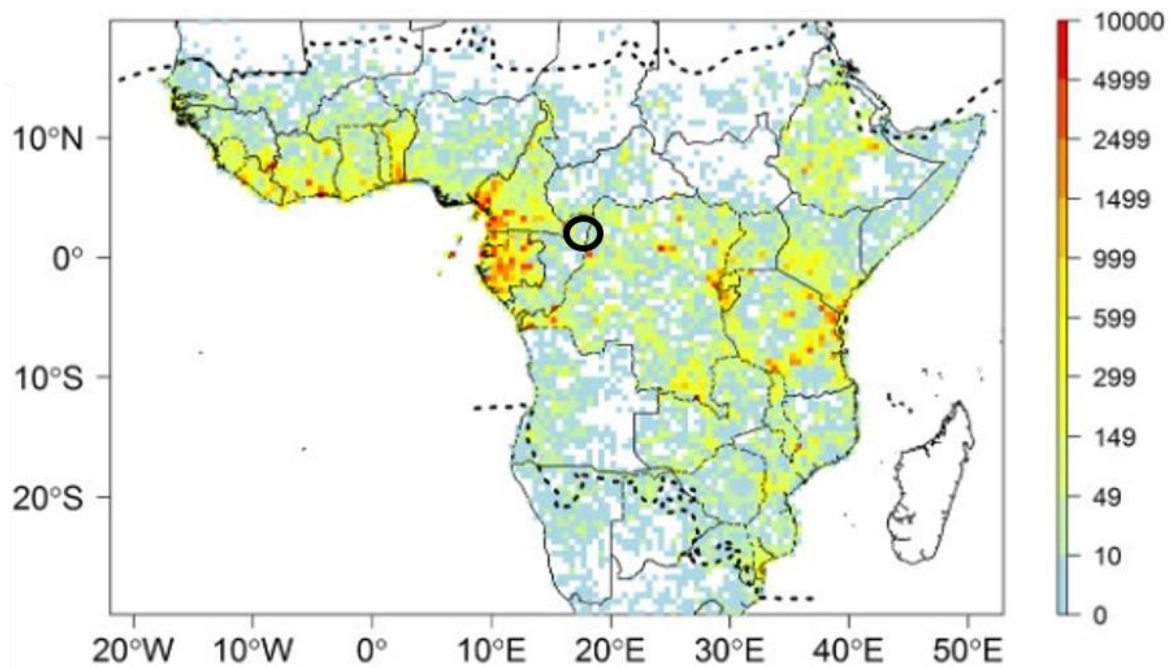


# 1 General Introduction

## 1.1 Lianas and their importance in tropical forests

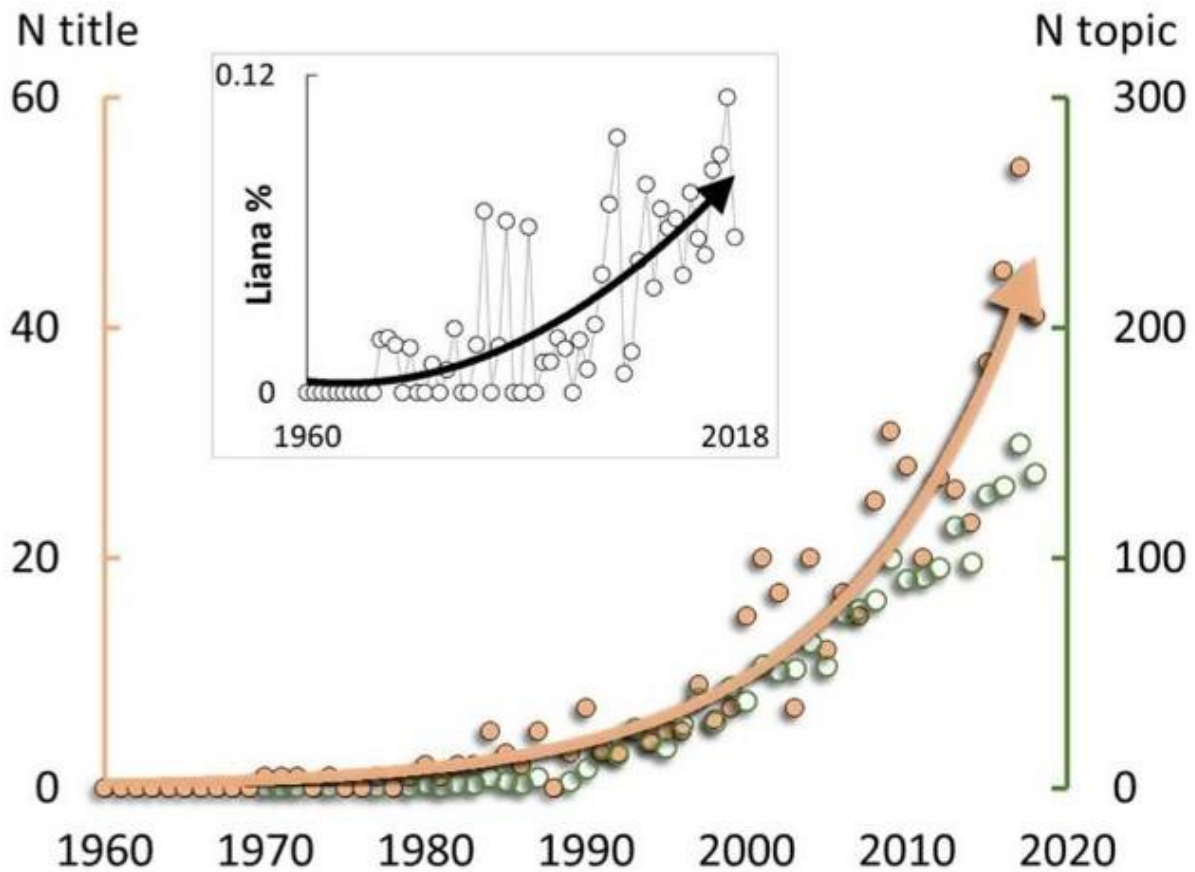
### 1.1.1 Tropical forests, Central Africa, lianas and historical lack of studies

Tropical forests are one of the most important ecosystems on Earth, performing a multitude of functions with global implications (Watson et al. 2018). They account for one-third of the productivity and evapotranspiration of the Earth's land surface (Malhi 2012) and are considered a key element of global climate regulation by acting as a significant carbon sink and mitigating climate change (Pan et al. 2011; Alkama and Cescatti 2016; Grassi et al. 2017; Luysaert et al. 2008). In addition to their ability to store carbon, tropical forests harbor unparalleled biodiversity (Gibson et al. 2011) and serve as hotspots for over half of all plant and animal species (Myers et al. 2000). A great biodiversity in species composition and individuals contribute to the ecological stability and resilience of tropical forests (Donohue et al. 2016). Throughout history, tropical forests have provided food and water to indigenous peoples and invaluable resources for human health and economic revenues (Watson et al. 2018). Today, these species-rich ecosystems are suffering from losses in biodiversity and carbon storage capacity due to deforestation and degradation (Vancutsem et al. 2021; Hansen et al. 2013). Recent increases in natural and anthropogenic disturbances leading to significant loss of forest cover and changes in precipitation patterns due to global change have exacerbated the vulnerability of tropical forests (Malhi et al. 2014). Conservation measures and sustainable management strategies are urgently needed to mitigate the impacts of global change and anthropogenic pressures. The preservation of tropical forests requires a comprehensive understanding of the different components of tropical forests and their interactions, distribution, and responses to global change (White et al. 2021). A thorough understanding of tropical forest ecology will enable us to more accurately predict their dynamics and support effective conservation and sustainable management strategies that are essential for the future conservation of tropical forests (Réjou-Méchain et al. 2021). Although Central African forests represent the second largest block of humid tropical forests after the Amazon, many regions remain poorly studied scientifically (Figure 1; Sosef et al. 2017), which affects our understanding of forest functions, compositional changes, and forecasting of the different components of tropical forests.



**Figure 1.** Map of botanical records distribution based on herbarium records, silica gel samples and plot data across tropical Africa, per 0.5° sampling units. The black circle represents the study area where I conducted my thesis and illustrates the lack of botanical knowledge in this region. The illustration was taken from Sosef et al., 2017 and modified.

An increasingly recognized component of tropical forests are lianas. They have attracted the interest of scientists since the 19th century because of their unique life history and one of the most complex vascular systems in the plant kingdom (Darwin 1875), but until recently have received relatively little attention in ecological studies (Schnitzer and Bongers 2002; Marshall et al. 2020). The huge diversity of growth forms, taxonomic uncertainties, lack of botanists, and difficulties in field identification have led to the omission of lianas from most contemporary studies of community ecology (Schnitzer and Bongers 2002). Overall, our understanding of the ecology of lianas and their role in the ecosystem has lagged far behind that of trees, and this is even more true in Central Africa where the literature is scarce. In neotropical forests, lianas may account for 35% of woody plant diversity and 25% of plant density (Schnitzer et al. 2012; Schnitzer 2015), invade more than half of the canopy tree crowns (Ingwell et al. 2010), and significantly alter the carbon cycle of tropical forests (Porcia e Brugnara et al. 2019). Lianas also create vertical stratification by bridging the gap between soil and tree canopies and providing pathways and nutrient resources for animals (Thiel et al. 2021; 2023). With the increasing recognition of the importance of lianas to forest dynamics (Laurance et al. 2014; Tang, Kitching, and Cao 2012; Schnitzer and Bongers 2005; Putz 1984), the number of liana studies has grown exponentially in the last decade, nearly doubling from the 1980s to 2010 (Figure 2).



**Figure 2.** Exponential increase of liana studies in the last decades. The illustration is taken from Marshall et al., 2020. Primary y-axis shows the number of papers per year with primary focus on lianas (i.e., title mentions of “liana” or “lianas”; N title; peach-coloured points). Secondary y-axis shows the number of papers per year with more general inclusion of lianas (i.e., title, keywords or abstract mentions; N topic; green points).

### 1.1.2 Definition of lianas and the lianescent habit

Lianas are long stemmed and slender terrestrial plants found on all continents and which have evolved in more than 130 angiosperm families (Gentry 1991). They are characterised by a distinctive growth habit and physiological strategies in their climbing behaviour. After germination on the ground, most lianas initially go through a self-supporting phase in the young, early stages of their development. During this juvenile phase, many liana species exhibit characteristics similar to trees or shrubs in that they mechanically form stiff and upright stems (Caballé 1998; Darwin 1875; Putz 1984; Putz and Chai 1987). These allow lianas to search for hosts using a variety of exploratory strategies thanks to different specialised structures called climbing mechanisms (Rowe and Speck 2015). Lianas are able to climb trees using tendrils, prehensile or angular branches, hooks, spines, adhesive roots or hairs, or simply twining or scrambling (Figure 3). Twining species and lianas with tendrils often exhibit active behaviour



in seeking support through circumnutation. In contrast, liana species with more passive climbing mechanisms such as hooks, adventitious roots or hairs, or spines can show further strategies for attaching and climbing (Melzer et al. 2010; Sperotto et al. 2020).



**Figure 3.** Diversity of climbing mechanisms of lianas in northern Republic of Congo. (a) *Fabaceae* spp, adherent hairs; (b) *Strychnos aculeata*, spines; (c) *Artabotrys* spp, hook; (d) *Clerodendrum* sp1, angular branches; (e) *Luffa cylindrica*, tendril, (f) *Loeseneriella* sp2, twining; (g) *Urera* spp, adherent roots and (h) *Strychnos* sp2, tendril-like hook.

After a variable young exploratory phase, many liana species lose their ability to support themselves and become flexible as they begin to climb trees to reach the canopy (Darwin 1875; Caballé 1998; Isnard and Silk 2009; Putz 1984). The physiological change in the lifestyle of lianas to a lianescent, climbing form is related to the development of a diversity of complex vascular organisations (Chery et al. 2020; Angyalossy, Pace, and Lima 2015; Hegarty 1991), which give liana stems sufficient flexibility to climb and adapt to different types of supports, but also toughness to survive and heal from environmental hazards (Rowe and Speck 2015; Fisher and Ewers 1991; Putz and Holbrook 1991; Dobbins and Fisher 1986; Putz 1984). Once adult lianas begin climbing, they do not invest in structural support such as trees and need smaller diameters to reach the canopy (Francis E. Putz 1984a; Kurzel, Schnitzer, and Carson 2006). The leaf mass production of lianas of 2 cm in diameter have been found comparable to the leaf mass production of canopy trees of 10 cm in diameter (Gerwing and Farias 2000; Gerwing et al. 2006). Investing less biomass into diameter to reach the canopy than trees, lianas tend to have a greater ratio of leaf area-stem diameter (Hegarty and Caballé 1991; Medina-Vega et al. 2021). This allows lianas to form a monolayer of leaves above the canopy, reducing light availability and competing directly with trees for aboveground resources (Avalos, Mulkey, and Kitajima 1999; Visser et al. 2018). In fact, lianas can occupy 30% of the forest leaf area, while accounting for less than 5% of the biomass of woody stems (Geertje M. van der Heijden et al. 2013). In addition, lianas are

thought to be in direct competition for belowground resources with trees because they are better able to explore and capture soil resources (C. G. Collins, Wright, and Wurzbürger 2016; Smith-Martin et al. 2019; De Deurwaerder et al. 2018). As a result of the competition and mechanical stress of lianas on trees, lianas have mostly been studied at the community level for their impact on tree demography and forest dynamics.

### 1.1.3 Liana impact on tree and stand-level dynamics

Lianas have been shown to be aggressive competitors of trees (Putz 1984; Schnitzer and Bongers 2002; Reis et al. 2020). They are mainly known to have negative effects on trees, ranging from seedling recruitment and tree floristic diversity to tree growth, carbon storage, and water assimilation (Laurance et al. 2014). Indeed, in Bolivia, lianas were found to limit natural tree regeneration, negatively affecting tree seedling growth (Pérez-Salicrup 2001). Competing severely with tree seedlings, their impact can lead to potential shifts in the diversity of tree floristic composition in tropical forests. In early-late secondary succession forests in Panama, lianas were even shown to reduce diversity, recruitment, and survival of shade-tolerant tree species by half (Schnitzer and Carson 2010). As a result, they can lead to significant reductions in the carbon uptake of tropical forests. They have been found to decrease the aboveground net carbon uptake by 76% each year in Panama again, in part due to the negative effects of lianas on tree growth (van der Heijden, Powers, and Schnitzer 2015). Whilst they reduce tree carbon sequestration, lianas do not particularly compensate through their carbon uptake. In Peru, they were shown to reduce annual aboveground tree biomass gains by 10% and offset only 29% of the loss (Van der Heijden and Phillips 2009). According to a dynamic global vegetation model, accounting for lianas reduces accumulated aboveground forest biomass by 19% (Porcia e Brugnera et al. 2019). Moreover, through their negative impact on tree growth, lianas significantly alter the height-diameter allometry of trees, being lower than would be expected for infested trees (Loubota Panzou et al. 2022), and can lead to arrested ecological successions. Lianas can keep forest succession statically in a liana-dominated, low canopy state for many years, significantly limiting forest resilience (Schnitzer, Dalling, and Carson 2000; Tymen et al. 2016; Foster, Townsend, and Zganjar 2008). In Panama, an estimated 7.5% of new canopy gaps created annually are stuck in a liana-dominated gap-phase regeneration (Schnitzer, Dalling, and Carson 2000).

Most of these studies, conducted mainly in neotropical forests, have found a significant negative impact of lianas on tree growth in liana-infested forests at the individual tree level (Becknell et al. 2021; Ingwell et al. 2010; Van der Heijden and Phillips 2009; Venegas-González et al. 2020). However, Tymen et al. (2016) found higher tree growth rates at the stand level in a liana-infested forest than in a high canopy forest in French Guiana because gap dynamics were higher in the liana-infested

forest and fast-growing tree species therefore recruited more. Thus, while lianas negatively affect individual trees, e.g., by directly competing for light, liana infestations can also lead to faster stand-level dynamics by promoting gap dynamics. Porcia e Brugnera et al. (2019) even modelled that the negative effect of lianas was cancelled out in old successional forests, through a large biomass increase of late-successional trees. The effects of lianas on forest dynamics appear to be scale-dependent and more complex than previously thought.

While most tree crowns seemed to be infested with lianas in tropical forests (74% of canopy trees  $\geq 20$  cm dbh in Panama, Ingwell et al, 2010; 86% of trees  $\geq 10$  cm dbh in Bolivia, Perez-Salicrup et al, 2001), liana infestations appear to be highly dynamic in time. Ingwell et al. (2010) found that 11% of trees severely infested with lianas were liana-free after 10 years, while 5% of liana-free trees became severely infested during the same period. The effect of lianas on trees might not last throughout its life, depending on the residence time of lianas in canopies. The mean residence time of large lianas ( $\geq 10$  cm in DBH) was estimated between 13 and 19 years in Peru (Phillips et al. 2005), shorter than the age of most trees. Overall, they found that large lianas had a three times higher turnover rate than large trees (Phillips et al. 2005). The effect of lianas on trees might also depend on how and when its considered. It's than important to further explore how lianas develop within tree communities to beter understand what impact lianas actually have on natural dynamics and long-term recovery of tree populations.

While most studies have found that lianas primarily affect regeneration of non-pioneer tree species (Schnitzer, Dalling, and Carson 2000), with higher infestation levels of shade-tolerant trees (Schnitzer and Carson 2010; Schnitzer and Bongers 2002; Van der Heijden, Healey, and Phillips 2008) and indirectly promote the density and diversity of pioneer trees (Tymen et al. 2016), some recent studies have found conflicting results with alternative interpretations of the effects of lianas on tree species depending on their identity. For instance, in Panama, Visser et al. (2018) found that fast-growing pioneer tree species experienced the greatest decline in growth, survival, and reproduction. They suggested the survivorship bias as an explanation for these inconsistent results, consisting in underestimating the effect of lianas on pioneer trees because most infested individuals are already dead, leading to a disproportionate liana-free surviving pioneer tree individuals. In Brazil, lianas negatively impacted the growth of only two of five tree species during the wet season, both of which were canopytrees, while the remaining three were classified as forest understory trees (Venegas-González et al. 2020). The effects of lianas on tree demography appear to be dependent not only on scale and when the effects are considered, but also on the identity of the tree species. To better predict

the effects of lianas on trees, it is necessary to know more precisely how they develop over time, and to understand the dynamics of lianas.

#### 1.1.4 The temporal dynamics of liana infestation and abundance

In neotropical forests, a growing number of studies indicate that liana abundances are increasing due to the combined effects of climate change and anthropogenic disturbances (Laurance et al. 2014; Phillips et al. 2002; Schnitzer and Bongers 2011). However, in the absence of data on other tropical forests, particularly African forests, it is highly uncertain whether this increase is occurring throughout the tropics. The only studies conducted in Central Africa showed a decline or static state of liana abundance over long periods of time (Bongers et al. 2020; Bongers and Ewango 2015; G. Caballé and Martin 2001; Ewango 2010; Thomas et al. 2014). In Gabon, Caballé and Martin (2001) recorded a 20% decline in liana stem density (stems  $\geq$  5 cm DBH) in 13 years of monitoring. In the Democratic Republic of Congo (DRC), Bongers et al. (2020) recorded an overall decline of 33.5% of liana abundance (stems  $\geq$  2 cm DBH), concerning over half of the studied liana species, also in 13 years. In Cameroon, Thomas et al. (2014) recorded a 16% decline in liana stem density (stems  $\geq$  1 cm DBH) over the 10-year monitoring period. Thus, the increase in liana abundance observed in the Neotropics is probably not a pantropical trend. Even in Brazil, liana density was found not to have changed during a 10 years monitoring (Gerolamo et al. 2018). The main factors determining liana abundance and composition in the Neotropics and other tropical regions may differ. Our knowledge of current trends in liana abundance in tropical regions is still quite limited due to the lack of long-term monitoring of lianas, particularly in regions other than the neotropics. In addition, the factors contributing to changes in liana populations and composition are still largely unknown. Understanding the spatial and temporal drivers of lianas is critical to better predicting their impacts on forest functions in different tropical regions, although several suspected mechanisms have already been proposed (Schnitzer and Bongers 2011).

#### 1.1.5 Factors influencing liana structure and floristic composition

Lianas are plants that require supports to reach the forest canopy and thus are strongly influenced by the surrounding forest structure (Balfour and Bond 1993; Hegarty and Caballé 1991). Their abundance has been systematically found to vary along forest stand structure gradients, such as canopy height and disturbance. Taller canopies have been found to be associated with lower liana abundance (Dalling et al. 2012; Villagra et al. 2021) and lower tree infestation probabilities (S. J. Wright et al. 2015; Tymen et al. 2016). Forest disturbances in particular have been found to play a key role in the spread of lianas due to their ability to quickly invade spaces through clonal reproduction (Ledo and

Schnitzer 2014; Stefan A. Schnitzer et al. 2021; Villagra et al. 2021). Indeed, most liana species thrive in canopy gaps through the production of multiple new clonal stems (Putz 1984a; Stefan A. Schnitzer et al. 2012; Waite et al. 2023; Rocha et al. 2022). However, a recent finding from Thailand challenges these assumptions, made primarily in Central and South America, and showed that liana abundance can also increase along forest successional gradients (Lomwong et al. 2023).

In addition, abiotic factors such as topography and soil chemistry may also shape liana communities, although their climbing lianescent form is thought to make them less dependent on physical and chemical habitat variables than trees, as they rely more heavily on their physical support (Ledo and Schnitzer 2014; Dalling et al. 2012). Nevertheless, lianas have been found to thrive to a lesser extent than trees on slopes and in areas with shallow water tables in Central and South American forests (Dalling et al. 2012; Gerolamo et al. 2018). A recent study has even shown that liana abundance increased along a precipitation gradient with rainfall seasonality in Panama (Parolari et al. 2020). Soil nutrient availability also influences liana abundance, with richer soils favouring higher liana abundances. However, recent results from Asia challenge previously established conclusions that abiotic factors play a lesser role in the distribution of liana structure, finding a much stronger influence of soil properties on liana abundance than forest structure (Liu, Sterck, Medina-Vega, et al. 2021).

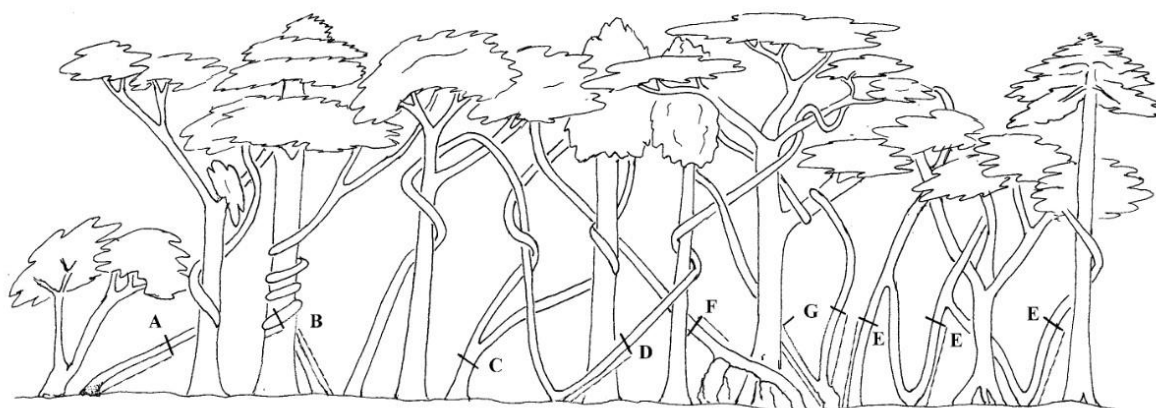
The floristic composition of liana communities is less studied than their structure, but also appears to be related to forest structure, forest type, and abiotic variables (Dalling et al. 2012; Mumbanza et al. 2020; Lomwong et al. 2023; DeWalt et al. 2006; Rocha et al. 2022; Liu, Sterck, Medina-Vega, et al. 2021; Parolari et al. 2020). Few studies have linked floristic distribution of lianas to forest structure. In Panama, certain liana species showed a clear preference for habitats with lower canopy height (Dalling et al. 2012). A study conducted in Central Africa consistently found significant differences in liana species composition between different forest types within the same landscape (Mumbanza et al. 2020). In Thailand, Lomwong et al. (2023) found that different dominant liana species occurred at different stages of forest succession. Both topography, soil properties, and rainfall precipitation were found to influence the floristic composition of lianas (Dalling et al. 2012; DeWalt et al. 2006; Parolari et al. 2020). Recent results even suggest that hydrological gradients (Rocha et al. 2022) and local soil properties such as pH and phosphorus content (Liu, Sterck, Medina-Vega, et al. 2021) have a relatively greater influence on liana species distribution than forest disturbance.

These inconsistencies highlight the lack of understanding we currently have to explain changes in liana abundance and floristic composition within forests and across the tropics (Muller-Landau and Pacala 2020). To better understand the role of lianas and quantify their impact on tropical forest

functions, we need to be able to accurately estimate the spatiotemporal distribution of lianas and accurately quantify liana biomass.

### 1.1.6 Liana estimations and limits of traditional methods

Historically, the study of lianas in tropical forest ecology relied primarily on ground-level observations, considering lianas as a single light-demanding functional plant type, and using basic measurements such as stem diameter. Even then, there were difficulties for the identification of lianas (see section 2.3. and discussion point 6.4.1) and in measuring liana stems due to the diversity of liana stem forms and life histories. Because of their anatomical diversity, lianas can be cylindrical or flat or have more irregular shapes such as strands or lobes. Because of their clonal reproductive ability, lianas can be multi-stemmed by splitting off their main stem at different heights (Figure 4, C), sprout multiple clonal stems directly from the same root (Figure 4, G), or even take root after descending from the canopy to form a loop before ascending again (Figure 4, D). Overall, there is a tremendous complexity and diversity of liana-tree situations (Figure 4) due to the ability of lianas to adapt to different environments and environmental hazards. To facilitate comparisons of different studies and to improve our understanding of global patterns of liana communities, protocols for ground-based censuses of liana stems have been standardized internationally over the past two decades. Today, most community-level liana studies are conducted in field plots where lianas are inventoried at a distance of 1.3 m along their stem from the last rooted point (Gerwing et al. 2006; Schnitzer, Rutishauser, and Aguilar 2008).

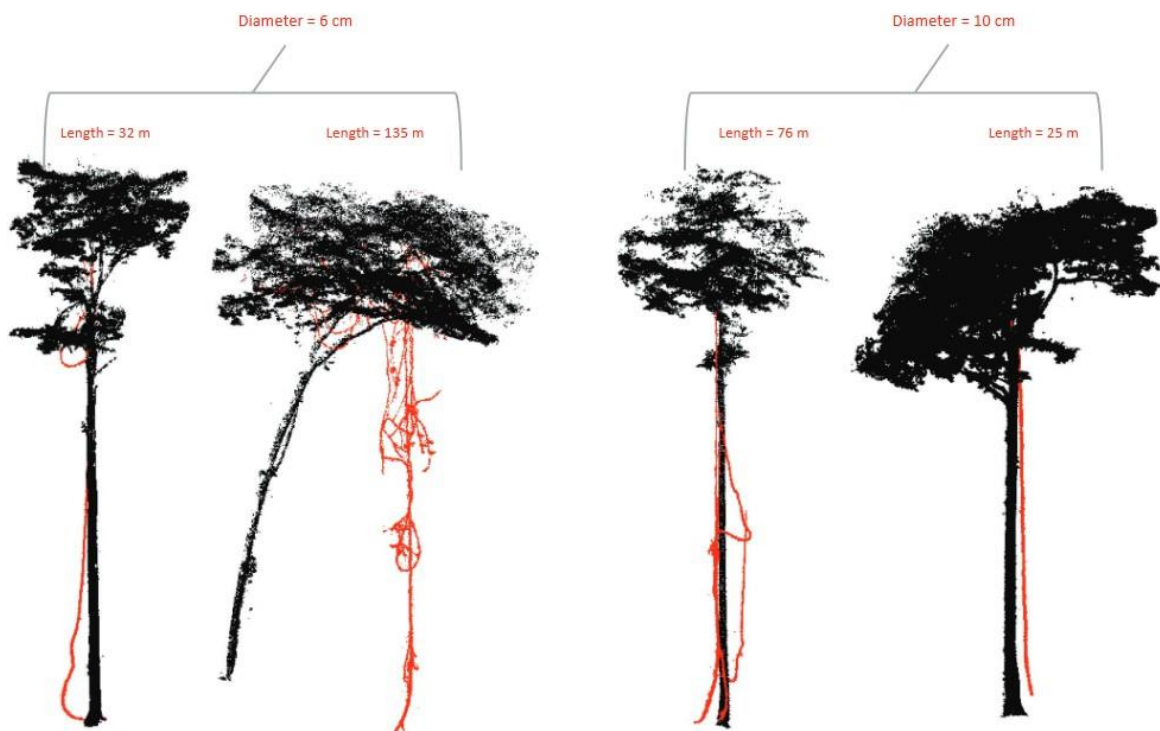


**Figure 4.** Diversity of liana-tree situations and recommendations for diameter measurement points. This illustration is taken from Gerwing et al., 2006.

Nevertheless, stem inventories are both time and labor intensive methods, which has led to the development of liana infestation indices such as the Crown Occupancy Index (COI), a ground-based measurement of liana infestation that is much less time consuming than traditional dendrometric measurements (Ingwell et al. 2010; S. J. Wright et al. 2015). The COI is a semi-quantitative index that assesses relative liana leaf cover in tree crowns from the ground based on five categories: (0) no liana leaves in the crown, (1) 1–25%, (2) 26–50%, (3) 51–75%, and (4) > 75% of the tree crown is infested with liana leaves (Clark and Clark 1990). There are positive results on the accuracy of the COI in estimating liana infestation and its relationship with diameter-derived metrics such as basal area and stem abundance (Van der Heijden et al. 2010). However, in tropical forests, visibility of the entire tree crown from the ground is limited in most cases, and assessing accurate COI is excessively difficult and can be prone to errors (Waite et al. 2019). One study examined the relationship between traditional ground-level measurements (liana stem abundance, basal area, and biomass) and the actual extent of liana leaves over tree crowns, assessed by a canopy crane (Cox et al. 2019). Alarming, they found no significant relationship between ground-based classical liana measurements and liana leaf cover above the canopy. Although liana stem diameters can now be accurately measured from the ground, there is still uncertainty about how accurately they are linked to and estimate the actual leaf deployment of lianas in the canopy and thus liana biomass (Van der Heijden et al. 2022). This uncertainty is important to consider to better interpret conclusions drawn from ground-based measurements.

As for trees, liana biomass has usually been estimated using allometric equations to avoid time-consuming destructive approaches. Allometric equations have been developed to estimate liana biomass using liana stem diameter only, because the stem length of lianas in the field is difficult to measure from the ground (Miao et al. 2016). Available allometric equations, such as the most commonly used pantropical equation by Schnitzer, DeWalt, and Chave (2006), (i) were developed using data mainly from neotropical forests and do not include central African datasets, and (ii) are based on a limited number of observations, replicates within species, and within diameter ranges along ontogeny (Schnitzer, DeWalt, and Chave 2006; Smith-Martin et al. 2020). Because of their narrow stems, it is assumed that lianas allocate more biomass to their leaves than to their stems (Avalos, Mulkey, and Kitajima 1999). This assumption may not be entirely accurate because of lianas extremely long and variable stem lengths, which can easily reach tens of meters, and potentially lead to different allocation patterns of biomass from stem width to stem length (Smith-Martin et al. 2020). Given the diversity of biomass allocation patterns in lianas, which depend on species, forest type, and abiotic conditions, allometric models for estimating liana biomass are also prone to major errors (Miao et al. 2016; Smith-Martin et al. 2019; van der Heijden et al. 2022). In particular, in central African forests, where there is a severe lack of data to calibrate models, liana biomass was found to vary fivefold

depending on the allometric equation used to calculate biomass estimates (Miao et al. 2016). In fact, a study using terrestrial laser scanning (TLS) showed that existing pantropical allometries for liana biomass overestimated biomass by more than 130% and other regional allometries underestimated biomass by 81% (Krishna Moorthy et al. 2020). Given the wide range of liana growth strategies (and thus biomass allocation patterns) that appear to be structurally and mechanically independent of diameter growth (Figure 5; Putz and Mooney, 1991), questions remain about the relevance of constructing allometries based solely on diameter.



**Figure 5.** TLS imagery of four liana-tree situations illustrating the diversity of growth forms and biomass allocation patterns between stem diameter and length. The illustration is taken from Van der Heijden et al., 2022 who adapted it from Krishna-Moorthi et al., 2020.

There is a crucial need for more accurate methods to estimate lianas to better understand their contribution and role in forest functions, which requires a better mechanistic understanding of the distribution patterns of lianas in different forests worldwide (van der Heijden et al. 2022). Further studies are needed to reveal liana patterns and their diversity among species and regions in forests and forest canopies, which are often considered the most important forest layer in ecosystem dynamics. Today, new methods are increasingly being used to study liana ecology and community patterns in forests. New tools are being used, such as remote sensing, which provides better access to the distribution of lianas across the canopy, and functional ecology, which takes into account the



functional diversity of lianas and the diversity of biomass allocation patterns among species, pushing aside the notion that lianas are a light-demanding, functionally homogeneous plant group.

## 1.2 Emergent methods to study liana ecology

### 1.2.1 Remote sensing

Due to recent advances in remote sensing technology, it is now possible to easily reach the most inaccessible layer of the forest, the canopy, and collect high-resolution data. This allows more accurate detection of liana leaf coverage of individual tree crowns locally, via drones and regional liana infestation rates via satellite imagery (van der Heijden et al. 2022). In order to map the distribution of liana leaves across tree canopies, it is important that lianas exhibit a distinct spectral signature distinguishable from trees. Liana leaves typically have different chemical properties than tree leaves and have different pigment concentrations. For example, liana leaves in dry forests have been found to have lower concentrations of chlorophyll and carotenoids than tree leaves (Sánchez-Azofeifa et al. 2009). Lianas appear to have cheaper leaves than trees, thinner and more efficient at light interception, with lower photosynthetic pigments (chlorophyll and carotenoids) and perhaps flatter leaf angles over tree crowns (Visser et al. 2021). This difference in chemical composition and structural properties has resulted in different spectral responses between liana and tree leaves, with lianas generally exhibiting significantly higher light reflectance than trees across different spectral bands, indicating a generally higher brightness (Visser et al. 2021). In particular, the most pronounced reflectance differences between liana and tree leaves occur around 550 nm in the green domain (the chlorophyll and carotenoid absorption region; (Asner and Martin 2012; Castro-Esau 2004; Chandler et al. 2021), as well as in the near-infrared (NIR, 780 nm to 1400 nm) and shortwave infrared domain (SWIR, 1400 nm to 3000 nm; (Chandler et al. 2021; Visser et al. 2021).

The spectral differences between liana and tree leaves have allowed local studies to visually identify and accurately delineate manually liana leaves over tree crowns using high-resolution images up to ~2 cm/pixel, from drones (Figure 6, Waite et al. 2019). Access to the actual extent of liana leaves in the canopy can now allow to test the accuracy of commonly used ground-based liana measurements (metrics derived from diameter and the COI). Although Waite et al. (2019) found a significant positive relationship between the actual liana leaf cover over tree crowns and the COI, more than 25% of trees had been misclassified based on their infestation rates. Most of these errors occurred when liana infestations were low and accounted for nearly half of the misclassified trees. Ground-based data generally provide approximate estimates of liana distribution above the canopy with considerable

uncertainty, which affects our understanding of liana-tree interactions. For that reason, I wanted to explore the link between drone and ground based liana estimates to better understand the interactions between trees and lianas and potential avenues to more accurately estimate liana infestation and burden on trees, in chapter 1. The emergence of easy-to-acquire drone data may revolutionize this aspect by providing a very high-resolution view of liana distributions above the canopy and a high frequency of image collection thanks to relatively low acquisition costs. Increasing drone assessments may improve our ability to explicitly incorporate competition for light between lianas and trees into ecological models to more accurately assess the role of lianas in forest functions.



**Figure 6.** High-resolution images taken by drone illustrating visual identification and delineation of liana cover over tree crowns. The illustration is taken from Waite et al., 2019.

Nevertheless, manual delineation of liana patches in drone data requires considerable time and expertise, which can be problematic for studies at regional scales. Differences in liana spectral responses have also been tested recently for detecting and monitoring liana infestation rates at larger

scales across forest canopies using emerging satellite and airborne remote sensing tools (Chandler et al. 2021; Chandler et al. 2021b; Marvin, Asner, and Schnitzer 2016). While these recent studies were able to produce maps of liana infestation at large scales and monitor changes in infestation over time using machine learning (support vector machine algorithms and neural network classifications), they were unable to accurately detect low levels of liana infestation at this scale and only found reliable results for severely infested trees (> 50% or 75% liana infestation). The difficulty of detecting more subtle variations and lower levels of liana infestation is likely due to (i) lower image resolutions for airborne and satellite data compared to drone data, with resolutions ranging from approximately 30 m/pixel to resolutions of 1-3 m/pixel (Visser et al. 2021; Chandler et al. 2021; Chandler et al. 2021b; Marvin, Asner, and Schnitzer 2016); (ii) some overlap between the spectral signatures of lianas and trees, potentially confounding pixel-based predictions (Chandler et al. 2021; Visser et al. 2021); and (iii) a large diversity of liana spectral responses among liana species, combined with the presence of untangleable multiple liana species in a single tree crown (Hesketh and Sánchez-Azofeifa 2012; Sánchez-Azofeifa and Castro-Esau 2006; Visser et al. 2021). While new emerging remote sensing tools such as drone, airborne and satellite data can help fill many knowledge gaps in liana ecology and monitor lianas over long periods of time and large areas (van der Heijden et al. 2022), they are limited in providing a mechanistic understanding of liana ecology and the mechanisms underlying liana increase, and the inconsistencies between studies discussed in Sections 1.1.4. and 1.1.5.

## 1.2.2 Functional ecology

### 1.2.2.1 Plant strategies and the economic spectra

Functional ecology plays a crucial role in deciphering the intricate relationships between plant traits and their distribution patterns in different environments. Functional traits are specific attributes of organisms, such as trees or lianas, which are directly linked to plant function and generally play a key role in plant responses to environmental constraints (Lavorel et al. 1997; Violle et al. 2007). Understanding the functional strategies of different plant species can therefore provide valuable insights into the mechanisms that determine their spatial distribution and coexistence in different ecosystems. For example, leaf and wood economic spectra provide a framework for deciphering how plants allocate resources in response to environmental gradients and competitive pressures, providing valuable insights into the adaptive strategies of tropical tree species (Wright et al. 2004; Chave et al. 2009; Baraloto et al. 2010; Reich 2014).

The leaf economic spectrum (LES) focuses on traits that describe the investment and reinvestment strategies of plants in photosynthate and mineral nutrients, to build and maintain leaves

to ensure their survival, producing enough surplus resources for the continuity of future generations (Wright et al. 2004). The LES opposes low-cost and short-lived leaves with rapid return-on-investments to expensive and long-lived leaves with slower return-on-investments (Baraloto et al. 2010). It includes traits such as specific leaf area (SLA), leaf nitrogen content, or laminar toughness, which reflect the trade-off between resource acquisition and conservation strategies. As a result, species with high SLA and leaf nitrogen content tend to prioritize rapid growth and resource acquisition, whereas species with high laminar toughness adopt a more conservative approach to resource utilization. Therefore, the performances of species with mostly rapid resource acquisition strategies may thrive in resource-rich environments, while species with traits geared towards resource conservation may dominate in more resource-poor environments (Reich 2014). Conversely, the wood economic spectrum (WES) reflects tradeoffs between mechanical support and water transport efficiency (Chave et al. 2009). It includes traits related to wood density, vessel anatomy, and hydraulic properties. For trees, vessel traits were mainly related to species growth, while wood density was also related to survival (Poorter et al. 2010). This suggests that species with wide vessels that are efficient for water transport, and cheap mechanical structures (low wood and vessel density) tend to favor rapid growth, while species with small vessels and higher wood density tend to favor survival and mechanical strength (Poorter et al. 2010; Van Gelder, Poorter, and Sterck 2006).

The study of functional traits has helped elucidate the niche differentiation and competitive interactions underlying the spatial distribution of tropical tree species and shed light on questions related to community assembly, biodiversity maintenance, and responses to global change. In essence, functional ecology serves as a bridge between plant traits, ecological processes, and the spatial distribution of species, providing a more comprehensive perspective on the complex interactions and dynamics of tropical ecosystems. Moreover, this knowledge is critical for informed conservation and management strategies in the face of ongoing environmental change. However, in tropical forests, functional ecology and strategies have been studied primarily to understand tree demography and dynamics. Lianas have not been explicitly considered in most key studies describing leaf and wood economic spectra and associated plant performances (Wright et al. 2004; Baraloto et al. 2010; Poorter et al. 2010; Reich 2014).

In the wake of breakthroughs describing plant strategies, lianas have received little attention. In the worldwide wood economic spectrum, only few lianas have been considered compared to trees, and were mainly characterized by wider and numerous vessels that optimize water transport (Chave et al. 2009; Ewers, Fisher, and Chiu 1990; Caballé 1993). Therefore, lianas have mostly been considered as a single functional plant group in most studies in community ecology, comparison of trees and

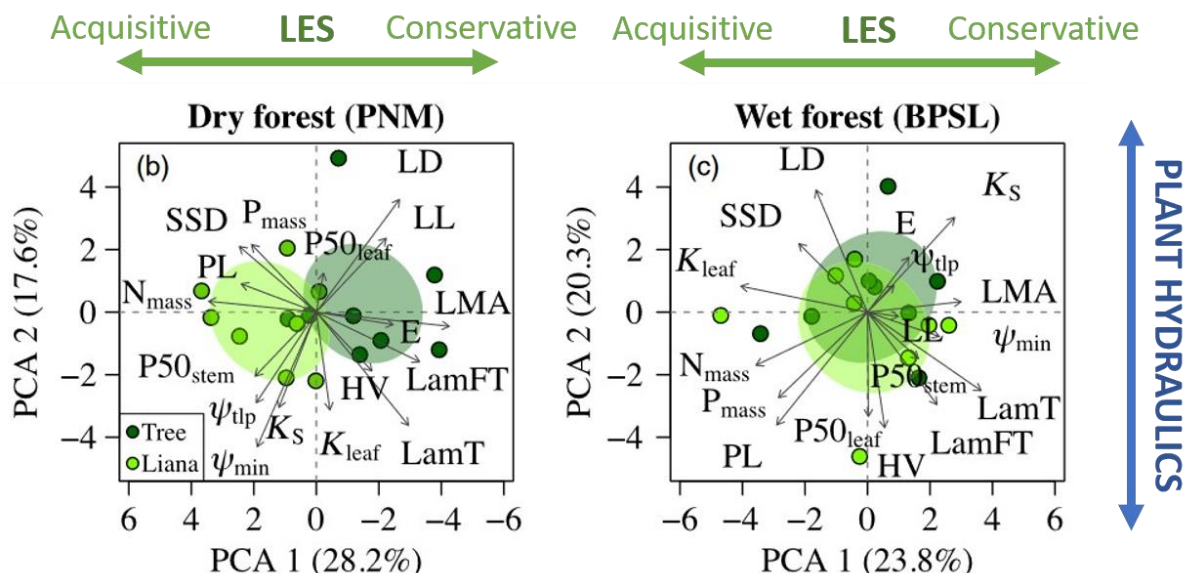
lianas, or vegetation models (Chen et al. 2015; Stefan A. Schnitzer, Kuzee, and Bongers 2005; Porcia e Brugnera et al. 2019; Zhu and Cao 2010; Meunier et al. 2021). Overall, only a small number of studies and species were conducted and collected, respectively, while trees were commonly categorized into functional groups (Meunier et al. 2020). However, several recent studies have shown that the traits of lianas largely overlap with those of trees and do not belong to a distinct functional group (Werden et al. 2018; Smith-Martin et al. 2019), and studies on the functional ecology of lianas have begun to increase in the last decade.

The existence of different niches and light requirements for different liana species has even been suggested as a possible explanation for the contradictory results observed in the different studies with respect to liana dynamics and structural and floristic distribution. For example, the increase in liana abundance observed with forest succession in Thailand, which contradicts neotropical assumptions about canopy gaps and disturbance-induced abundance (see Section 1.1.5.), was explained by the increasing abundance of shade-tolerant liana species with forest succession that are better adapted to thriving under lower light conditions (Lomwong et al. 2023). Lianas exhibit great variability in life history and a range of ecological strategies that are still not well understood. Compared to what we currently know about tree life history and forest ecology, which can be traced back to the 15th century (Fuller 1917), liana ecology is still considered a relatively new branch of science. Functional ecology and studies that combine functional traits from plant biology and their relationships with the environment have led to a mechanistic understanding of the spatiotemporal dynamics of tree populations. Further research through the lens of functional ecology for lianas are critically needed to provide a better mechanistic understanding of their ecological preferences, resource partitioning among species, their distribution in different local environments, and to improve our ability to predict the current and future dynamics of lianas in tropical forests.

#### 1.2.2.2 Emergent studies about liana functional ecology and underlying mechanisms of their distribution along different environments at the community level

Lianas exhibit a diversity of growth strategies that have only recently begun to be characterized through the lens of functional ecology. Consistent with previous studies that considered lianas on the acquisitive side of the ecological spectrum, Werden et al. (2018) found that the 7 studied liana species exhibit significantly more acquisitive leaf strategies than trees. However, using a larger number of liana species, Medina-Vega et al. (2021) discovered that the leaf strategies of lianas and trees largely overlapped along the leaf economic spectrum (LES; Figure 7). More specifically, lianas and trees differed in their leaf strategies only in the studied dry forest, whereas they overlapped with trees in the studied wet forest. Considering lianas as a single functional group can easily lead to

misinterpretation. Sun et al. (2022) found, using trait mean values, that liana seedlings differed significantly from trees by having a higher mean SLA or mean specific stem length, suggesting a higher potential growth rate and more acquisitive strategies, consistently with studies considering lianas as a single acquisitive plant group. However, considering all traits on the “fast-slow” spectrum and not just the mean individual trait values, Sun et al. (2022) found that half of the liana species belonged to the conservative side of the spectrum, with most liana species functionally similar to trees. Along the WES, almost all recent studies that have tackled the subject from a liana perspective have found overlapping water-use strategies with trees (Figure 7; Werden et al. 2018; Medina-Vega, Bongers, Poorter, et al. 2021; Meunier et al. 2020; van der Sande et al. 2019). In French Guiana, Meunier et al. (2020) observed that values of wood density, vessel area, and vessel diameter within a single study site were comparable in magnitude to those found in tree surveys across various tropical forests and pantropical liana datasets. This highlights the wide diversity of WES strategies among liana species, both within and among different environments. Consistently, even among a small number of liana species, Werden et al. (2018) found that lianas tend to be distributed all along the water-use strategies continuum rather than falling into clearly defined functional categories. In contrast to the assumption that lianas are more hydraulic efficient with wider wood vessels than trees, they found that lianas appear to fall under the “packing-limit” tradeoff, or also commonly known as the hydraulic safety-efficiency tradeoff, in which species have either many small or a few large vessels to maximize hydraulic efficiency while investing in mechanical structure.



**Figure 7.** Overlapping strategies between lianas and tree along the leaf economic spectrum (LES; PCA 1) and water-use strategies (PCA 2) in a dry and wet forest in Panama. The illustration is taken from Medina-Vega et al., 2021 and modified.

Concerning the coordination of life history strategies between the different organs of lianas, there is still ambiguity between studies. While nutrient acquisitive liana species have been found to be positively associated with a high leaf hydraulic conductance suggesting a hydraulic (water-use) efficiency strategy, life strategies between leaf nutrient acquisition and stem hydraulics have been found to be independent (Medina-Vega et al. 2021; Rocha et al. 2022). This independence suggests that liana species are potentially able to pursue multiple combinations of strategies depending on resource availability. However, other studies have found that stem hydraulic efficiency was strongly associated with high leaf gas exchange rates, while it was hydraulic safety that seemed independent of other morphological or photosynthetic traits (van der Sande et al. 2019). This would give lianas the potential to maintain high hydraulic efficiency (and growth rates) as well as some resilience to cavitation, which is important for their safety under drier environmental conditions. In fact, others have found that, although the leaf and wood strategies of lianas exhibit some coordination, there are nevertheless still two independent spectra, one focused on tissue toughness and water-use and the other on nutrient and carbon acquisition. Each spectra showed coordinated traits and life history strategies across different organs of the liana (Liu et al. 2021). For example, along the tissue toughness spectrum, they have found that stem toughness (via wood density) was positively associated with leaf toughness (via leaf density and dry matter content). Liana species tend to invest in either soft tissues for quick and cost-efficient growth, or persistent tissues to conserve resources and improve plant survival. Overall, the common assumption that lianas are mainly light-demanding and follow acquisitive strategies is currently under-revision, although there is still a critical need for additional studies on lianas' functional strategies, associated plant performance, and distribution in different environments.

Recent studies challenged the notion that lianas are exclusively light-demanding and suggested that species-specific niches contribute to variations in liana behavior. These studies have shown that forests with an open canopy and greater light availability provide more favorable conditions for lianas with acquisitive plant strategies, i.e., low wood density and high SLA and leaf P concentrations, as shown for trees (Villagra et al. 2021; Liu et al. 2021; Mumbanza et al. 2022). Lianas that followed more conservative strategies were more likely to be found in undisturbed old successional forests (Liu et al. 2021; Villagra et al. 2021). In addition, abiotic factors such as hydrological gradient, soil, or water niches also resulted in different species distributions, both floristically and functionally (Rocha et al. 2022; Liu et al. 2021). Liana species with larger stomata, low wood density, and a higher proportion of self-supporting juvenile xylem, but also lower SLA, occurred preferentially in valleys and topographic water niches, i.e., areas with high soil moisture availability due to strong water accumulation. However, while multivariate strategies (i.e., acquisitive or conservative, tough or

soft tissues) are considered more informative, especially for trees, individual traits have been found to better predict species niche dimensions for lianas (Rocha et al. 2022; Liu et al. 2021). This suggests that different individual traits (strategy components) may have relatively different roles and importance in different niche contexts.

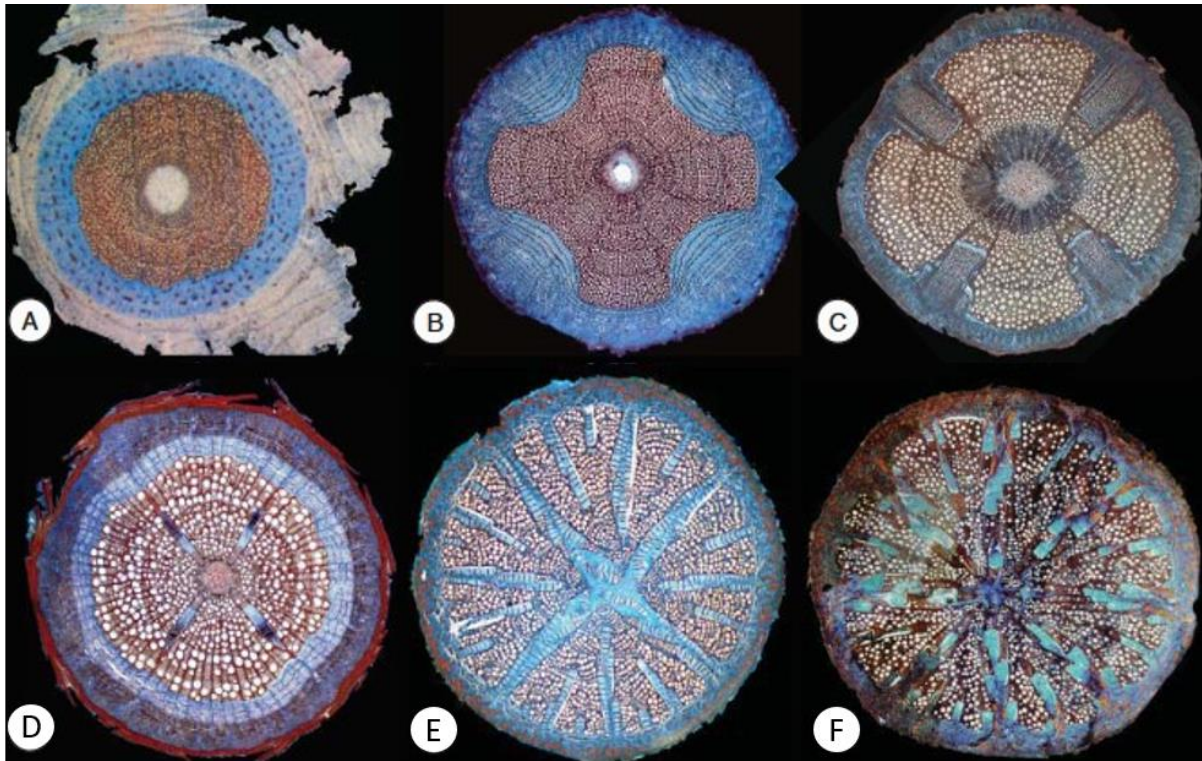
Recent studies have used several traits from the leaf economic and wood economic spectra (LES and WES) to describe liana strategies that are generally considered important for plant strategies and performance (see Section 1.2.2.1.; Wright et al. 2004; Chave et al. 2009), and yet none of the traits (with the exception of stomatal density) were found to be significantly related to the relative abundance of lianas (Liu et al. 2021). The mechanisms underlying liana abundance are still not clear. Even for saplings and the juvenile stage of lianas, while tree sapling abundance is positively associated with shade tolerance traits (such as high wood density or low SLA), liana sapling abundance does not appear to be related to any functional traits (van der Sande et al. 2019). Although significant progress has been made in the field of liana ecology, we still need to further explore the different life strategies of lianas and provide a deeper understanding of their shifts under different local environmental conditions. Classically circumscribed plant functional traits may not reflect changes in the life history of lianas and their connections to the environment as clearly as in trees (Liu et al. 2021). Lianas differ significantly from trees in their mechanical structure and encounter distinct physiological constraints. As mentioned in Section 1.1.2, they initially go through a self-supporting phase, but then rely on external supports for growth and undergo significant changes in their properties and tissue organization as they mature (Rowe, Isnard, and Speck 2004; Rowe et al. 2006). The role of stem traits can vary significantly in lianas, especially during the climbing phase, depending on the life history of different species (Letcher and Chazdon 2012). The large diversity and complexity of tissue arrangements and vascular systems in lianas may reveal different functions and solutions for coping with different environmental conditions (Rocha et al. 2022). Therefore, exploring anatomical stem characteristics offers promise for a better understanding of the life history of liana species and their environmental shifts and interactions. For this reason, I will particularly explore the possible relationships between some anatomical functional traits beyond the classically circumscribed traits of recent community ecology studies in my chapter 3.

### 1.2.2.3 Liana cambial variants and associated biomechanical properties

While the unique physiological characteristics of lianas and their associated original anatomical configurations have been documented for decades since the 19th century, they have rarely been integrated into community-level trait-based approaches. In the early stages as self-supporting and host-seeking stems, lianas develop what is known as “juvenile wood” to provide mechanical



stability to the stem (Fisher and Ewers 1991; Rowe, Isnard, and Speck 2004; Rowe and Speck 2005). This wood is characterised by specific structural features, including narrow and sparse vessels, thick-walled fibrous cells, and limited, often lignified axial parenchyma (Angyalossy et al. 2012; Caballé 1998). It is produced by the bifacial vascular cambium (hereafter referred to as cambium), which produces secondary plant tissues in all angiosperms. The cambium produces secondary xylem (wood) in a centripetal direction and secondary phloem (phloem) in a centrifugal direction (Philipson, Ward, and Butterfield 1971). As lianas mature and become climbers, their mechanical needs change and they require flexible and resilient stems in their quest for reaching the light (Obaton 1960; Putz and Holbrook 1991; Rowe and Speck 2005). However, this flexibility comes at the cost of vulnerability to environmental factors such as wind and falling branches that can damage their small and slender diameter stems (Ménard et al. 2013). To address these challenges, many liana species have evolved complex woody forms known as “vascular cambial variants” (Carlquist 1991). These variants involve different arrangements of lignified tissues, xylem and/or fibres, alternating with softer tissues such as parenchyma and phloem (Figure 8; Angyalossy et al. 2012; Angyalossy, Pace, and Lima 2015; Caballé 1998; Chery et al. 2020; Philipson, Ward, and Butterfield 1971). These cambial variants are thought to enhance stem integrity and protect vital functions. Experimentally, they have been found to resist mechanical disturbances by allowing controlled splitting and separation of the stem rather than catastrophic cross-sectional ruptures (Dobbins and Fisher 1986; Fisher and Ewers 1991).



**Figure 8.** Diversity of cambial variants of lianas of the Bignoniaceae family. The illustration is taken from Angyalossy et al., 2015 and modified. (A) *Podranea ricasoliana*, stem with regular secondary growth. (B) *Perianthomega vellozoi*, stem with 4 arcs. (C) *Fridericia samydoides*, stem with 4 phloem wedges. (D) *Amphilophium crucigerum*, stem with included phloem wedges. (E,F) Stems with multiple dissected phloem wedges. (E) *Dolichandra unguis-cati*. (F) *Dolichandra unguiculata*.

Many studies have been conducted at the botanical family, genus, or species level, such as Bignoniaceae (Figure 8; Angyalossy et al. 2012) or Paulinia L. (Chery, da Cunha Neto, et al. 2020) on the diversity of cambial variants; and some studies have tested the biomechanical properties of lianas such as stiffness and flexibility during their development in numerous species from different phylogenetic groups (Putz and Mooney 1991; Rowe et al. 2006; Rowe and Speck 1996). All have suggested that the ability of lianas to endure significant stem deformation without loss of function depends on the complicated and heterogeneous anatomy of their stems. However, despite the extensive knowledge of the phylogenetic and functional diversity of liana stems, there are surprisingly few studies exploring the relationship between liana anatomical characteristics and its role at the community level. Community-level studies are difficult due to the destructive nature of the methods needed for anatomical studies, which are often prohibited in permanent plots. In addition, detailed functional and anatomical studies are time consuming, limited in the number of replicates, and often specific to local effects on individuals (Rowe and Speck 2015). On top of that, because botanical identification of liana species from the ground is difficult, there has thus been a gap in our understanding of the relationship

between individual level traits, such as secondary cambial growth, and liana ecological dynamics. That is why I will explore in my chapters 2 and 3 the relationships between functional traits and strategies, and patterns at the community level.

## 1.3 Objectives and scientific production of my thesis

### 1.3.1 Problematics and objectives of my thesis

A deeper understanding of liana ecology, particularly the links between traits, anatomy, and the community structure of lianas, is needed to better predict their spatiotemporal distribution, dynamics, and effects on forest functions. The goal of my thesis is to expand our knowledge of liana ecological strategies, from macroanatomical diversity to community-level patterns, using both ground-, drone-based field data and lab trait measurements. My studies were conducted in an experimental site in northern Republic of Congo, an area that is poorly studied for lianas. Through the lens of functional ecology, I investigate (i) the link between commonly used ground-based liana measurements and drone-based measurements of liana leaf cover over tree crowns; (ii) the influence of local topography, forest structure, and tree composition on liana community structure and floristic and functional composition; and (iii) the strategies associated with liana macroanatomical diversity, their links to the leaf economic spectrum, and their patterns across the phylogeny and along environmental gradients. More specifically, I will address the following questions:

- Do commonly used ground-based measurements of lianas predict drone-based measurements of liana leaf coverage over tree crowns? To what extent is this relationship mediated by the functional composition of lianas?
- How are liana communities distributed along environmental gradients? To what extent do forest structure and composition, and topography influence the structure, floristic, and functional composition of liana communities?
- What are the different ecological strategies of lianas within a community? What is the anatomical diversity of liana species, and are cambial variants and derived functional traits associated with different functional strategies? How are they integrated, and what are their contributions to the classical economic spectra?

I will explore these questions through 3 different chapters in the form of scientific articles. These articles are currently either accepted in a scientific journal or still in preparation. For the latter, they will likely continue to evolve until they are published. Each chapter presents several complementary approaches aiming at characterizing the functional ecological strategies of lianas from individual to

community level observations. A final chapter provides a cross-cutting discussion and concludes my thesis with perspectives.

## 1.3.2 Scientific production

### 1.3.2.1 Publications

**Kaçamak, B.**, Barbier, N., Aubry-Kientz, M., Forni, E., Gourlet-Fleury, S., Guibal, D., Loumeto, J.-J., Pollet, S., Rossi, V., Rowe, N.P., Van Hoef, Y., & Réjou-Méchain, M. (2022). Linking Drone and Ground-Based Liana Measurements in a Congolese Forest. *Frontiers in Forests and Global Change*, 5, 803194. <https://doi.org/10.3389/ffgc.2022.803194>

**Kaçamak, B.**, Réjou-Méchain, M., Rowe, N.P., Rossi, V., Barbier, N., Bazan, S., Forni, E., Guibal, D., Harris, D., Loubota Panzou, G. J., Loumeto, J.-J., Marcon, E., Pinho, B. X., Zombo, I., & Gourlet-Fleury, S. Local forest structure influences more the structure than the floristic and functional composition of liana communities in a moist forest in Northern Congo. *In preparation for Journal of Ecology*.

**Kaçamak, B.**, Réjou-Méchain, M., Bazan, S., Forni, E., Gourlet-Fleury, S., Guibal, D., Grolleau, M., Harris, D., Loumeto, J.-J., Rossi, V. & Rowe, N.P. Liana traits and macro-anatomy from the Republic of Congo: linking cambial variants and life history strategies. *In preparation*.

### 1.3.2.2 Conference and talks

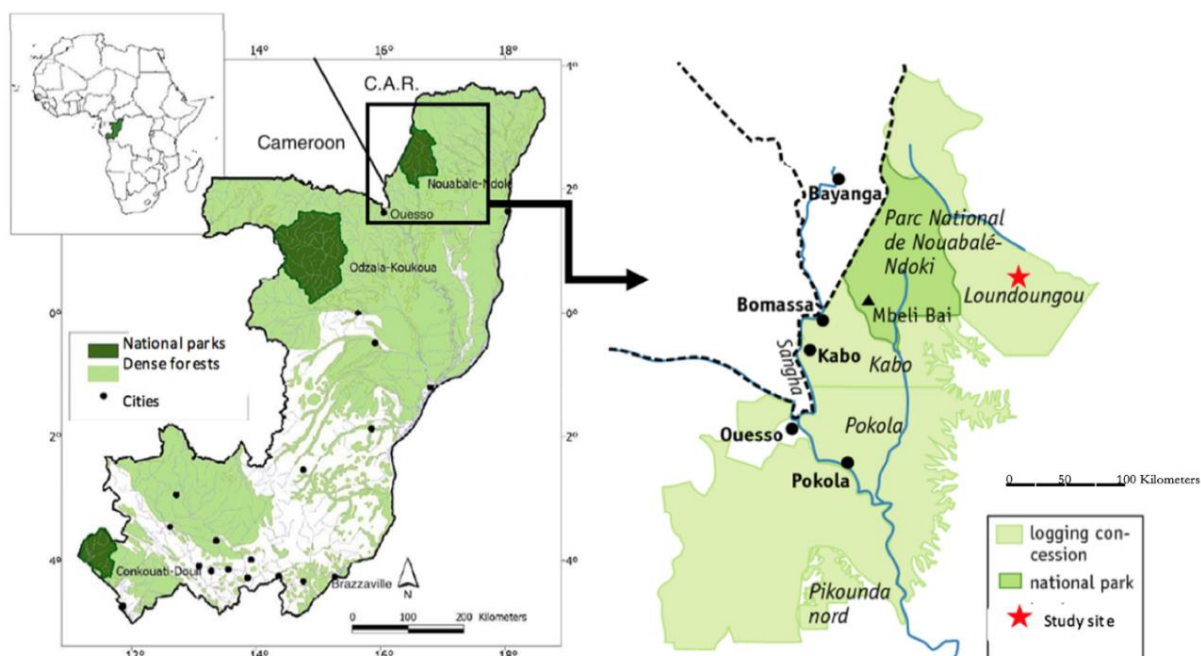
**Co-chair and organiser of session** “Tropical lianas: functional traits, ecology and impact in the tropics” at GTOE (European Conference of Tropical Ecology) in Montpellier, France

**Oral presentation** about “Local forest structure drives liana community structure, functional and floristic composition in a moist forest of northern Congo” at GTOE (European Conference of Tropical Ecology) in Montpellier, France

**Oral presentation** about “Liana communities in northern Congo” at the seminar “Focus on lianas” with Stefan Schnitzer at UMR AMAP, Montpellier, France

## 2 Study area and liana botanical identifications

### 2.1 General description



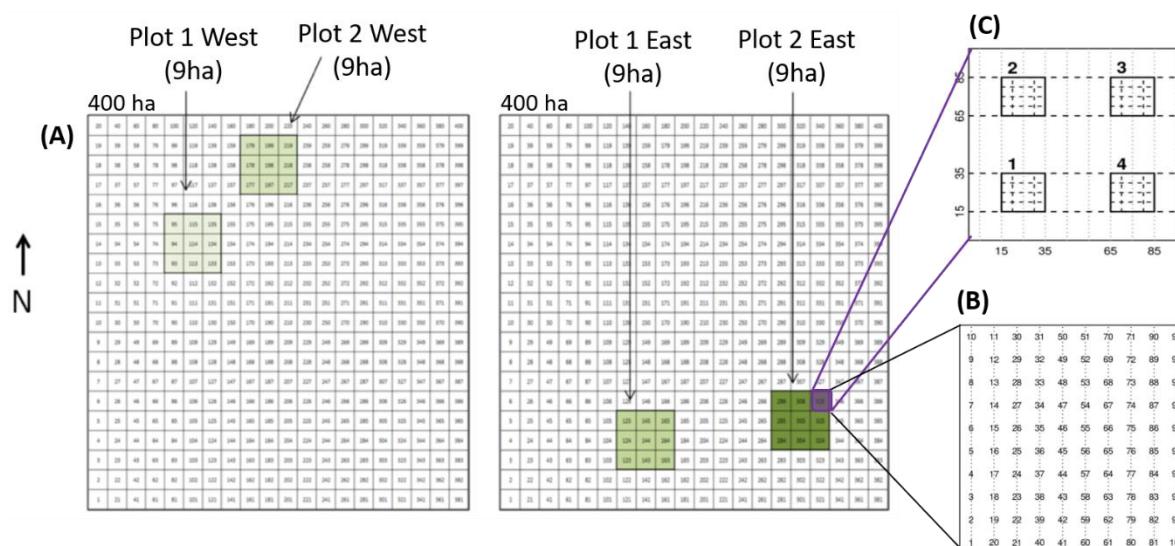
**Figure 9.** Study area and study site of Loundoungou-Toukoulaka (red star). Map adapted from WCS (Stephen, 2014; Meder, 2014).

The study site is located in central Africa, in the north of the Republic of Congo, in the Likouala Province (north of Ouessou; Figure 9;  $2^{\circ}27'11.87''$  N and  $17^{\circ}02'32.17''$  E). The study site was settled in 2013-2014 by the Cirad within the Loundoungou-Toukoulaka forest management unit (UFA) in a forest concession managed by the logging company CIB-Olam (Forni et al. 2019). Loundoungou is located on a plateau with a predominantly low and flat elevation ranging from 395 to 470 m a.s.l. (above sea level; Freycon 2014). It is located in the transition zone between the alluvial deposits of the Congo Basin and the Carnot Sandstone Plateau (Boulvert 1996; Penel et al. 2022). The geologic substrate is Cenozoic alluvium consisting of limestones and Quaternary alluvium (Forni et al. 2019). The soils are mainly composed of sands and clays and vary from sandy-clay to clay-sandy in the highest and lowest elevations of the plateau. The soil type can be classified as Xanthic Acrisols (Freycon 2014). The study area is also characterized by the presence of a large number of large termite mounds, from 1.5 to 6 mounds per ha with a radius of  $9.9 \pm 3.3$  m and a height of  $4.1 \pm 1.5$  m (Freycon et al. 2018; Penel et al. 2022). The climate of Loundoungou is classified as a “tropical monsoon” climate” (type Am) according to KöppenGeiger’s classification (Peel, Finlayson, and McMahon 2007). It is characterized by

a mean annual temperature of 25 °C and rainfall of 1605 mm/year (unpublished data from 2003 to 2017 from a local station in Pokola, 140 km from the study area). There are four main seasons in the year, two dry seasons, a short one from June to August and a long one from December to March, and two wet seasons from April to June and from September to November. The vegetation in Loundougou belongs to the semi-deciduous forest type (Réjou-Méchain et al. 2021) with 240 identified tree species dominated mainly by the families Euphorbiaceae (20%), Fabaceae (12%), Meliaceae (9%), Ebenaceae (8%), and Annonaceae (7%) (Forni et al., 2019). Tree density at Loundougou is  $346.8 \pm 5.8$  trees/ha with a biomass of  $432.6 \pm 13.8$  Mg/ha (Forni et al. 2019). Giant herbs, from the order Zingiberales are another life form widespread in the study area and overall particularly in lowland forests of central and western Africa (Pouteau et al. under review), that can interact with trees or lianas. The Loundougou study site was originally selected in 2013 to compare different silvicultural treatments. To minimize abiotic effects, it was located in an area homogeneous in terms of soils, topography, and vegetation, with a difference of only 23 meters in elevation between the most distant plots. Little is known about the history of human activities in this area. Aside from hunting and a small amount of logging (0.3 trees/ha) in late 2018, there is no evidence of recent human activity in the last century.

## 2.2 Experimental designs

The experimental site consists of permanent plots embedded in two 400-ha blocks, west and east. Within each block, two 9-ha permanent plots were established in 2014 (Figure 10, A) in which all trees  $\geq 10$  cm at 1.3 m (DBH- diameter at breast height) were marked, identified, and positioned and are measured annually according to international protocols (Picard and Gourlet-Fleury 2008) by the CIB-OLAM logging group. Each 9-ha plot is subdivided into nine 1-ha subplots. Prior to my arrival in the project, an inventory of lianas and giant herbs was conducted in the study area from April to July 2017. All giant herbs (GH) from the orders Commelinales and Zingiberales were recorded on a systematic 10-m grid in each 1-ha subplot (i.e., 100 sampling points per subplot; Figure 10, B). Their foliar cover projected on the ground was measured using a semi-continuous index from 1 to 3, where 1 represents low cover of less than 20%, 2 represents cover between 20 and 70%, and 3 represents high cover (> 70%). Lianas were sampled in four 20 x 20 m quadrats embedded in each 1-ha subplot, for a total of 144 quadrats covering an area of 5.76 ha (Figure 10, C). All woody lianas  $\geq 1$  cm DBH were marked, identified with vernacular names, and their diameter measured according to international protocols (Gerwing et al. 2006; Schnitzer, Rutishauser, and Aguilar 2008). In late 2018, highly selective logging was conducted in the western block (0.3 logged trees/ha), while the eastern block was left untouched as a control. The inventories of trees, giant herbs, and lianas are described in more detail in the different chapters of the thesis.



**Figure 10.** Experimental design of the permanent plots of Loundoungou-Toukoulaka; (A) the two blocks of 400 ha and the four permanent plots of 1-ha where trees are inventoried annually; (B) giant herbs inventory systematic grid on 1-ha plots; (C) liana inventory quadrats of 20 x 20 m within the 1-ha plots.

## 2.3 Field missions and lab work

During my thesis I conducted several field missions (Figure 11), to collect additional data; one in the context of a pre-doctoral internship (2018), one in the context of a research prize that I won with the European GrowBot project (2020), and two under my doctoral contract (2021 and 2022):

- In April-May 2018 (1 month), I collected 284 herbarium and silica gel leaf samples, which I used to work on botanical identification of liana species (see Section 2.3 below for details) and measure some leaf morphological, physiological, and chemical functional characteristics for 64 liana taxa (described in Chapter 2). I also collected 39 stem samples for 34 liana taxa outside of the permanent plots, on which I subsequently measured wood infradensity (described in Chapter 2, and Chapter 3).
- In February 2020 (3 weeks), we conducted a field mission where high-resolution drone RGB, multispectral, and LiDAR data were collected above the study area. I concomitantly conducted a campaign to validate and associate tree crown delineations on drone images acquired in 2018 and 2019 to tree field inventory numbers, and validate from the ground liana leaf cover observed on drone images. For each tree (277 in total), the COI and all lianas  $\geq 1$  cm in diameter climbing or visibly entering/leaving the tree crown were identified and measured (615 lianas measured). Using Lidar, drone and ground data, I semi-automatically segmented all tree crowns from two permanent

plots (18 ha) and manually delineated all lianas on drone images in the study area (36 ha; methods described in Chapter 1).

- In September-October 2021 (2 months), I conducted a field campaign with an intern to continue the validation of tree crowns from drone images and field inventory numbers. We validated an additional 1217 trees and measured 2002 lianas from the ground with an intern that I supervised for 6 months. I also collected 172 stems for 60 liana taxa outside of the permanent plots, on which I subsequently measured several functional anatomical traits (described in Chapter 3).

- In April-May 2022 (1 month), I participated to the re-launch of the liana and giant herbs inventory in the same quadrats as 2017 to monitor liana dynamics following 2018 logging activities. In particular, I was responsible for starting the liana inventory. I trained a local team for three weeks on liana measurement and identification protocols so that they could continue independently afterwards for six months (described in the Perspectives).



**Figure 11.** Different field missions conducted during my PhD. (A-C) 2018 field mission: (A) Loundougou camp base, (B) field team with Isaac, Aimée, Urbain, Raoul, me, Eric and Latifa and (C) Marien Fongo, one of the local botanical experts on lianas. (D-E) 2020 field mission: (D) field and drone team with Eric, Robin, me, Ati, Maxime, Pachtely and Nicolas, (E) me and a twinning big liana. (F-H) 2021 field mission: (F) nap time with Yorick and me on a big liana, (G) field team with Carla, Ati, Pachtely



and me; (H) macro-anatomical image acquisitions after field days. (I) 2022 field mission liana inventory team with Ibrahim, Dambilo, Pachtely, me and Cyril Dzebou, the principal local botanical expert on lianas.

The most exciting aspect of my thesis was that I had the opportunity to apply, adapt, and learn many different tools and methods from different disciplines. Following my different field missions, I performed a variety of different laboratory work ranging from DNA extractions, gene sequencing, chemical analyses, morphological trait measurements, and herbarium determinations on liana leaves to wood density measurements and cutting, processing, and analysing cross sections on liana stems. I have also worked with drone RGB, multispectral, and LiDAR data, from rasterizing digital models from point clouds to manual and semi-automatic delineation of lianas and tree crowns.

## 2.4 Phylogeny, botanical identification and liana field identification booklet

As mentioned in the introduction, there is a lack of botanical records in the north of the Republic of Congo (Sosef et al. 2017), and this is especially true for lianas. While some identification manuals have been developed for tree species in the region, such as the “Sangha Trees: an illustrated identification manual” by David J. Harris and Alexandra H. Wortley, there is no equivalent for lianas. Due to a lack of expertise in liana taxonomy in the region, lianas were initially identified by a local botanist (Cyril Dzebou) using vernacular names in the regional language of Enyellé (Likouala region; Pandzou, n.d.) during the first liana inventory in 2017. However, a vernacular name may represent more than one species if they have similar uses, and a species may have several vernacular names at different ontogenetic stages (Palma and Heath 2021). For example, the liana “Epougne”, known for its drinkable water in the stem, refers to two different liana species: *Milletia barteri* and *Milletia multiflora*, from the Fabaceae family. Conversely, *Turraea vogelii* of the Meliaceae family is called “Dzola”, but also “Diwolaka” when fruits are present. Another example is one of the most common vernacular names in our study area, “Mbizo”. “Mbizo” represents two different species, *Dalhousiea africana* (the most common species) and *Leucomphalos brachycarpus*, both from the Fabaceae family. Although they are quite similar, they have notable differences in the botanical characteristics of their leaves and stems. Thus, working with vernacular names could lead to considerable uncertainties in regarding their scientific names and possibly uncertainties in subsequent analyses of floristic and functional compositions. In order to analyse the liana inventory data, I first focused on evaluating the taxonomic coherence of vernacular names and, when possible, assigned botanical scientific names to the lianas. I worked on botanical identification of lianas through herbarium comparisons of the flora

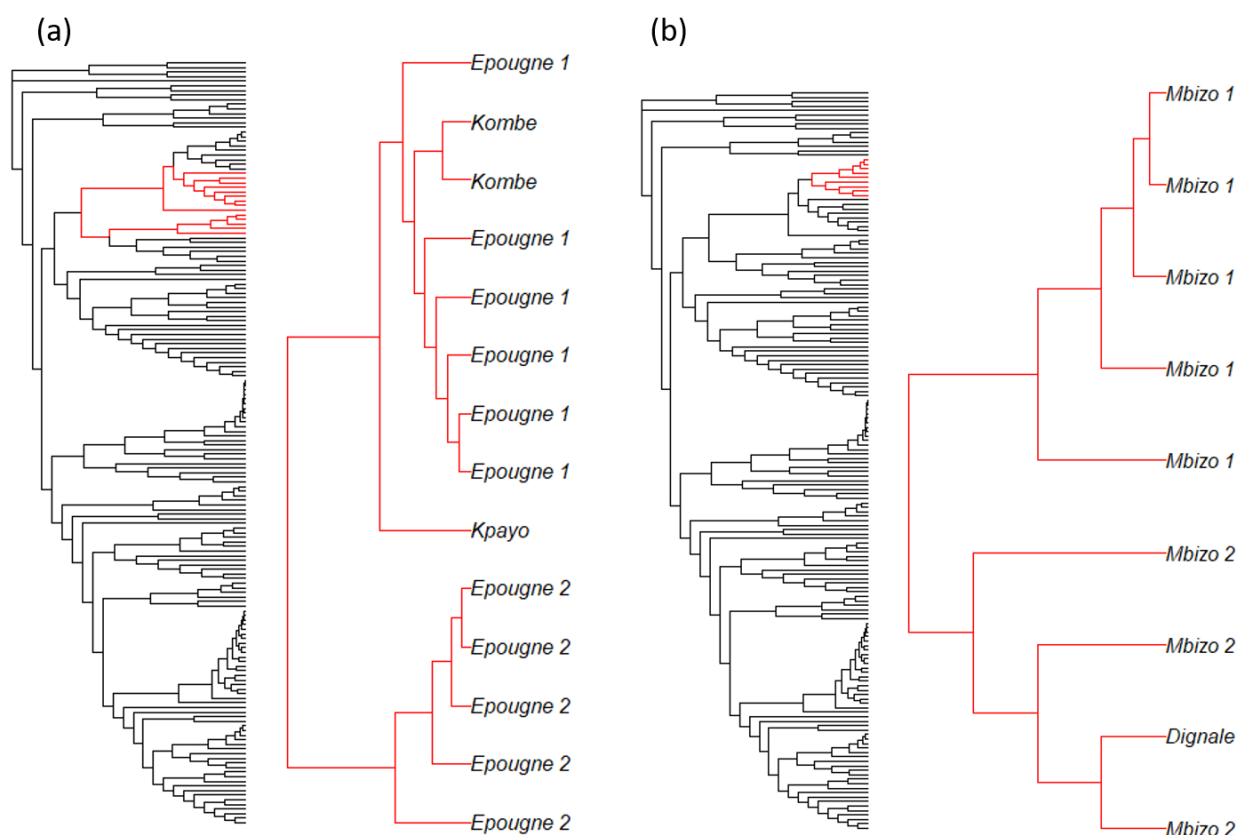
of Cameroon and Gabon mostly and online open-access flora. I also generated and analysed DNA sequence (matK and rbcL markers) to construct a phylogenetic tree of liana species in our study area. Finally, I initiated a field booklet for botanical identification of liana species for our upcoming field missions, which is constantly updated during each field mission with the help of local botanists.

#### 2.4.1 Taxonomic coherence of liana species

To check the taxonomic coherence of the vernacular names, I collected herbarium and silica gel samples of leaves during my first field mission in 2018 with the same field workers as during the 2017 liana inventory. We took care to indicate the different “qualities” for single taxa to verify their taxonomic coherence. Leaf samples were collected within and around the four 9-ha permanent plots in shaded areas in the forest understory on leafy shoots of liana sprouts. I collected two herbarium specimens from each plant. I took one of the specimens to France and stored it at the herbarium ALF at Cirad in Montpellier. The other specimen was deposited at the National Forest Research Institute (IRF) in Brazzaville. I also dried some leaves with zeolite beads for genetic analyzes. I maximized the number of samples collected for the most abundant lianas and for those where taxonomic uncertainty was greatest (where we suspected multiple species behind the vernacular taxa or where the botanical genera were known to contain several lianescent species (maximum of 17 samples per taxa, average of 4 samples per taxa).

I successfully performed DNA extractions from 192 dried liana leaf tissue samples, ensuring that at least one extraction per vernacular name was successful. I then sequenced two specific plastid loci, matK and rbcL, which are recognized as the best candidates for barcoding terrestrial land plants (Group Plant Working Group1 et al. 2009). All DNA extractions were performed using a Qiagen kit (QIAamp 2010), and we performed polymerase chain reactions (PCR) according to the protocol described in (Dunning and Savolainen 2010) for matK and rbcL. Each isolate was sequenced using the Sanger method (Gonzalez et al. 2009) in both the forward and reverse directions. I used the Geneious software (Kearse et al. 2012) to generate consensus sequences and aligned all sequences in the MEGA software (Kumar et al. 2018). I then concatenated the rbcL and matK sequences and identified the most optimal nucleotide substitution model for generating pairwise evolutionary distances between samples using MEGA as the model with the lowest BIC, leading to the selection of the GTR+G+I model. I used the selected substitution model to generate a maximum likelihood phylogenetic tree and fit a chronogram to generate an ultrametric tree (Supplementary S1, and more details in Chapter 3,). The phylogenetic tree was used to check the taxonomic coherence of the liana taxa, especially for taxa representing different species. We were able to show that these species were correctly divided into different "qualities" by local botanists, such as “Epougne” into “Epougne 1” and “Epougne 2” and

“Mbizo” into “Mbizo 1” and “Mbizo 2” (Figure 12), proving that we can use vernacular taxa in further analysis.

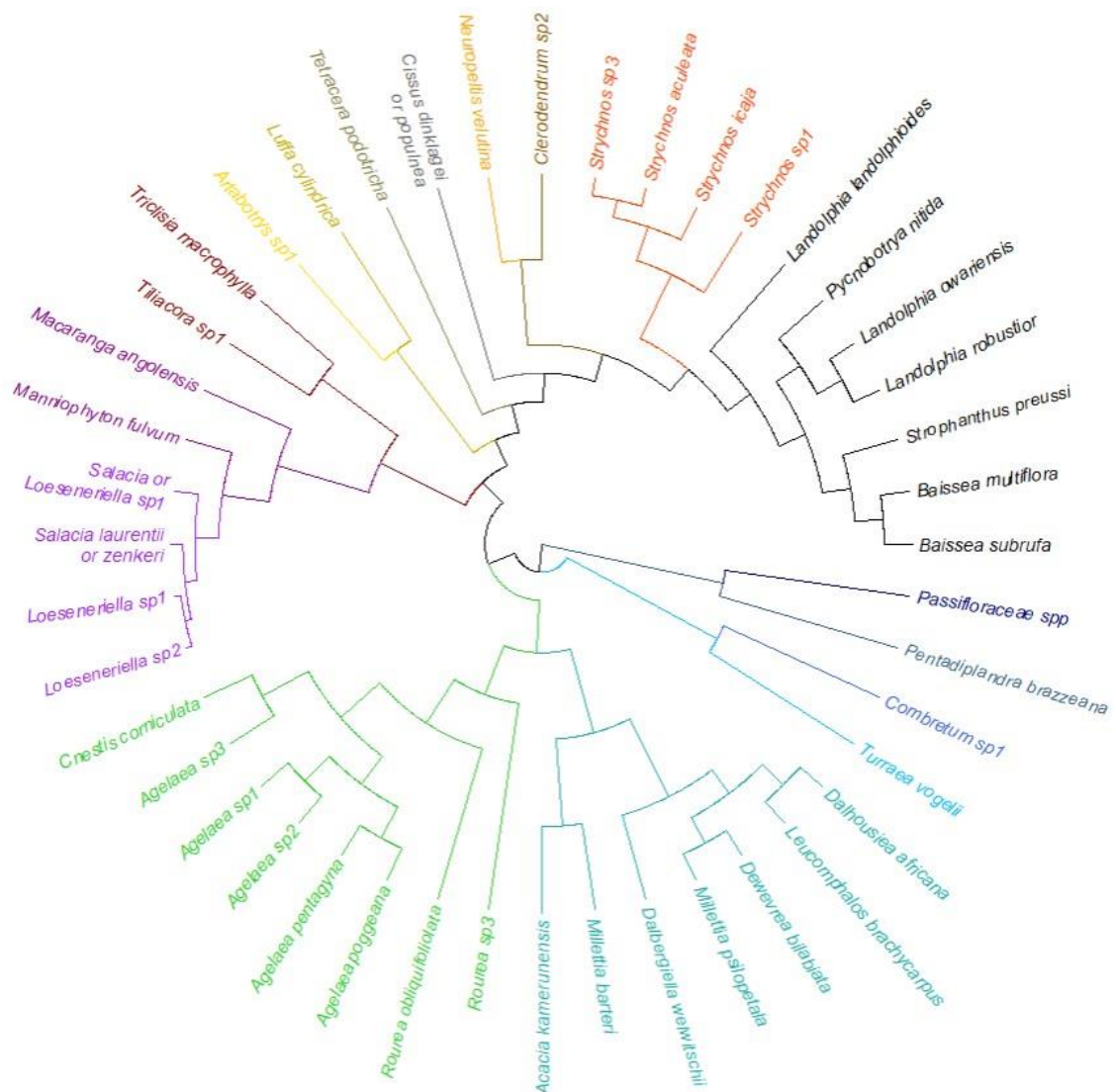


**Figure 12.** Taxonomic coherence of (a) the taxa “Epougne” and (b) the taxa “Mbizo”.

#### 2.4.2 Botanical identification of liana species

The phylogenetic tree provided some insight into the phylogenetic dependence of the liana samples. In addition, I used the Basic Local Alignment Search Tool (BLAST), an algorithm for comparing DNA sequences and identifying similar sequences above a certain threshold in GenBank (Benson et al. 2009), to narrow the identification of each liana herbarium sample to a taxonomic group. Using taxa identification keys based on vegetative or fertile characteristics (when available), primarily in the flora of Gabon and Cameroon and other open-access herbarium databases, I then identified all liana herbarium samples, some at the species level, but others only at the morphospecies, genus, or family level, as most identification keys depend on fertile characteristics of the lianas. Through this work, 57.7% of the 2017 inventoried lianas were identified at the species level, 9.2% at the morphospecies level, 30.8% at the genus level, 0.5% at the family level, and we were unable to identify 1.8% of the individuals (see Chapter 2). After pruning the phylogenetic tree to keep only one sample of each liana species and the species for which we also had functional trait data (see Chapters 2 and 3), we

constructed a phylogenetic tree for the most common and main liana species in our study area, that I used in my thesis (Figure 13).

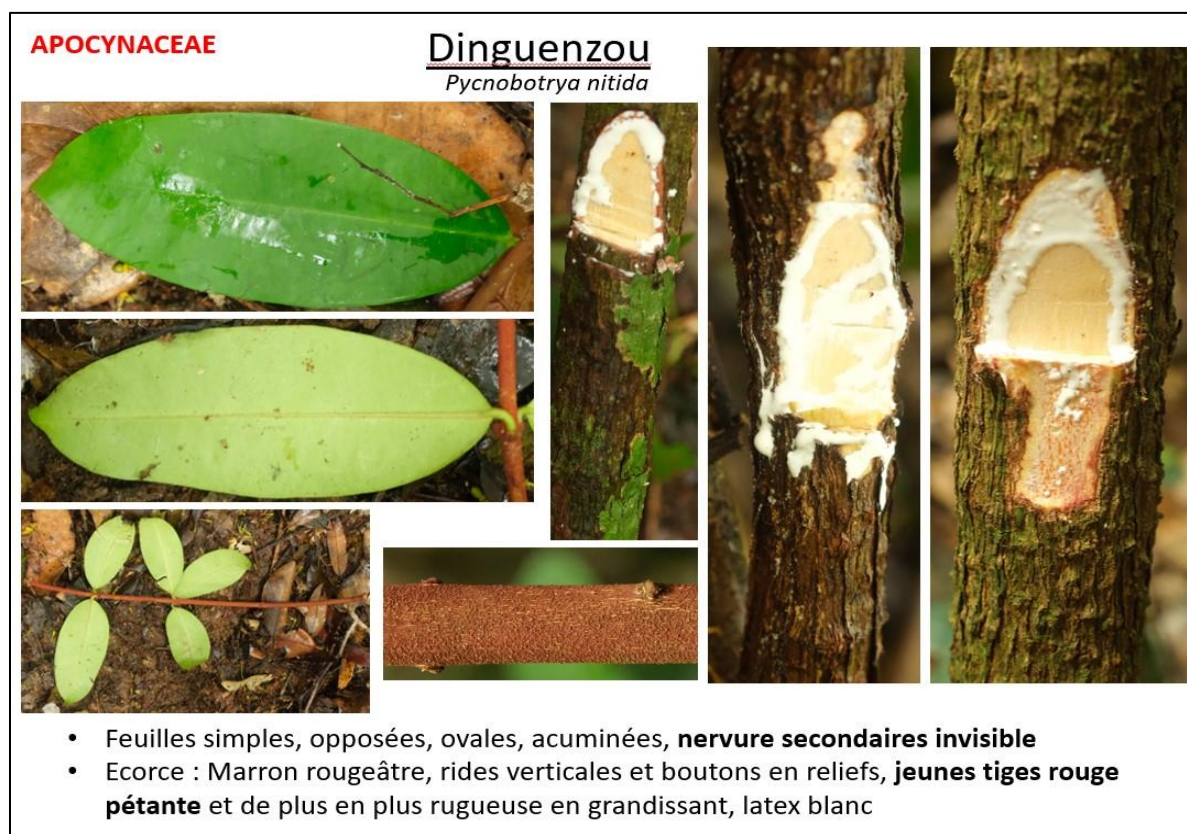


**Figure 13.** Ultrametric phylogenetic tree of liana species of Loundoungou. Colors represent different botanical families.

### 2.4.3 Liana field identification booklet

Because of the difficulty to find botanists in the region and the difficulty of accessing fertile parts of lianas, I have begun to make a field identification booklet for lianas, with simple botanical descriptions of the vegetative parts of lianas, such as leaves, stems, the color of the inner bark and wood, and climbing mechanisms. Since the vegetative parts are mainly the material available from the ground to identify liana species, I also included field pictures of leaves, stems, and a slash cut of their wood and bark to aid in identification (Figure 14). During each field mission, I worked with local

botanists to clearly separate all vernacular names by "qualities", to ensure we could distinguish all the different morphospecies, and went through all the liana species of the booklet to validate their descriptions. The booklet has been improved during each field mission and now contains 100 liana species. It has become an indispensable tool in the field, notably to train, communicate and exchange with local experts. Some copies have been given to local experts and botanists for the education of future generations and to the botanist in charge at the logging company. It is planned to publish the booklet in an open-access database that will serve as a basis for future research studies in the area and further improvements.



**Figure 14.** Example of the description page of “Dinguenzou”, *Pycnobotrya nitida* from the Apocynaceae family, from in the liana field identification booklet.

### 3 Chapter I: Drone and ground estimations of lianas and the role of functional composition

In this chapter, I investigate the liana community at the scale of individual trees to better understand how lianas colonize trees and how we can combine ground and drone data to have more accurate estimations of liana infestation. Liana growth and biomass allocation patterns, between diameter-derived metrics and leaf cover over tree crowns, are explored more mechanistically through the functional composition of liana species that infest individual trees. This chapter demonstrates the potential and need for combining multiple data of different natures (liana leaf cover with drones, individual ground metrics, and individual liana functional traits) to increase our knowledge of liana ecology, but also to better predict aboveground competition of lianas with trees and its effects on their growth. Better data and estimates on lianas will allow to draw broader conclusions about liana-induced effect on forest functions. This chapter also allows to have a first look at the importance of functional composition and the role of functional traits in those liana estimates, and to better understand how heterogeneously lianas might develop on trees and the diversity of biomass allocation patterns.



Keywords: Central Africa, Woody vines, Strategy, Canopy, Competition, UAV systems, Remote sensing.

## Linking drone and ground-based liana measurements in a Congolese forest

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*Published in Frontiers in Forests and Global Change, doi: [10.3389/ffgc.2022.803194](https://doi.org/10.3389/ffgc.2022.803194)*

### Abstract

Lianas are abundant and diverse in tropical forests and impact forest dynamics. They occupy part of the canopy, forming a layer of leaves overtopping tree crowns. Yet, their interaction with trees has been mainly studied from the ground. With the emergence of drone-based sensing, very high-resolution data may be obtained on liana distribution above canopies. Here, we assessed the relationship between common liana ground measurements and drone-determined liana leaf coverage over tree crowns, tested if this relationship is mediated by liana functional composition, and compared the signature of liana patches and tree crowns in our drone images. Using drone platforms, we acquired very high resolution RGB and multispectral images and LiDAR data over two 9-ha permanent plots located in northern Republic of Congo and delineated liana leaf coverage and individual tree crowns from these data. During a concomitant ground survey, we focused on 275 trees infested or not by lianas, for which we measured all lianas  $\geq 1$  cm in diameter climbing on them ( $n=615$ ) and estimated their crown occupancy index (COI). We additionally measured or recorded the wood density and climbing mechanisms of most liana taxa. Contrary to recent findings, we found significant relationships between most ground-derived metrics and the top-of-view liana leaf coverage over tree crowns. Tree crown infestation by lianas was primarily explained by the load of liana climbing on them, and negatively impacted by tree height. Liana leaf coverage over individual tree crowns was best predicted by liana basal area and negatively mediated by liana wood density, with a higher leaf area to diameter ratio for light-wooded lianas. COI scores were concordant with drone assessments, but two thirds differed from those obtained from drone measurements. Finally, liana patches had a higher light reflectance and variance of spectral responses than tree crowns in all studied spectra. However, the large overlap between them challenges the autodetection of liana patches in canopies. Overall, we illustrate that the joint use of ground and drone-based data deepen our understanding of liana-infestation pathways and of their functional and spectral diversity. We expect drone data to soon transform the field of liana ecology.

# 1 Introduction

Lianas are essential components of tropical forests. They may represent up to 20% of woody plant diversity and 40% of stem density in Neotropical forests (Dalling et al., 2012). Because they do not invest into structural support at the adult stage, often using trees to rise to the forest canopy, lianas tend to exhibit a large leaf area-stem diameter ratio compared to trees (Hegarty & Caballé, 1991; Medina-Vega et al., 2021). They can invade more than half of canopy tree crowns (Ingwell et al., 2010), forming a monolayer of leaves overtopping trees and limiting their light acquisition (Avalos et al., 1999; Visser et al., 2018). They are also suspected to better explore and capture soil resources than trees (Collins et al., 2016; Smith-Martin et al., 2019). They thus are in direct competition with trees for both below-ground and above-ground resources (Avalos et al., 1999; De Deurwaerder et al., 2018), reducing forest tree diversity, growth and carbon storage and strongly limiting forest resilience (Laurance et al.; Schnitzer & Carson, 2010; Tymen et al., 2016; van der Heijden et al., 2015). Therefore, accurately estimating liana infestation is important to quantify its effects on forest functions and predict tropical forests dynamics.

Lianas have mostly been studied through ground-level observations, using common measurements such as stem diameters, following international standardised protocols (Clark & Clark, 1990; Gerwing et al., 2006; Schnitzer et al., 2008). However, while they typically represent less than 5% of woody stem biomass, they can occupy up to 30% of the forest leaf area (van der Heijden et al., 2013). To our knowledge, only one study has looked into the relationship between estimates derived from classical ground measurements (i.e., liana stem density, basal area and biomass) and the top-of-view liana leaf coverage over tree crowns, measured by a canopy crane (Cox et al., 2019). This study found no significant correlations between ground-derived estimates and the liana leaf coverage, raising important questions about the conclusions drawn from ground-based measurements on the aboveground impact of lianas on trees. Understanding the relationship between ground-based measurements and the top-of-view liana leaf coverage over tree crowns is thus important to better interpret the conclusions drawn from classical ground measurements and to better understand liana impact and proliferation in tropical forests.

One mechanism that could blur the relationship between ground-based measurements and the top-of-view liana leaf coverage on tree crowns is that lianas do not constitute a homogenous functional group. A recent study has indeed shown that liana trait variations are comparable in magnitude to tropical tree trait variations, within and across studies (Meunier et al., 2020). Indeed, lianas possess a wide range of strategies for climbing and colonizing trees, allowing them to adapt to different



environments (Darwin, 1875; Hegarty, 1991; Putz & Holbrook, 1991; Rowe & Speck, 2015). For instance, physiologically, different wood densities may enable lianas to have different growth-survival strategies. As shown for trees, low wood densities tend to characterize acquisitive species, with high growth rates, large and thin leaves, high photosynthesis rates, large wood vessels and high hydraulic conductance (Baraloto et al., 2010; Buckton et al., 2019; Chave et al., 2009; Poorter et al., 2010; Van Gelder et al., 2006; Werden et al., 2018). These characteristics may in turn impact the patterns of biomass allocation between foliage and woody structures in liana species, as shown for trees where the biomass allocated to the foliage decreases with wood density (Mensah et al., 2016). Furthermore, different climbing mechanisms enable lianas to have different exploration strategies to reach the canopy (Darwin, 1875; Isnard & Silk, 2009; Putz, 1984). Active climbers, such as lianas with tendrils or twining species, exhibit a support-seeking behaviour through circumnutation, whereas other climbers, for example climbing with hooks, spines or root climbing attachment, have developed entirely different mechanisms to attach and climb (Melzer et al., 2010). Attachment modes and climbing behaviours have been long known to be of key interest for understanding liana ecology (Putz, 1984). For instance, Bongers et al. (2020) recently found that climbing strategies was significantly related to the recruitment rates of lianas in Central Africa.

With the development of new emerging remote sensing tools such as unmanned aerial vehicles (hereafter referred to as drones), we can now acquire very high-resolution data in which patches of liana leaves can be visually detected on individual trees (Waite et al., 2019). These high-resolution images provide us with accurate estimations of liana leaf distribution above individual tree crowns and allow us to assess the accuracy of commonly used ground-based liana infestation estimates such as the Crown Occupancy Index (COI). This index is a semiquantitative ground-based assessment of relative liana leaf cover over trees (Clark & Clark, 1990). Some studies have looked into the accuracy of the COI to estimate liana loads through its relationship with metrics derived from common ground liana measurements (density, basal area), with positive conclusions (van der Heijden et al., 2010). As a consequence, liana-infestation has been monitored through time using the COI, as it is much less time-expensive than classical dendrometric measurements (Ingwell et al., 2010; Wright et al., 2015). However, using high resolution drone data in Malaysia, Waite et al. (2019) showed that even if a significant positive correlation between the COI and the relative liana leaves coverage over tree crowns exists, ground-based COI estimates were prone to errors, with more than 25 % of trees incorrectly classified from the ground. Most of these errors occurred for low infestation levels, representing nearly half of the wrongly classified trees. Given the importance of the COI in current liana studies, the accuracy of this index should be further evaluated in different forest contexts.

One important condition for detecting liana leaves in remote sensing products is the existence of different spectral responses between liana and tree leaves. Lianas tend to have different leaf chemical properties than trees, resulting in higher reflectance across the solar spectrum, with higher differences between trees and lianas observed around 550 nm (green domain; Asner & Martin, 2012; Castro-Esau, 2004; Chandler et al., 2021; Li et al., 2018) and in the near infrared (NIR; 780 nm to 1400 nm; Li et al., 2018) and shortwave infrared (SWIR; 1400 nm to 3000 nm; Chandler et al., 2021; Visser et al., 2021). Some studies have used these differences in spectral responses to detect liana infested trees and monitor infestation rates at the scale of the canopy (Chandler et al., 2021; Li et al., 2018; Marvin et al., 2016). For instance, Li et al. (2018) obtained an accurate classification of liana infested and non-infested trees using a deep self-encoding network at the scale of the canopy, using high-resolution multi-spectral (475 nm (blue) to 840 nm (NIR)) drone data. However, as most previous studies, they solely focused on the presence or absence of lianas and did not quantify the degree of infestation of trees. All studies aiming at quantifying the degree of liana infestation found reliable results only for highly infested trees (> 50 or 75% of infestation by lianas) and could not accurately estimate nor detect low liana infestation rates (Chandler et al., 2021; Marvin et al., 2016). A recent study even showed that lianas and trees do not differ significantly in their spectral signatures at the leaf level (Visser et al., 2021). Nevertheless, radiative transfer modelling has suggested that lianas display a lower light absorption and greater projected leaf area, due to flatter leaf angles. This results in a higher reflectance at the canopy scale, especially in the near and shortwave infrared regions and when liana leaves are aggregated within large patches (Visser et al., 2021). Most of these studies were, however, conducted in Neotropical forests while much less is known about the spectral properties of lianas in the paleotropics. Given that lianas are present in more than 133 families of angiosperms (Gentry et al., 1991), probably generating a large range of spectral signatures as observed for trees (Féret & Asner, 2012; Rocchini et al., 2016) and that spectral signatures partly depend on local environmental conditions (Asner & Martin, 2012; Medina-Vega et al., 2021), the extent to which liana leaves can be detected from their spectral signatures should be further investigated, especially with the use of very high-resolution drone data and focusing in other tropical regions than the Neotropics. Furthermore, with the recent advances in processing Light Detection and ranging (LiDAR) data, we now can semi-automatically delineate individual tree crowns thanks to dedicated algorithms (Aubry-Kientz et al., 2019) and thus better disentangle the spectral response of tree crowns from that of liana patches.

In this study, we investigated the relationship between ground-based liana measurements and liana leaf coverage over tree crowns quantified through high-resolution drone images. More specifically, we assessed whether ground-based measurements accurately predict liana leaf coverage over tree crowns and whether these two measurements are mediated by liana functional composition.

We also separated the signatures of liana patches and tree crowns both in the visible and non-visible domain to evaluate the extent to which they overlap. We hypothesise that (i) classical ground-based liana measurements are significantly correlated with drone-based liana leaf coverage estimates; (ii) liana wood density and climbing mechanisms both influence liana leaf coverage over tree crowns; (iii) the COI is not an accurate measure of liana leaf coverage for low infested trees, as found by Waite et al. (2019); and (iv) spectral responses of liana patches and tree crowns significantly differ in multispectral data, with higher reflectances of lianas both in the green and near infrared domain, as previously found in the Neotropics.

## 2 Material and methods

### 2.1 Study site

Our study took place in Central Africa, in the north of the Republic of Congo, in the Likouala province (2°27'11.87" N and 17°02'32.17" E). Mean annual rainfall is 1605 mm/year (unpublished data obtained from 2003 to 2017 using a local station at Pokola, 140 km away from our study site). The climate is characterized by two dry seasons with a short one from June to August and a long one from December to February. The Loundougou site is located on a plateau, the geological substrate consists of limestone and alluvium from the Quaternary. Soils can be classified as Xanthic Acrisols, sandy-clay to clay-sandy, representative of the highest and lowest elevations of the plateau (Freycon, 2014). The studied landscape is generally low and flat, between 395 and 470 m asl (Freycon, 2014). The vegetation is a semi deciduous forest characterized by the abundance of trees belonging to the Fabaceae, Annonaceae and Malvaceae families (Réjou-Méchain et al., 2021).

The experimental study site was settled in 2013-2014 in the Forest Management Unit (UFA) of Loundougou-Toukoulaka, in a concession managed by the logging company CIB-Olam. The experimental design aims at comparing different silvicultural treatments among four 9-ha plots that were established in similar soil, topography and initial vegetation conditions (using preliminary inventories). In the present study, we focused on two 9-ha permanent plots that experienced highly selective logging operations at the end of 2018 (0.3 trees logged per ha on average). Other human activities are unlikely to have induced major disturbances in the recent decades. Inside each plot, all trees  $\geq 10$  cm dbh (diameter at breast height) have been identified, located, and their diameter measured each year since 2015 following international standards (Picard & Gourlet-Fleury, 2008), for a total of 6380 trees  $\geq 10$  cm dbh measured in 2019.

## 2.2 Drone-based data and pre-field inventories analyses

Drone-based acquisitions were performed at three different periods: in June 2018, April 2019 and in February 2020. In 2018 and 2019, Red Green Blue (RGB) images were acquired over the experimental site using an EBEE 03-907 drone, from the manufacturer SENSEFLY, operated by a private company (Sylvafrica). In 2020, we acquired three drone datasets: Red Green Blue (RGB), multispectral and LiDAR data. All flights were conducted under homogeneous sunlit conditions. RGB data were acquired with a Mavic 2 Pro drone, using an integrated three-waveband (RGB) camera (20MP Hasselblad L1D-20c gimbal). The flight trajectory was calculated and conducted with the UGCS software. The acquisitions were made in three flights covering the whole study site in less than 1-hour between 7 and 8 am, on the 14th of February, with an overlap of 90% between flight lines. This short time of acquisition of all RGB data allowed us to obtain Digital Numbers (DN) values under homogeneous sunlight and atmospheric conditions, and were hereafter assumed as a proxy of relative radiometric responses (radiometric corrections were not possible in our study). Multispectral data were acquired in the red (660 nm +/- 40 nm), green (550 nm +/- 40 nm), red-edge (735 nm +/- 10 nm) and near-infra red (790 nm +/- 40 nm) regions using a Parrot Sequoia camera mounted on a DJI Matrice 600 drone. The flight trajectory was also calculated and conducted using UGCS. The acquisitions were made in two overlapping flights over the studied area, on the 13th of February, the first at 8 am and the second at 15 pm, with an overlap of 90% within flight lines. Data from an incident light sensor located above the drone was used for conversion of DN values into bottom-of-atmosphere (BoA) reflectance in the Pix4D software (<https://www.pix4d.com/>). However, as the Pix4D routine did not yield satisfactory results, analyses based on the BoA reflectance values of trees versus lianas were restricted to 60% of the studied area, i.e., using only the first flight to minimize atmospheric effects and avoid inter flight radiometric corrections.

All drone imagery data were processed through Pix4D to produce orthomosaics at spatial resolutions of 10 cm (2018), 5 cm (2019), 3 cm (2020 RGB) and 17 cm (2020 Multispectral). Pix4D used structure from motion algorithms, and other algorithms, to build a dense point cloud from which a digital surface model (DSM) was derived and used to produce an orthomosaic. In all cases, pixels were represented by a minimum of five overlapping images, with a total of 1095 images over 1292 ha (2018), 248 images over 80 ha (2019), 1153 images over 56 ha (2020 RGB) and 2011 images over 450 ha (2020 Multispectral). We used both the Pix4D algorithms of noise filtering, to remove outliers in the generated points cloud, and of surface smoothing (type Sharp), to flatten erroneous small bumps in the DSM.

Finally, very high-resolution LiDAR data were acquired on the 9th of February 2020 over the whole study site. A YellowScan Surveyor Ultra sensor (combining a Velodyne Ultra Puck, 600kHz, 905 nm wavelength LiDAR scanner and an Applanix 15 IMU) was flown mounted on the DJI Matrice 600 UAV platform at 60 m above SRTM elevation at a speed of 8 m/s, with an interline distance of 50 m. A multiple return acquisition resulted in a point density of 372 points/m<sup>2</sup>. We used a Reach RS2 GNSS base station for PPK differential positioning with a global accuracy of less than 4 cm on the X and Y axis (average accuracy of 3.7 cm on all trajectories) and less than 7 cm on the Z axis (average accuracy of 6.3 cm on all trajectories). Trajectories were post-processed in PosPac UAV v9 and point clouds were processed in LASTools (Isenburg, 2014) to derive a 1-m resolution Digital Terrain Model (DTM) using the `lasground` (with the `wilderness` option) and `las2dem` functions. We then normalized the point clouds (using the `lasheight` function) and assessed the maximum height values with a 1m-grid in the normalized point cloud (`lascanopy` function) to create a Canopy Height Model (CHM), representing the top-of-canopy height above the ground.

Prior to the field inventory (see next section), we conducted preliminary analyses on the 2018 and 2019 drone datasets in order to facilitate our upcoming fieldwork. Through a visual interpretation of RGB mosaics, we manually delineated what was seemingly liana leaf cover patches over individual tree crowns, using the QGIS open source software (version 3.10). We then validated the presence of lianas in these tree crowns using binoculars in the field to assess the accuracy of these preliminary delineations from the ground. This assessment also both helped our tree selection and liana delineation afterwards on the 2020 drone images (see section 2.4.1.2).

## 2.3 Field inventories

We conducted a field campaign concomitantly with the third drone acquisition in February 2020. Using the field application of QGIS, Qfield (<https://qfield.org/>), we validated and corrected (if needed) the delineation of individual tree crowns and the presence of liana leaf coverage observed on the 2019 RGB images, and recorded the corresponding tree field inventory number for each tree crown. In almost all cases the preliminary delineations of lianas were validated with the presence of liana leaf coverage patches over tree crowns, with only a few errors due to the occurrence of hemi-parasite and hemi-epiphyte plants. Because the number of liana-infested trees was much smaller than that of non-infested ones, we focused our field investigations on trees that were identified as liana-infested in our preliminary analyses and measured non-infested trees in an opportunistic way. It enabled us to optimize our time during our 3-week field mission and to ensure the measurement of numerous liana-infested trees. In total, we were able to link individual tree crowns delineated on drone images with tree ground survey numbers for a total of 275 trees, infested or not by lianas, with diameters ranging

from 12.9 cm to 170.7 cm dbh (median of 55.7 cm dbh). All studied trees had a crown entirely visible from drone images, as estimated from the field.

For each tree, we estimated the liana leaf coverage from the ground using the widely used Crown Occupancy Index (COI; Clark & Clark, 1990; van der Heijden et al., 2010). This semi-quantitative index expresses the relative coverage of liana leaves in the tree crown using five categories: (0) no liana leaves in the crown, (1) 1–25%, (2) 26–50%, (3) 51–75%, and (4) >75% of the tree crown covered by liana leaves. For each tree, the COI was systematically assessed by two observers, equipped with binoculars, who observed tree crowns from every visible and accessible angle, discussed their estimates and agreed on the final COI score.

All woody lianas  $\geq 1$  cm in diameter climbing on the studied trees, or visibly entering or leaving the tree crown, were identified by vernacular name and their diameters were measured following international protocols using a manual calliper for small lianas and a tape for large ones (Gerwing et al., 2006; Schnitzer et al., 2008). In total, we measured 615 lianas belonging to 54 vernacular taxa climbing on 104 trees. For each tree, we computed four stand level liana measurements: liana stem number ( $N_L$ ), liana basal area ( $BA_L$ ), liana maximum diameter ( $D_{max,L}$ ), liana mean quadratic diameter ( $QMD_L$ ).

We measured or recorded two functional traits: the stem wood infradensity and the climbing mechanism. For stem wood infradensity, we collected stem cylinders of more than 2 cm in diameter at 1.3 m from the stem root, out of the permanent plot to avoid destructive measurements within the plots. In total, we collected stems belonging to the most abundant 20 vernacular taxa, representing 83 % of the 615 liana stems inventoried. Wood samples of approximately 2 cm of length were debarked and saturated with water under pressure and the Archimedes thrust was measured following the protocol described by Birouste et al. (2014). Wood samples were first dried in an oven at 45°C for a week to avoid damaging the water saturated materials with sudden extreme temperatures. Then, we rose the temperature to 103°C for 24 hours to eliminate all water residuals. Finally, the anhydrous masses of wood samples were measured, to assess the wood infradensity, hereafter named wood density.

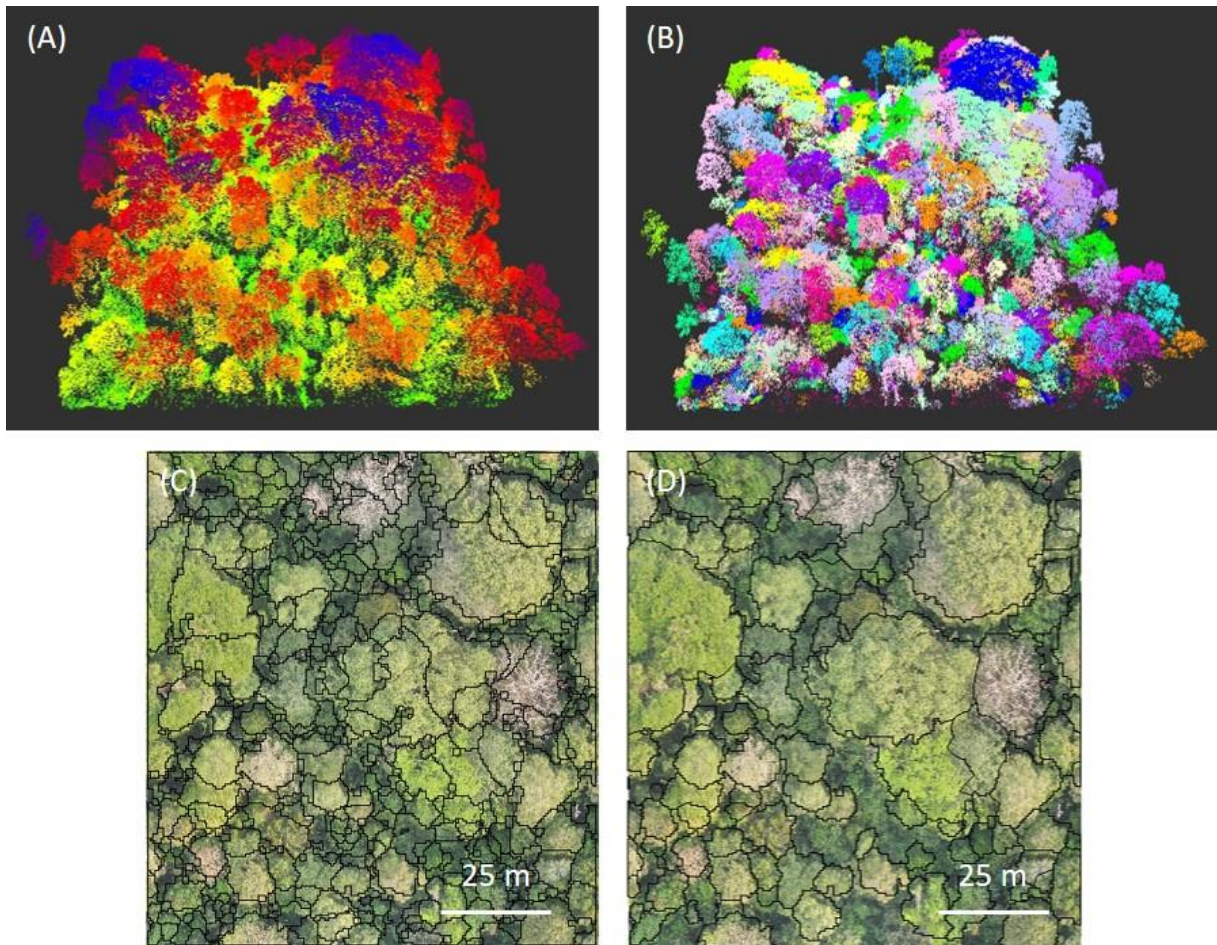
Liana climbing mechanisms were recorded for 34 vernacular taxa, representing 92% of the 615 liana stems inventoried. Climbing mechanisms were assigned to each vernacular name following the classification proposed by Sperotto et al. (2020). We classified as “active” climbing mechanisms twining lianas, lianas with tendrils, prehensile branches and lianas with angular branches. We classified as “passive” climbing mechanisms lianas with hooks, spines, adhesive roots and simple scrambling lianas.

## 2.4 Data analysis

### 2.4.1 Geospatial analysis

#### 3.1.1.1 Tree crown segmentation

We used the LiDAR data to delineate tree crowns on the two 9-ha plots. After normalising the point cloud with the Digital Terrain Model (DTM), we removed the ground points and reduced randomly the density of the point cloud to 40 points/m<sup>2</sup> to limit computing time. We then used the Adaptive Mean Shift approach (AMS3D; Ferraz et al., 2012) implemented in the open Computree software (Piboule et al., 2013). This approach composes a normalized point cloud into 3D clusters, corresponding to individual tree crowns, by finding local maxima giving a certain cylinder size. We deliberately parametrized the model to over-segment tree crowns (Figure 1, A and B) because it is then easier to manually merge over-segmented crowns than to segment under-segmented crowns. After extracting the projected shapes from Computree, we manually cleaned the segmentation in QGIS, using our field observations and high resolution RGB and multispectral images (Figure 1, C and D). In total, we delineated 1626 individual canopy tree crowns over the 18-ha study area. We finally assigned to each tree its maximum height using the LiDAR-derived CHM model built at 1-m resolution.



**Figure 1.** An example of tree crowns segmentation of a 1-ha subplot, with the AMS3D approach. (A) the point cloud before the segmentation, coloured by height (green to blue) and (B) after the segmentation, coloured by individual tree. The projected 2D shapes of individual tree crowns (in black) before manual cleaning in (C) and after in (D) over an RGB image.

### 3.1.1.2 Liana delineation and spectral signatures of lianas

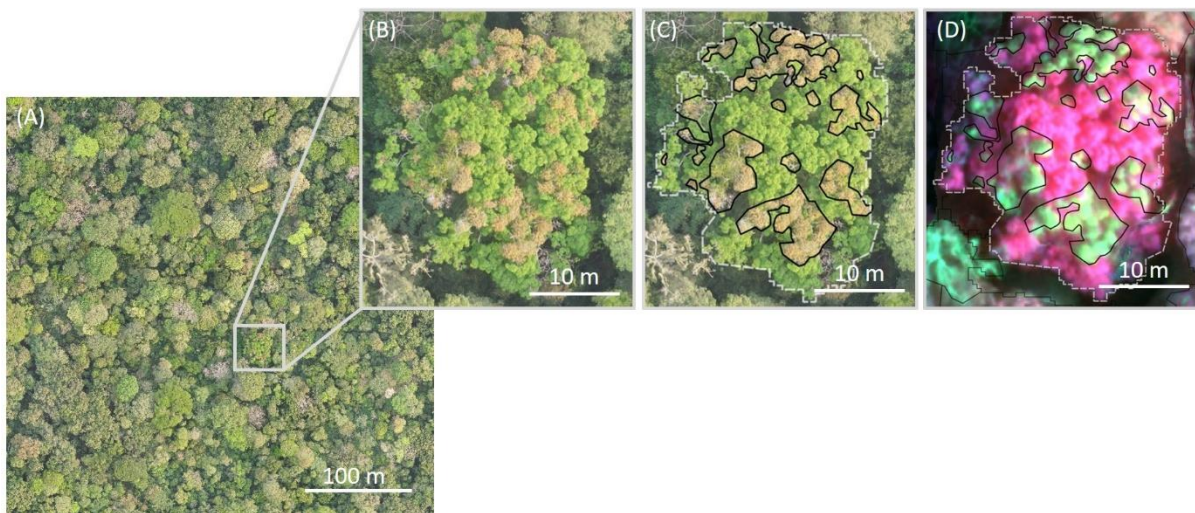
In all the studied trees validated from the ground, liana leaves were clearly distinguished visually from leaves of their host trees in the visible (RGB) and/or non-visible (Red-Edge and Near Infrared) domain (Figure 2). We thus delineated all visible liana leaf coverage over the two 9-ha plots, manually from QGIS, combining our spatialized field observations and a careful visual interpretation using the different 2020 spectral bands available.

Using the 2020 RGB images, we then selected pixels that were likely dominated by leaves, either from trees or lianas, to quantify the photosynthetic surface of trees and lianas. To do this, we first only selected pixels belonging to a segmented tree crown (see previous section), ignoring canopy gaps and below-canopy vegetation. We then filtered out woody pixels (in our case DN values  $> 190$  in the blue waveband) and pixels corresponding to small gaps in the tree crown (DN values  $\leq 100$  in the green



waveband). Using this dataset, we finally estimated the relative area of liana leaves over the total canopy photosynthetic surface.

To test whether liana leaves expressed a singular spectral response, we averaged pixel DN (RGB data) and reflectance (multispectral data) values for each individual liana patch and liana-free tree crown for all bands independently to minimize the noise associated with pixel-level information. We submitted object-level averaged DN and reflectance values to a Principal Coordinate Analysis (PCA) and compared the liana and tree leaves responses along the first two PCA axes using Wilcoxon tests, to test for difference in signal average, and F-test, to test for difference in signal variance. As mentioned earlier, this analysis was conducted on only 60% of the study area to minimize atmospheric and radiometric bias in multispectral data. Considering multispectral data in DN values instead of reflectance values in the PCA led to the same results (not shown).



**Figure 2.** Example of the manual delineation of liana leaves using RGB and multispectral data. (A) RGB mosaic of one of the two 9-ha plots. A liana-infested tree crown is illustrated before (B) and after (C-D) the manual delineation of lianas (in black lines) and the LiDAR segmentation of the tree crown with the AMS3D approach (in white dotted lines) on RGB (C) and multispectral (D) images.

## 2.4.2 Statistical analyses

### 3.1.1.3 Relationship between the COI and liana leaf coverage over tree crowns

We used the whole dataset (275 trees) to study the relationship between the COI determined from the ground and the proportion of photosynthetic surface of lianas on tree crowns determined by drone-based data. We modelled with an ordinal probit regression the relationship between the different ground-determined COI categories (0, 1, 2, 3 or 4) and the proportion of photosynthetic surface of lianas (aka drone-determined liana leaf coverage) on tree crowns.

### 3.1.1.4 Relationship between stem ground measurements and liana leaf coverage over tree crowns

We performed all statistical analyses at the scale of individual trees. We divided our dataset in four categories by the type of infestation of the host tree:

- (i) trees that were not infested by lianas. These trees did not have any visible liana climbing on them or coming from adjacent trees from the ground (COI of zero), and did not have any liana leaves visible on the crown from the drone images (n=161 trees);
- (ii) trees that were identified as infested by lianas. These trees were identified as infested either from ground measurements or/and drone observations;
  - (ii)-a trees that were identified as infested from both ground measurements and drone observations (n=87 trees);
  - (ii)-b trees that were identified as infested only from ground measurements, with no visible liana leaves on the crown from drone images (n=17 trees);
  - (ii)-c trees that were identified as infested only from drone observations, with no visible lianas climbing on them or coming from adjacent trees from the ground (n=10 trees).

Because including category (i) may lead to an overestimation of model performance, with an inflation of zero values, we only considered infested trees of category (ii) when analysing the relationship between ground measurements and liana leaf coverage. We also discarded infested trees of the category (ii)-c because we either failed to find the corresponding lianas rooted point in the ground or the leaves most probably belonged to epiphytes (see discussion). Thus, ground measurements and liana leaf coverage comparison were done on a total of 104 trees (categories (ii)-a and (ii)-b). Our infested tree selection was the same as Cox et al. (2019) except that, here, we also included trees with lianas climbing on them without any visible leaves from above.

First, we modelled with a Bernoulli probit-regression, the probability that a tree infested from ground measurements had visible liana leaves on the crown from drone images. This model was calibrated on the 104 trees of (categories (ii)-a and (ii)-b). Second, we modelled with a log-linear regression, the liana leaf coverage for trees infested from ground measurements and with visible liana leaves on the crown from drone images. This model was calibrated on the 87 trees of (categories (ii)-a).

For the two models, the predictors were selected among the four tree-level liana measurements calculated at the tree level ( $N_L$ ,  $BA_L$ ,  $Dmax_L$ ,  $QMD_L$ ), the LiDAR-derived total tree height (H) and the interactions between  $N_L * QMD_L$  and  $H * QMD_L$ . We selected the predictors using a stepwise approach

(backward/forward) based on the Bayesian Information Criterion (BIC; the best model has the lowest BIC).

Hence, the products of these two models could lead to a model of the liana leaf coverage for trees defined as infested from ground measurements.

### 3.1.1.5 Influence of liana functional traits on liana leaf coverage

To study the influence of growth strategies on liana leaf coverage, we analysed the relationship between the residuals of the selected linear log-log regression model and two liana functional traits averaged at the tree level: the basal-area weighted wood density of lianas ( $WD_L$ ) and the climbing mechanisms of lianas ( $Mecha_L$ ).  $WD_L$  was estimated for every infested tree for which we knew the wood density of liana individuals for more than 80% of the total liana basal area ( $n= 57$  trees) using the equation as follows:

$$WD_L = \frac{\sum_{i=1}^n (WD_i * BA_{Li})}{\sum_{i=1}^n BA_{Li}}$$

With  $n$  the total number of liana stem climbing on the host tree,  $WD_i$  the wood density for liana species  $i$  and  $BA_{Li}$  the total liana basal area for individuals belonging to the liana species  $i$ . on the host tree We calculated the climbing mechanism index ( $Mecha_L$ ) indicating the mean liana growth strategy through the following equation:

$$Mecha_L = \frac{\sum_{i=1}^{n_a} BA_{i_a}}{\sum_{i=1}^{n_a} BA_{i_a} + \sum_{i=1}^{n_b} BA_{i_b}}$$

With  $n_a$  the total number of liana stems with active climbing mechanisms,  $n_b$  the total number of liana stems with passive climbing mechanisms and  $BA_{i_a}$  and  $BA_{i_b}$  the basal area of all lianas having an active and passive climbing mechanism, respectively. We calculated  $Mecha_L$  for every infested tree for which we knew the climbing mechanism of more than 80% of the total liana basal area ( $n= 70$  trees).

We did not include directly functional traits variables into the regression models but decided to look at their relationship with the residuals of the models (response minus fitted values), because we did not have trait data information for the whole dataset.

All analyses were conducted on R version 4.0.3 (R Core Team, 2020), using the libraries sf (Pebesma et al., 2018), raster (Hijmans, 2021), lidR (Roussel et al., 2020), MASS (Venables & Ripley,

2002), reshape2 (Wickham, 2007), ggplot2 (Villanueva et al., 2016), DescTools (Signorell et al., 2021), dplyr (Wickham et al., 2021) and RcmdrMisc (Fox et al., 2020).

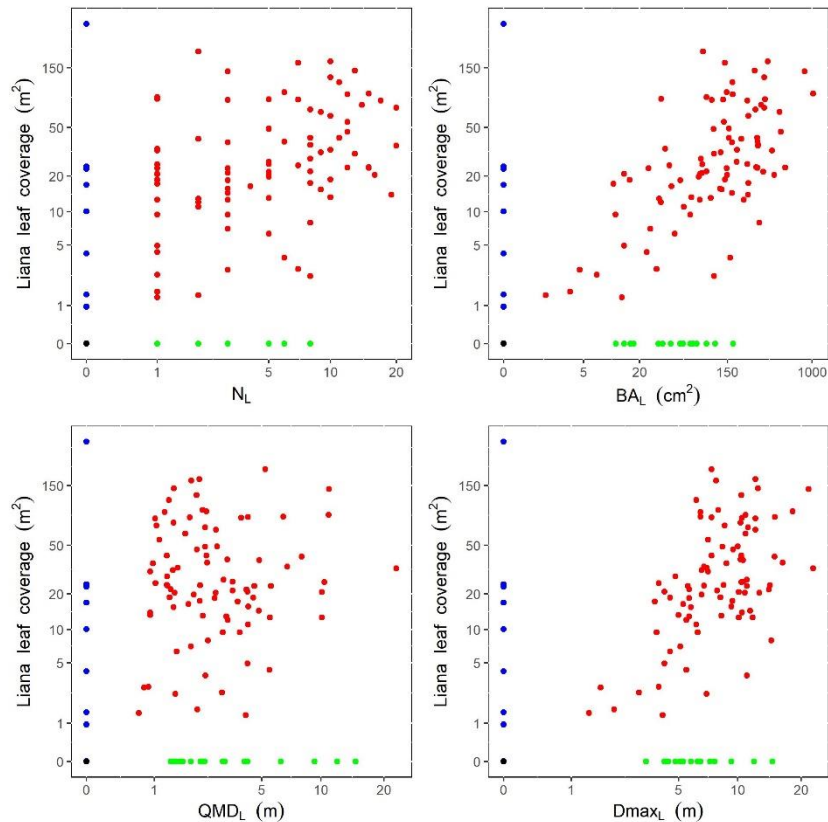
## 3 Results

### 3.1 Amount of liana infestation estimated from the ground and from drone data

Drone- and ground-based measurements indicated that 35% and 38% of the selected 275 trees were infested by lianas, respectively. These numbers are unlikely to be representative because we deliberately sampled a higher proportion of liana-infested trees than non-infested trees. However, at the scale of the study sites (the two 9-ha plots), drone-based measurements indicated that 16.6% of canopy trees (n=270) were infested by lianas and that liana leaves covered 6.2% of the total canopy photosynthetic surface (n=594 patches). At the scale of the 275 trees dataset, ground-based measurements indicated that liana-infested trees were infested by an average of 5.9 lianas (range of 1 to 20) with a mean quadratic diameter of 3.5 cm (range of 0.7 to 22.8 cm) and an average basal area of 157.8 cm<sup>2</sup> (range of 1.6 to 1027.5 cm<sup>2</sup>). Using herbariums, we identified a total of 54 liana taxa, although this estimate might be underestimated because some vernacular names cannot yet be assigned to a single species (work in progress). Wood density also varied markedly among liana taxa, ranging from 0.29 to 0.52 g cm<sup>-3</sup> (mean of 0.42 g cm<sup>-3</sup>), and the basal-area weighted wood density of lianas at the scale of an individual tree,  $WD_L$ , ranged from 0.37 to 0.52 g cm<sup>-3</sup> (mean of 0.44 g cm<sup>-3</sup>). Finally, the dominant climbing mechanisms was active (64% of individuals), with 47% of the total stems belonging to twining lianas.

### 3.2 Link between drone and ground-based liana measurements

Eighty four percent of the trees hosting lianas had visible liana leaves on their tree crowns in drone images (category (ii)-a; red dots in Figure 3). Thus, 16% of the trees observed as infested from the ground did not have any visible leaf coverage on their crowns when drone data were acquired (category (ii)-b; green dots in Figure 3). Most of these trees consistently had a COI score of 0 (n=5) or 1 (n=11), except one tree that had a COI score of 3. For this tree, our field note indicated that the COI score was uncertain due to the co-existence of a hemi-epiphyte (*Ficus* sp.) and a mix of old and young liana leaves. Finally, we observed liana leaves in the crown of 10 trees (4%; category (ii)-c; blue dots in Figure 3) for which we failed to assign any corresponding liana stems on the ground.



**Figure 3.** Relationships between liana ground measurements and liana leaf coverage estimated from drone data for the 275 studied trees. Colours illustrate the different infestation categories, black for category (i), red for (ii)-a, green for (ii)-b and blue for (ii)-c. Axes are shown in log scale. For  $N_L$ , Spearman's  $\rho = 0.43$ ,  $p$ -value  $< 0.001$ ; for  $BA_L$ , Spearman's  $\rho = 0.58$ ,  $p$ -value  $< 0.001$ ; for  $QMD_L$ , Spearman's  $\rho = 0.004$ ,  $p$ -value =  $0.97$ ; for  $Dmax_L$ , Spearman's  $\rho = 0.48$ ,  $p$ -value  $< 0.001$ .

### 3.2.1 Link between liana leaf coverage and classical ground-based liana measurements

For trees identified as infested either from the ground or drone data (category (ii)), we found that ground-derived liana stand metrics were significantly correlated with the liana leaf coverage measured on drone data (Spearman's  $\rho = 0.43$  to  $0.58$ ;  $p$ -value  $< 0.001$ ; Fig. 3), except for liana mean quadratic diameter ( $p$ -value= $0.97$ ).

The infestation status of tree crowns (infested or not) was first best predicted by liana basal area and total tree height, with a predominant positive effect of liana basal area and a negative effect of tree height (Table 1). The selected model classified 86% of the 275 trees accurately but tended to overestimate the number of tree crowns infested by liana leaves using ground-based measurements as predictors (Table 2).

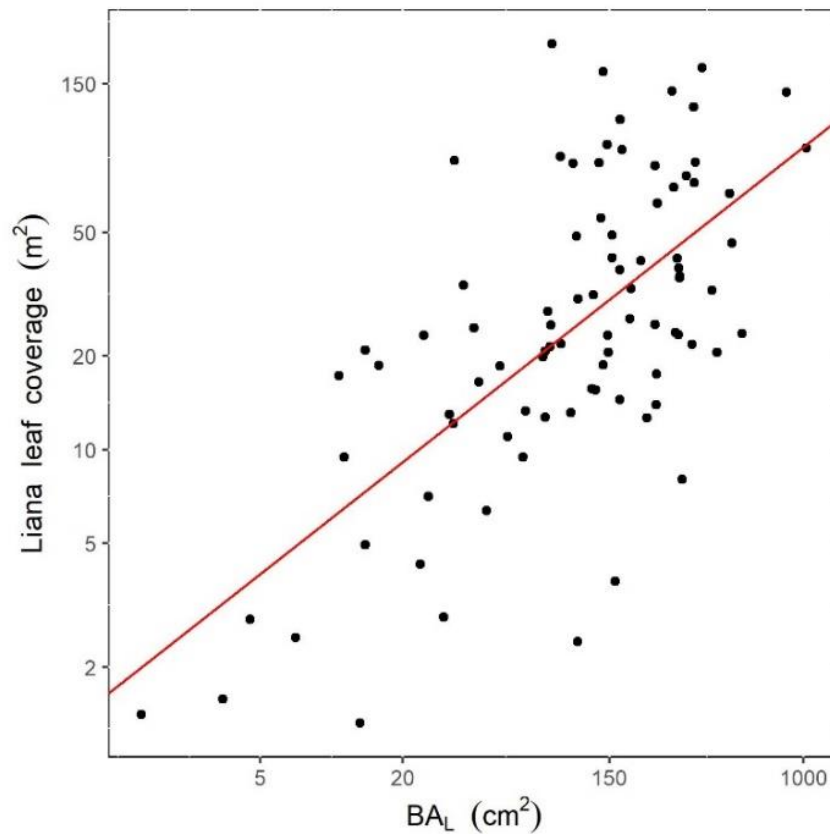
**Table 1.** Estimates of parameters of the model selected to predict liana infestation status (tree crowns infested or not). Parameters associated with variables that were not selected by the BIC step procedure are not reported.

	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	1.4791	0.2754	5.371	<0.0001 ***
BA <sub>L</sub>	1.3630	0.4258	3.201	0.0001 **
Height	-0.4791	0.1937	-2.474	0.01337 *

**Table 2.** Error matrix showing the number of tree crowns predicted to be infested by liana leaves using ground-based measurements as predictors and drone observations as reference data. Agreements between predictions and observations are represented in bold.

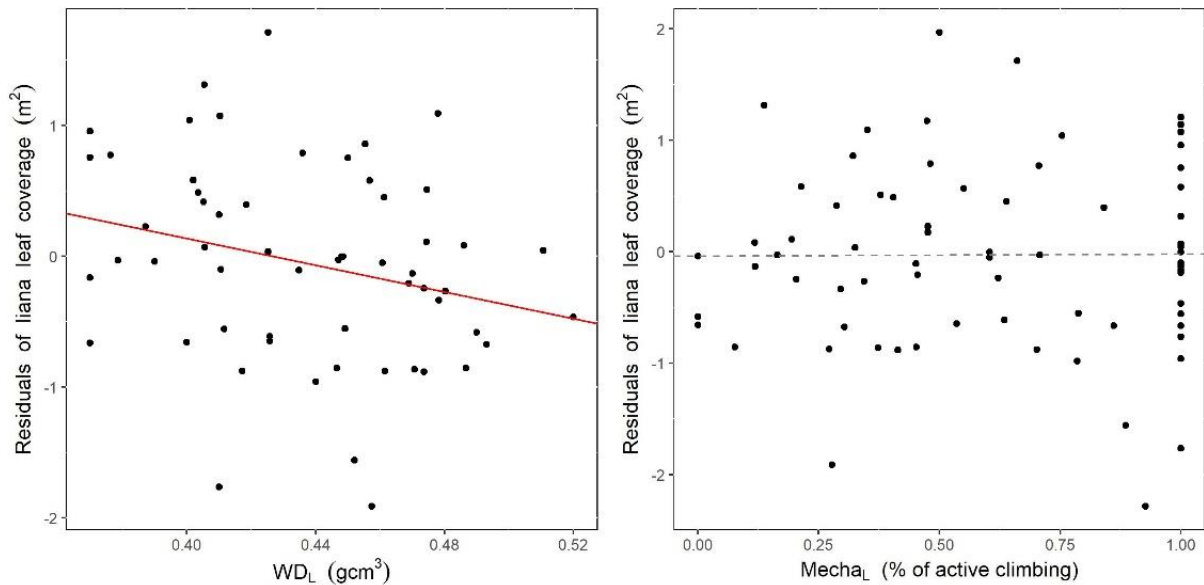
		Drone observations	
		Not infested	Infested
Predictions from ground measurements	Not infested	5	2
	Infested	12	<b>85</b>

When focusing on trees being interpreted as liana-infested from both ground and drone observations (category (ii)-a; n=87), our BIC selection procedure only retained the total liana basal area per tree as a predictor of liana leaf coverage over tree crowns, with a significant positive effect, explaining 43% of the total variance (intercept = 0.42; slope = 0.60; p-value < 0.001; Fig. 4).



**Figure 4.** Relationship between total liana basal area measured from the ground and leaf coverage estimated from drone data for 87 tree crowns. The red line illustrates the predicted linear log-log model. Axes are shown in log scale.

We then found a significant, albeit weak, negative effect of liana basal area weighted wood density on the residuals of the selected model predicting liana leaf coverage (intercept = 2.18; slope = -5.10;  $p$ -value = 0.048; Fig. 5). Trees hosting lianas with lower wood densities thus tend to have a larger liana leaf coverage over their crowns. By contrast, we did not detect any significant effect of liana climbing mechanisms on the model residuals ( $p$ -value = 0.96).



**Figure 5.** Relationship between the basal area weighted liana wood density (A), or the percentage of active climbing mechanism (B), and the residuals of the selected linear model predicting liana leaf coverage from total liana basal area. The red (significant slope) or dotted grey (non-significant slope) lines illustrate the predicted linear model between the two variables.

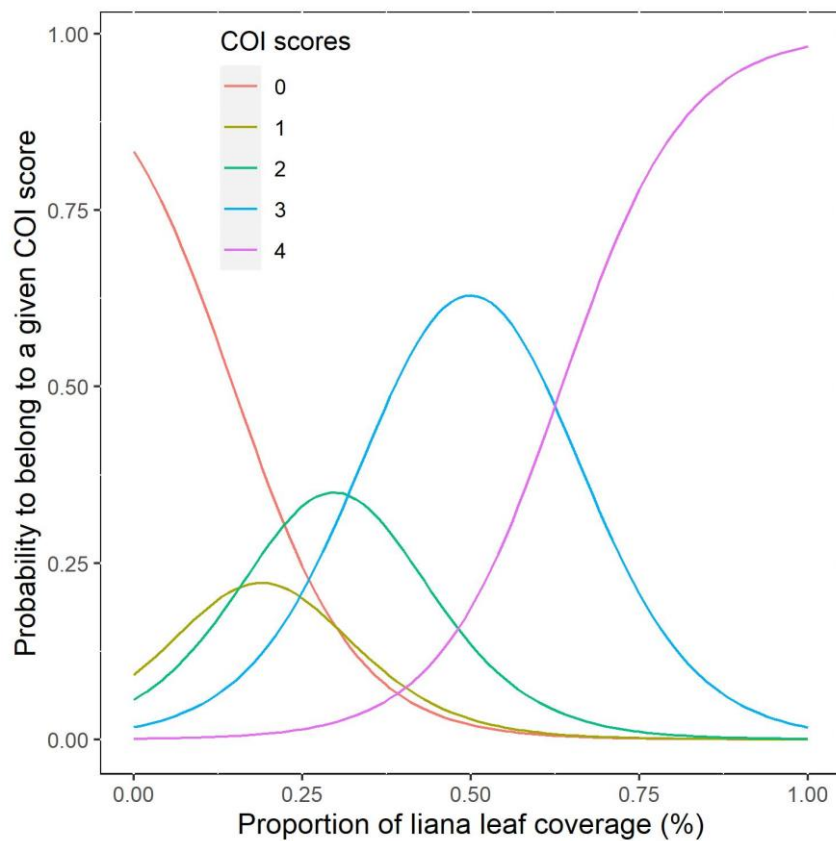
### 3.2.2 Link between liana leaf coverage and the COI

COI scores estimated from the ground and from drone data were significantly concordant (Kendall's  $W = 0.94$ ,  $p$ -value  $< 0.001$ ,  $N = 275$ ), with the same classification for 72% of the studied trees (Table 3). However, most of these agreements were due to trees identified as non-infested by the two approaches (95% of the trees identified as non-infested from the ground were also identified as non-infested by drone measurements). When the comparison was restricted to trees observed as infested from the ground, only 32% of them were assigned to the same COI category using both approaches, with an overestimation of the ground-based compared to the drone-based estimates (Table 3). For 22% of the trees, the classification varied by one class and, for 6% of the trees, it varied by two or more classes. The probit model confirmed that a large overlap exists between the probabilities of belonging to the different categories along the gradient of infestation, even if the ranks were fairly well-preserved among categories on average (Figure 6).



**Table 3.** Confusion matrix showing the number of trees classified into the five COI classes from ground and drone-based measures. Agreement between the two approaches are illustrated in bold.

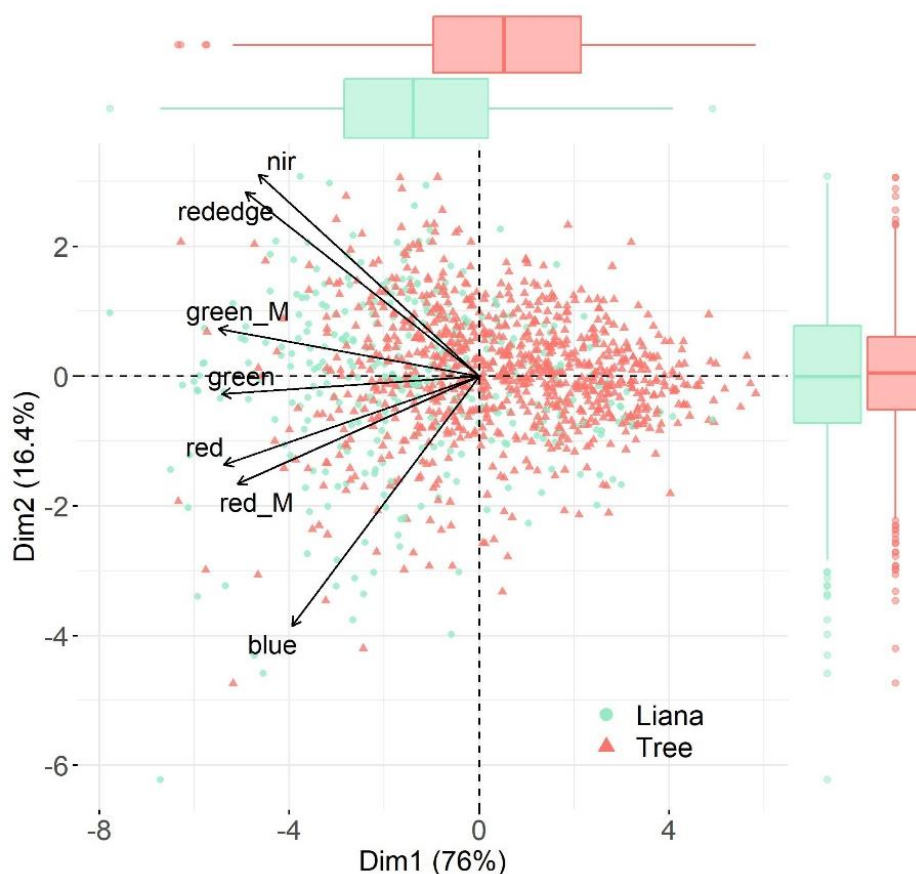
		Ground data COI				
		<b>0</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>
Drone data COI	<b>0</b>	<b>166</b>	11	0	1	0
	<b>1</b>	8	<b>10</b>	11	7	1
	<b>2</b>	1	0	<b>9</b>	14	5
	<b>3</b>	0	0	2	<b>11</b>	11
	<b>4</b>	0	0	1	3	<b>3</b>



**Figure 6.** Probabilities that a tree belong to a given COI score determined from the ground according to the level of infestation measured with drone data.

### 3.3 Spectral signatures of lianas and trees in drone images

The PCA performed on liana patches and liana-free tree crowns signal averages resulted in a first dominant axis (76% of the inertia) negatively correlated with signal intensity in all bands (Figure 7). The second axis, expressing 16% of the variance, tended to oppose invisible (near-infrared and red-edge) from visible bands. Despite a large overlap, we found that liana patches had significantly lower scores (higher DN and reflectance values) than tree crowns on the first axis (Wilcoxon's  $W = 82447$ ,  $p\text{-value} < 0.0001$ ) but exhibited no significant difference along the second axis ( $W=141893$ ,  $p\text{-value} = 0.21$ ). On the two PCA axes, the variance of the scores of individual lianas patches was significantly larger than that of trees (PCA Axis 1:  $F = 1.2$ ,  $p\text{-value} = 0.05$ ; PCA Axis 2:  $F = 1.6$ ,  $p\text{-value} < 0.0001$ ). Analyses conducted at the band level (Supplementary Figure S1) confirmed that liana patches tend to have greater DN and reflectance values than tree crowns in all the bands with a marked difference in the red and green domain compared to the other bands.



**Figure 7.** Plan 1-2 of a Principal Coordinate Analysis performed on RGB (red, green, blue) and multispectral (red\_M, green\_M, rededge, nir) bands. Tree and liana objects are represented in green and red, respectively; boxplots illustrate the differences between the scores of liana patches and tree crowns along the two first PCA axes.

## 4 Discussion

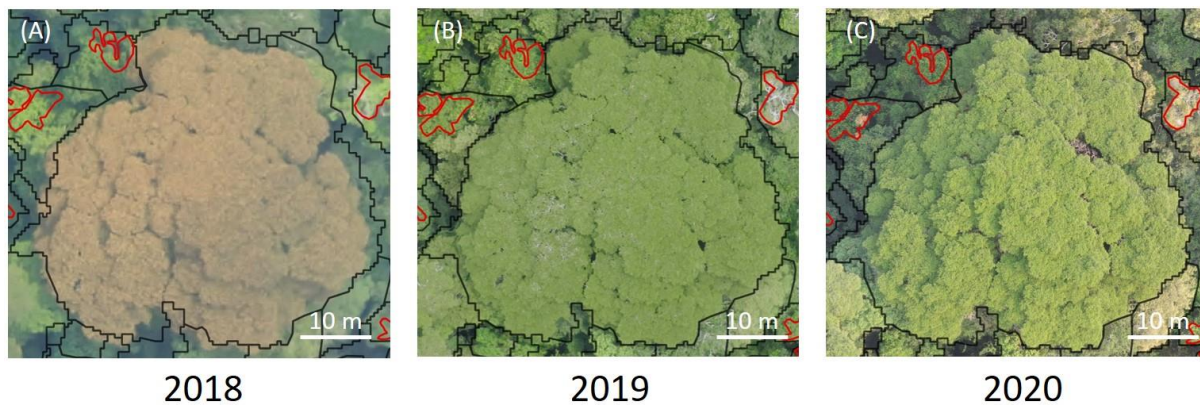
In this study, we used a combination of high-resolution drone images and field ground surveys to understand the links between below- and above-canopy liana distribution. We showed that the ability of lianas to reach the canopy depends mostly on their basal area and, to a less extent, on the total height of their host. Once the canopy is reached, lianas expand their leaves over tree crowns proportionally to their basal area, even though large variability in liana leaf cover exists for a given basal area. Some of this variability was explained here by a differential investment in leaf versus wood biomass with a larger leaf cover observed for liana species with lighter wood. We further showed that the widely used crown occupancy index (COI) provides reliable information on the liana infested status but that, in our case, this index tends to provide lower estimates of infestation levels compared to drone-determined liana leaf coverage. Finally, our results suggest that liana patches display a stronger light reflectance than tree crowns in all the studied bands but that their spectral signatures largely overlap with that of trees. The mechanisms underlying these results and their implications are discussed below.

### 4.1 Liana drone-based measurements can be linked to classical ground measurements, in most cases

Our results indicate that drone and ground data led to similar estimates of the number of liana-infested trees. The infestation status of tree crowns was indeed well predicted from ground data with 90% of the drone-based infested trees identified as such from a model using ground-derived estimates as predictors. This suggests that both methods are suited to study the number of tree crowns infested by lianas. We also found a significant correlation between classical ground measurements of lianas and drone-determined liana leaf coverage over tree crowns. This result is contradictory to that found by the only other study which has analysed the link between above and below canopy liana measurements, using a canopy crane to determine liana leaf coverage over tree crowns (Cox et al., 2019). This study surprisingly indicated that liana leaf coverage was unrelated to liana stem count, basal area, aboveground biomass or tree diameter at breast height and the authors interpreted this negative result by the fact that lianas tended to mostly spread through neighbouring tree crowns in their site. In our case, as discussed in the next section, we found strong significant correlations between the top-of-view liana leaf coverage and the ground-derived liana stem count, basal area, maximum diameter and tree height. This constitutes a reassuring result because liana infestation on trees has been extensively studied through ground measurements and estimations (Ingwell et al., 2010; Phillips et al., 2005; van der Heijden & Phillips, 2009; Wright et al., 2015). However, liana leaf cover was highly

variable for a given range of ground-based measurements, keeping in mind that we studied the relationship between both measurements in log-transformed scale. This indicates that a large variance in aboveground competition between lianas and trees cannot be captured by ground measurements.

Some liana-infested trees were not identified as such from the ground (10 trees, category (ii)-c). For one of these trees, the crown of which was heavily infested by lianas, our field notes indicated that it was impossible to follow any of the liana stems coming out or into the crown and measure them with certainty due to a poor visibility. For the other trees, a careful reanalysis of the drone images suggested that i) five of them were infested by hemi-epiphytes or epiphytes that we did not detect during our fieldwork; ii) four of them were trees with lianas coming from adjacent tree crowns, with probably remote rooting points of lianas that we missed from the ground. Once they reach the canopy, lianas can progress horizontally from crown to crown (Putz, 1984), sometimes up to relatively large distances (Ingwell et al., 2010), making the link between above and below-canopy views difficult to establish in some cases. Conversely, some trees identified with lianas climbing on them during the ground survey did not have liana leaf coverage over their crowns (17 trees; category (ii)-b). Four of these trees were trees with lianas climbing on them but which did not reach the canopy either because they still were at an early stage of development or because they appeared to have fallen at the time of the inventory, due to tree branch falls. For the other trees, lianas appeared to reach the canopy from the ground but were still invisible in drone images. One potential explanation is that these lianas were either deciduous or dying at the time of the 2020 drone acquisition. However, for all trees of this category, we did not find any visible leaves on the older drone data, up to two years before (2018 and 2019; Figure 8). Even if these lianas are not currently in competition with trees for light, they still may compete with trees for below-ground resources and induce significant mechanical stress on host trees (Ingwell et al., 2010), decreasing tree growth and survival rates (Schnitzer et al., 2005). This well illustrates that if most of the drone and ground measurements can be paired with confidence, exhaustive links are unlikely to be made due to the complexity of some liana infestation pathways and that both measurements can bring complementary information on the impact of liana on forest dynamics.



**Figure 8.** Example of a time series of photographs made by drone of a tree hosting a large liana of 6.3 cm dbh but that lacks any visible liana leaves in its crown. Black lines illustrate the tree crown limit and the red lines some delineated liana leaves belonging to other liana stems, as observed from the field. (A) Image at a resolution of 10 cm GSD from 2018. (B) Image at a resolution of 5 cm GSD from 2019. (C) Image at a resolution of 3 cm GSD from 2020.

## 4.2 The allometry between liana leaf coverage and ground measurements is mediated by liana wood density

We found that the probability of tree crowns to be infested by lianas depends strongly on the size of lianas and tree height. Larger lianas are developmentally older and have thus, on average, had more time to reach the canopy. However, the length-diameter allometry is known to be weak in lianas (Smith-Martin et al., 2019) with individuals of only 2 cm in diameter already reaching the canopy (Kurzel et al., 2006). Consistently, the total liana basal area was identified as the best predictor of tree crown infestation status (infested or not by lianas). Tree height also had a significant, yet smaller, effect on the probability of infestation of a tree crown in our statistical model. This result is consistent with previous studies where liana loads tended to be higher on smaller trees or lower canopy forests (Tymen et al., 2016; Wright et al., 2015). However, these results may originate from two non-exclusive mechanisms: lianas can more easily colonize small trees and/or liana infestation can lead to smaller tree heights by limiting their growth. By contrast, Marvin et al. (2016) found no strong associations between liana leaf coverage and canopy height but, as discussed in section 4.4, their remote sensing approach only enabled them to account for severe and high liana infestation levels, for which they had the lowest prediction error. Our findings also showed that if several ground-derived estimates can be successfully linked to liana leaf coverage, liana basal area was the best predictor, explaining 43% of the variance in the log-transformed space. This result is consistent with other studies that focused on the relationship between liana basal area and liana loads estimated from the ground (Ingwell et al., 2010; van der Heijden et al., 2010).

Our findings revealed that the large variability of liana leaf coverage for a given liana basal area can be partly explained by the functional composition of lianas. We indeed found a significant negative relationship between the drone-determined liana leaf coverage and mean wood density indicating that, for a given diameter, light-wooded lianas tend to invest in wider liana leaf coverages than hardwooded lianas. As introduced earlier, variations of wood density are well-known to express different growth strategies in trees (Baraloto et al., 2010; Buckton et al., 2019; Chave et al., 2009; Poorter et al., 2010; Van Gelder et al., 2006; Werden et al., 2018) but the implication of wood density variation on liana ecology has been much less studied. Our results show that wood density significantly vary among taxa and that this variation entails ecological trade-offs among lianas, with greater biomass allocation to leaves for lianas with softer wood, as previously found for trees (Mensah et al., 2016). This pattern suggests that light-wooded lianas allocate more resources into leaves, and thus to light acquisition, at the expense of wood material, which may entail a greater mortality, as observed for trees (Chave et al., 2009). By contrast, no significant effect of liana climbing mechanism was found on liana leaf coverage. Some studies have shown that climbing mechanisms have an effect on liana recruitment and distribution across different forest structures (Bongers et al., 2020; Dewalt et al., 2000). Indeed, it is expected that climbing mechanism has a primary role in the early life of lianas and may thus constitute a central trait to understand the spatial (horizontal) liana distribution (Dias et al., 2021). For instance, Dewalt et al. (2000) showed that lianas with tendrils were more abundant in low canopy forests. The absence of an effect of climbing mechanisms on liana leaf coverage may be due to the fact that the early-life influence of climbing mechanisms on liana ecology may vanish when lianas reach the canopy. In this study, we divided our dataset between active and passive climbing mechanisms following Sperotto et al. (2020). Further investigations using different classifications, such as the one used by Dewalt et al. (2000), may provide different insights on the role of liana climbing mechanisms in liana structure and dynamics.

### 4.3 The crown occupancy index should be used carefully

The crown occupancy index (COI) is widely used to estimate liana leaf coverage over tree crowns and is now routinely used in international protocols such as in the RAINFOR network (Lopez-Gonzalez et al., 2011). We found a significant concordance between the ground-determined COI scores and the drone-determined liana leaf coverage. This supports that the COI is a quite reliable estimate of liana infestation over tree crowns, and is an alternative worth considering against time-consuming dendrometric liana measurements (van der Heijden et al., 2010), at least when substantial time is dedicated to this measurement, as done in the present study. However, we found that two thirds of the infested trees were attributed to a (generally neighbouring) different infestation level from that

determined by drone. This mismatch between categories raises questions about the reliability of the use of the COI to monitor liana infestation over time (Ingwell et al., 2010; Wright et al., 2015). One clear difference between the ground-determined COI and the extent of the drone-determined liana leaf coverage over tree crowns was the overestimation of infestation levels from the ground. This result is expected not to be specific to our study case because, from the ground, tree crowns are rarely entirely visible, and thus the proportion of the tree crown covered by liana leaves could easily be overestimated (but see Waite et al. (2019)). Moreover, the results of our probit model supports the idea that dividing the COI in five infestation levels is too ambitious given the large variability of the ground estimates for a given drone-determined relative liana leaf coverage (Fig. 6). Our model indeed suggests that separating, or aggregating, infestation levels in three categories, as done by Rutishauser et al. (2011), is a more conservative approach. To summarize, if the COI might be a reliable estimate of the spatial distribution of liana load on trees, it should be interpreted carefully when used to detect changes of liana infestation over time. For the latter objective, multi-temporal drone acquisition appears as a more reliable and accurate approach.

#### 4.4 Lianas display (not enough) specific spectral signatures

The emergence of new remote sensing approaches and data, such as the use of high spatial and spectral resolution products, appeared as a promising way to monitor canopy liana infestation in space and time over large scales (Chandler et al., 2021; Marvin et al., 2016). A prerequisite to map liana distribution over tree crowns is that lianas should display a detectable signature over tree crowns (Visser et al., 2021). In our study site, our results suggest that liana patches exhibit significantly higher light reflectance than trees on average in all studied spectral bands, as found and predicted by Visser et al. (2021), who accounted for several parameters that were unavailable in our study, such as chemical and architectural leaf traits. Thus, the origin of these higher DN and reflectance values should be further investigated as it may be due to several non-exclusive origins, such as a higher leaf reflectance, lower gap fraction or flatter leaf angles, as shown in the neotropics by Visser et al. (2021). Note also that, in our study, we were unable to explicitly or accurately radiometrically calibrate our data due to a lack of reference data, such as those obtained with white panels or from ex-situ physical measurements. To minimize this aspect, we focused on data acquired during a single flight or within 1 hour, limiting the spatial extent of our analyses. Future works should thus provide more efforts to improve this calibration step to both enable the investigation of larger areas and to minimize the potential problems associated with illumination artifacts. Contrary to Chandler et al. (2021) and Visser et al. (2021), we did not find that the near-infrared region provided additional information for the discrimination of lianas versus trees (non-significant differences along the second PCA axis; Figure 7),

suggesting that visible bands already contained most of the information, even if our studied bands were limited to only two invisible bands. Interestingly, the variances of the scores along the two first PCA axes were significantly higher than those of trees, suggesting a higher spectral diversity and/or a higher variability in leaf optical properties (e.g., leaf area in vertical profiles and leaf angles; see Visser et al. (2021)) among lianas than among trees. Indeed, liana species have different leaf structure, pigment concentration or water content, resulting in a wide range of spectral responses (Sánchez-Azofeifa & Castro-Esau, 2006; Visser et al., 2021). Importantly, we found that the PCA scores of lianas versus trees largely overlapped, as acknowledged by previous studies (Chandler et al., 2021; Visser et al., 2021), potentially leading to a high rate of confusion in predictive models. It partly explains why reliable remote sensing predictions were obtained only for highly infested trees (> 50% of infestation; Chandler et al., 2021; Marvin et al., 2016; Visser et al., 2021). If the probability of identifying liana pixels among a set of pixels is rather low, the probability that the spectral signature of a given liana does not overlap with that of its host tree is much higher, as illustrated in Figure 2. Thus, developing approaches that classify pixels based on their contrast with surrounding pixels, and accounting for tree crown segmentation information, might be more promising than adopting a pixel-based approach. The rapid development of deep learning approaches on very high-resolution images, that specifically account for texture, thus constitutes a promising avenue (Li et al., 2018). Another efficient strategy has been recently adopted by Visser et al. (2021), who combined observations, trait measurements and radiative transfer modelling to understand the promise and limitations of monitoring liana infestation from remote sensing data. Finally, with the low cost associated with drone acquisitions, it is today possible to acquire drone data at a high frequency level, typically on a monthly basis. Assuming that the leaf phenology of a given liana and its host tree are decoupled in time, repeated drone acquisitions have the potential to better discriminate liana leaf patches over tree crowns using approaches accounting for intra-annual co-variability in spectral signals.

## 5 Conclusion

Combining drone-based and ground-based measurements has the potential to approximate the complex infestation pathways of lianas and their consequences on forest dynamics. Ground-based data on liana distributions and structure have been acquired for decades in tropical forests, providing key insights on liana ecology and on their impact on forest dynamics. However, as shown here, ground-based data approximate the above canopy distribution of lianas with important uncertainties, limiting our ability to understand tree-liana interactions in what is often considered as the most important



forest layer for ecosystem dynamics. The emergence of easy-to-acquire drone-data can make a difference on this aspect, providing a very-high resolution view of liana distribution above the canopy, thus improving our ability to integrate explicitly light competition between lianas and trees in ecological models. Drone-based determinations also open new opportunities to study liana infestation over large extents and over time, e.g. accounting for leaf phenology when acquisitions are done with a high frequency. However, drone-data also have serious drawbacks, especially when not paired with ground data. Given that current automatic approaches are not yet fully satisfactory due to a large overlap in the spectral signatures of lianas and trees, delineating manually liana patches in drone data requires significant time and a certain level of expertise. Furthermore, as seen in this paper, the functional composition of lianas can mediate the dynamics of infestation, something that would not have been seen using only drone data. Thus, we here advocate that combining ground- and drone-based data have the potential to take a major step forward in liana ecology, especially if the dynamics of lianas through time and space are studied in relation to their diverse ecological strategies.

## 6 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## 7 Author Contributions

Conceptualization: B.K. and M.R.-M.; ground data collection: B.K., S.P., Y.H. and M.R.-M.; drone data collection and pre-processing: N.B. and E.F.; formal analysis: B.K., M. A.-K., V.R. and M.R.-M.; wood trait measurements: B.K. and D.G.; writing (original draft): B.K. and M.R.-M.; writing (review and editing): all authors.

## 8 Funding

This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 824074 in form of a prize awarded to B. K. It also

benefited from financial support from the French National Research Institute for Sustainable Development. The studied experimental site has been settled within the DynAfFor project (French Fund for the Global Environment; grant numbers Nos. CZZ1636.01D and CZZ1636.02D). ; International Foundation for Science (grant number D/5822-1); F.R.S-FNRS (grant number 2017/v3/5/332 – IB/JN – 9500), Nature+ (asbl, Belgium) and the Republic of Congo (OGES-Congo). M.R.-M. was supported by the DESSFOR ANR project (ANR-20-CE32-0010).

## 9 Acknowledgments

We thank the CIB-Olam logging company that host and greatly facilitates the work conducted in this site. Last but not least, we are specifically thankful to Isaac Zombo, Marien Fongo, Patchely Mbondo, Ati Ngouabi, Fred Ngouabi and Cyril Dzebou for their invaluable help during the field missions.



## 4 Chapter II: Drivers of liana structure, floristic and functional composition

In this chapter, I examine the relationships between the liana community and the tree community and environmental factors. As a classic community ecology study, I focus on the factors that influence liana community structure and composition. Differently, I also consider the functional composition of lianas and the effects of tree community composition on the liana community composition. This study goes further into liana ecology to understand what mechanisms underlie liana distribution and composition shifts in local environments, highlighting (i) the functional heterogeneity of lianas, (ii) the importance of functional traits to understand floristic composition shifts and (iii) the need for more specific functional traits related to liana climbing form.



Keywords: ecological strategies, Congo, functional traits, DynAffor, tropical vines, species distribution.

## Local forest structure and host-specificity both influence liana community composition in a moist Central African forest

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### Abstract

Lianas are an important component of tropical forest diversity and dynamics, yet little is known about the drivers of liana community structure and composition, which spatial variation can provide important insights into tropical forest functioning. Combining LiDAR and field data, we investigated the influence of local topography, forest structure and tree composition on liana community structure and floristic and functional composition in a moist Central African forest. We inventoried all lianas with a stem diameter  $\geq 1$  cm in 144 20×20 m quadrats located in four 9-ha permanent plots, where all trees and giant herbs were inventoried in the northern Republic of Congo. To characterize liana functional strategies, we measured a set of resource-use leaf and wood traits of selected representatives of the main liana taxa. Local forest structure primarily influenced the structure of liana communities, with higher abundances and total basal area in relatively open-canopy forests where lianas appeared to compete with giant herbs. Liana floristic composition exhibited weak spatial structure at the study site level, but was marginally influenced locally by forest structure and topography. Only forest structure had a weak but significant effect on liana functional composition. Tall and dense forests were characterized by lianas with more conservative strategies—higher stem tissue density and lower  $PO_4$  leaf concentration and SLA values. Finally, we found evidence of host specificity with significant attraction/repulsion between liana and tree species. Liana community structure is strongly shaped by local forest structure in central African forests. On the other hand, despite a wide range of ecological strategies, the floristic and functional composition of lianas is only marginally determined by local forest structure. However, we show that the unexplained floristic variation can be partly due to significant host species-specificity between tree and liana species. Further exploration of liana traits targeting specific life histories will lead to a better understanding of how liana communities vary under local conditions and interact with tree communities.

# 1 Introduction

Lianas are increasingly recognized as important players in tropical forest dynamics (Marshall et al., 2020; Laurance et al., 2014; Tang et al., 2012; Schnitzer & Bongers, 2005; Schnitzer & Bongers, 2002; Putz, 1984). They contribute up to 40% of plant diversity and 25% of plant density (Schnitzer & Bongers, 2002) and significantly alter the energy balance and carbon cycling of tropical forests (Porcia e Brugnara et al., 2019). They are known to negatively affect tree growth, survival and regeneration through above- and below-ground competition, thus reducing tree diversity and forest carbon storage (Ingwell et al., 2010; Laurance et al., 2014; Phillips et al., 2005; Schnitzer et al., 2005, 2014; Schnitzer & Carson, 2010; van der Heijden et al., 2015; Van der Heijden & Phillips, 2009). Recent studies on lianas have mainly focused on their effects on forest dynamics, considering them as a single functional plant type. However, as noted nearly 50 years ago (Jacobs, 1976), their ecology remains “largely unknown.” Although much progress has been made in liana ecology since then, many of its aspects are still poorly understood (Schnitzer et al., 2014). Lianas occur in more than 133 angiosperm families (Gentry, 1991) and have recently been shown to exhibit great variability in life-history strategies, with a range of functional traits at least as great as that of trees (Medina-Vega et al., 2021; Meunier et al., 2020; Sun et al., 2022). Resource partitioning among different liana species with different ecological preferences is thus likely important, but remains poorly documented (Liu, Sterck, Medina-Vega, et al., 2021). This limits our ability to understand and predict current and future tropical forest dynamics (Marshall et al., 2020).

It has been hypothesized that the structure of liana communities is closely related to the local forest structure, whereas tree community structure is more dependent on abiotic factors such as topographic and edaphic gradients (Ledo & Schnitzer, 2014). Indeed, lianas require external physical supports to reach the canopy and are therefore expected to depend primarily on surrounding forest structure (Balfour & Bond, 1993; Hegarty & Caballé, 1991). Liana abundance has been shown to consistently vary along gradients of forest stand structure, including decreases in abundance along canopy height gradients (Dalling et al., 2012; Villagra et al., 2021). Also, forest disturbance is known to be a major driver of liana abundance (Ledo & Schnitzer, 2014; Schnitzer et al., 2021; Villagra et al., 2021) because most species have a high clonal reproduction rate that allows them to rapidly invade disturbed areas in canopy gaps (Dalling et al., 2012; Ledo & Schnitzer, 2014; Schnitzer et al., 2012, 2021; Waite et al., 2023). However, a recent study conducted in Thailand showed that both liana abundance and basal area increased significantly along a forest successional gradient (Lomwong et al., 2023). This result was inconsistent with previous studies mostly conducted in central and south America and was interpreted as the consequence of different light requirements in liana species, which allow more

shade-tolerant liana species to thrive in low light conditions (Lomwong et al., 2023). Abiotic factors, such as topography and soil conditions, also influence liana community structure. For instance, the abundance of lianas tend to be higher on slopes (Dalling et al., 2012), in forests with a shallow water table (Dalling et al., 2012; Gerolamo et al., 2018) and in nutrient-rich soils (DeWalt et al., 2006; Gerolamo et al., 2018; Lai et al., 2017). A recent study in Asia even showed that soil properties have a stronger influence on liana abundance than forest structure (Liu, Sterck, Medina-Vega, et al., 2021), which contrasts with previous findings from Neotropical forests (Dalling et al., 2012). Thus, the relative importance of forest structure and abiotic conditions on local liana community structure may be less clear than previously assumed.

The local drivers of the composition of liana communities are far less studied than their structure, in part due to difficulties in plant identification and taxonomic ambiguities (Schnitzer & Bongers, 2002). Since lianas are usually considered light-demanding species, as compared to trees (Collins et al., 2016), they are expected to occupy similar niches and respond to the same factors across continents. However, ecological strategies may differ among families (Putz & Mooney, 1991), leading to different light requirements and so responses to changing light conditions (Yuan et al., 2016). Consequently, liana community composition is expected to vary along environmental gradients, but few studies have confirmed this hypothesis (Dalling et al., 2012; DeWalt et al., 2006; Liu, Sterck, Medina-Vega, et al., 2021; Lomwong et al., 2023; Mumbanza et al., 2020; Rocha et al., 2022). Liana species composition have been found to differ significantly among forest type (Mumbanza et al., 2020), and along different forest successional stages (Lomwong et al., 2023). More precisely, different liana species dominated at different stages of forest succession (Lomwong et al., 2023). Forest structure seemed to impact liana taxonomic diversity and species distribution, with some species significantly associated with different canopy heights (Dalling et al., 2012). Like liana structure, liana floristic composition also appeared to be influenced by abiotic factors such as topography (Dalling et al., 2012) or soil properties (DeWalt et al., 2006). For example, both taxonomic and functional composition of lianas were recently found to be primarily related to a hydrologic gradient in the central Amazon and only slightly influenced by forest disturbances (Rocha et al., 2022). Local variations in soil pH and phosphorus levels also had a significant influence on the distribution of liana species in China (Liu, Sterck, Medina-Vega, et al., 2021). Thus, again, the relative importance of forest structure and abiotic on liana community composition remains unclear.

Because lianas physically depend on tree support and exhibit a wide range of climbing strategies, they closely interact with tree architecture and morphology (Hegarty, 1991). Therefore, the floristic composition of lianas may also be linked to the floristic composition of trees through host specificity,

regardless of the forest structure and abiotic environment. To date, host prevalence has been mostly studied from a tree perspective, with infestation probability depending on tree species identity, architecture, or morphology (Campanello et al., 2007; Carsten et al., 2002; Heijden et al., 2008; Loubota Panzou et al., 2022; Nesheim & Økland, 2007; Pérez-Salicrup et al., 2001). The few studies that have examined species-specific associations between lianas and trees considering liana species identity have found contrasting results. Uwalaka et al. (2021) found that host-specific relationships existed for three of the nine dominant liana species with significantly higher probabilities of colonizing certain tree species. In addition, Heymann et al. (2022) found that the liana *Marcgavia longilifolia* has significant host selectivity, with higher than expected colonization rates of the most common tree genera, while the second most common tree genus was rarely colonized. Song et al. (2023) found that all 15 most common liana species have varying species-specific interactions with the 20 most common tree species. In contrast, Vivek & Parthasarathy (2016) showed no host-specific relationships between tree species and the four dominant liana species, and no relationships between functional morphological traits of trees and lianas. To date, there is thus no consensus on whether liana species exhibit tree host specificity. This information is needed to better understand liana colonization strategies, unravel mechanisms of potential host selectivity, and better predict liana-tree dynamics over time and space.

The diversity of ecological strategies in lianas may be characterized by the association of different functional traits, which could explain the distribution of species along environmental gradients (Reich, 2014; Reich et al., 2003). Lianas are one of the most diverse and complex life forms with one of the widest ranges of growth strategies (Caballé, 1993; Darwin, 1875; Liu, Sterck, Zhang, et al., 2021), e.g., with different types of attachment and a distinct diversity of woody structures (Angyalossy et al., 2015; Hegarty, 1991; Isnard & Silk, 2009; Putz, 1984ab). Recently, advances have been made in characterizing these strategies through the lens of functional ecology. Mirroring the findings obtained on trees, it has been shown that forests with open canopies are thriving environments for lianas with acquisitive resource-use strategies, such as low-density woods and soft leaves (i.e. high SLA) with high nutrient concentrations (Mumbanza et al., 2022; Villagra et al., 2021). On the other hand, lianas with more conservative strategies are more likely to be found in undisturbed forests, i.e., with a greater number of twining species with low SLA (Liu, Sterck, Zhang, et al., 2021; Villagra et al., 2021). As for abiotic factors, lianas have been found to have different strategies along a hydrologic gradient, with species with lower SLA and wood densities occurring in valleys near the water table (Rocha et al., 2022). Overall, the common assumption that lianas are primarily light-demanding and pursue acquisitive strategies is currently under-revision (Liu, Sterck, Zhang, et al., 2021; Meunier et al., 2020; Sun et al., 2022). Studies have suggested that the different niches and light requirements of each species may be



a possible cause for the inconsistent results on the relative importance of drivers of liana structure and floristic composition across studies previously discussed (Lomwong et al., 2023). Despite recent advances in liana ecology, we still need to further explore the different life-history strategies of lianas and to understand how they vary under different local environmental conditions.

Here we examine distribution patterns of liana community structure and composition using a large liana inventory (144 20 × 20 m quadrats) in northern Republic of Congo — an area that is poorly studied scientifically (Sosef et al., 2017). We combine dendrometric measurements with various functional characteristics of leaves and stems of lianas, as well as drone-based measurements (stereophotogrammetry and LiDAR) to characterize the local environment, to answer the following main question and the three hypotheses derived from it (Hn): To what extent do forest structure, topography and tree composition influence the structure, floristic, and functional composition of liana communities?

(H1) Liana structure: we expect higher densities of small liana stems in relatively short-stature and open-canopy forests, but no major effects of local topography due to our homogeneous study are (see site description).

(H2) Floristic composition of lianas: we expect that (H2a) the floristic composition of lianas is mainly influenced by forest structure and hardly by topography, and (H2b) covariation in floristic composition of trees and lianas is only due to common environmental factors rather than host species-specificity.

(H3) Functional composition of lianas: we expect the abundance and occurrence of species with acquisitive resource-use traits to be higher in forests with shorter stature and more open canopies, due to higher light availability favoring fast-growing strategies.

## 2 Materials & Methods

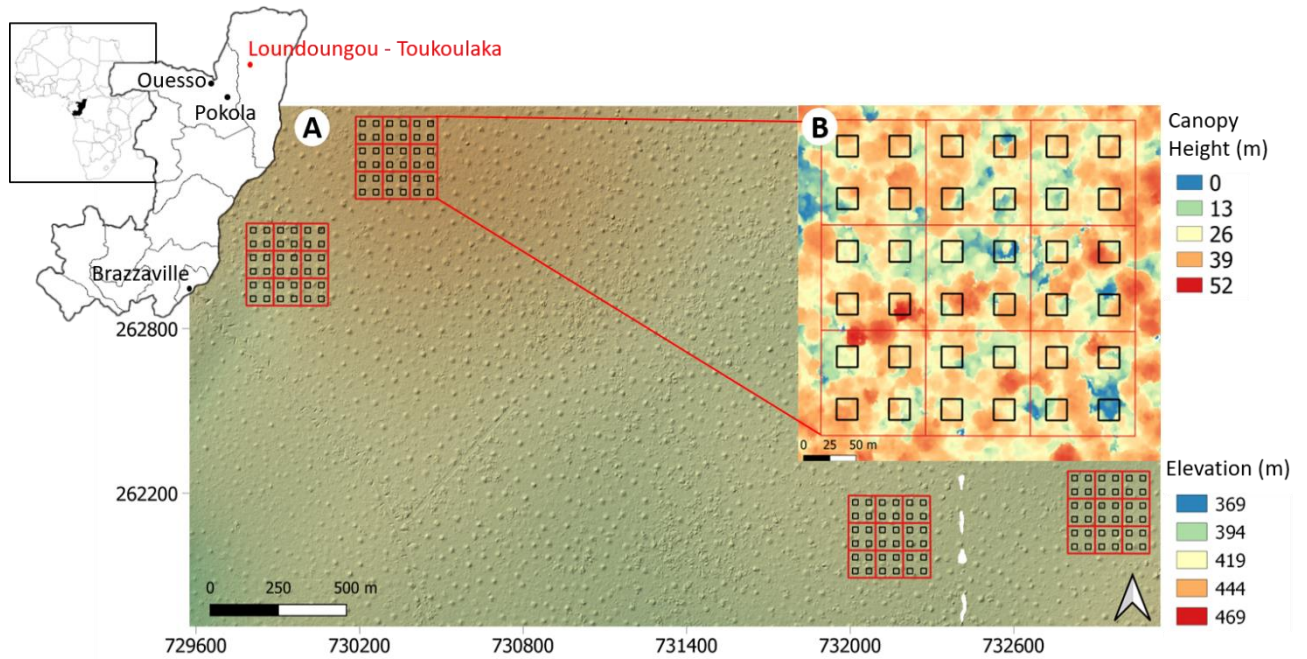
### 2.1 Study site

The study area is located in the Likouala Province in the north of the Republic of Congo (2°27'11.87" N and 17°02'32.17" E; Fig. 1). The mean annual rainfall is 1,605 mm/year (unpublished data from 2003 to 2017 obtained from the nearest station in Pokola, 140 km from the study area), with two dry seasons from June to August and from December to February. The site is located on a plateau with an elevation of 395 to 470 m a.s.l. and a geological substrate of Quaternary limestone and

alluvium. The soil type is classified as Xanthic Acrisols and shows little textural variation (from sandy-loamy to loamy-sandy) between the highest and lowest elevations of the plateau (Freycon, 2014). The vegetation corresponds to the semi-deciduous forest type with a large number of trees belonging to the Euphorbiaceae (20%), Fabaceae (12%), Meliaceae (9%), Ebenaceae (8%), and Annonaceae (7%) families (Forni et al., 2019; Réjou-Méchain et al., 2021). Little is known about human history in the area, but there is no evidence of recent human activity (< 100 years) in the study area, except for hunting and a recent, low intensity logging (0.3 trees/ha) that occurred at late 2018, after the liana inventory (see below).

## 2.2 Liana and tree inventory data

The experimental site was first established in 2014 in the Loundoungou-Toukoulaka forest management unit (UFA), conceded to the CIB-Olam logging company. The experimental design consists of four permanent 9-ha plots ( $300 \times 300 \text{ m}^2$ ) where all trees  $\geq 10 \text{ cm}$  DBH (diameter at breast height) were marked, identified, positioned, and their diameter measured every year since 2015 according to international standards (Picard & Gourlet-Fleury, 2008). To compare different silvicultural treatments, the experimental design of the plots was originally designed to minimize the effects of abiotic conditions, with a maximum elevation difference of only 23 meters, between the most distant plots (the four 9-ha plots were established within two pre-existing 400-ha blocks; Fig. 1).



**Figure 1.** Study site location and experimental design of the tree and liana inventories. (A) Lidar based hillshade elevation model with four 9-ha plots divided into 1-ha plots (red) where all trees  $\geq 10$  cm DBH were measured yearly. The high abundance of large termite mounds can be clearly seen; (B) Lidar based canopy height model of one 9-ha plot with 36 liana quadrats of 20x20 m (black), with 4 quadrats in each 1-ha plots.

Liana inventories were conducted from April to July 2017 within 144  $20 \times 20$  m quadrats (total area of 5.76 ha) established at regular intervals within the permanent plots (4 quadrats/ha; Fig. 1). All woody lianas and rattans  $\geq 1$  cm DBH were marked with paint and their diameter measured according to international protocols (Gerwing et al., 2006; Schnitzer et al., 2008). For each liana, the host tree and, if applicable, the identity of the second host tree were noted to assess whether lianas display host-specificity (see section 2.5.2.). Given the lack of expertise in liana taxonomy in this region, lianas were first identified using vernacular names in a regional language, Enyellé, from the Likouala region (Pandzou). Because a vernacular name may represent more than one species or a species may have multiple vernacular names at different ontogenetic stages, we conducted complementary work to assess the taxonomic coherence of vernacular names and, when possible, assigned botanical names to lianas. To this end, we collected leaf samples in May 2018 from 284 lianas identified by the same fieldworkers as in 2017. Leaf samples were collected primarily in and around the four 9-ha plots in shaded locations where lianas had sprouted yielding leafy shoots, maximizing the number of samples for the most abundant lianas (up to 17 samples per vernacular name; 4 samples on average). Two herbarium specimens were collected from each individual, one deposited in ALF herbarium at Cirad in

Montpellier (Bazan, 2021) and the other in the national Forest Research Institute herbarium in Brazzaville. A subset of the leaf material was dried with zeolite beads in ziplock bags for genetic analyses (see Appendix 1) to identify taxonomic groups, verify taxonomic coherence, and validate the scientific names of the lianas. 57.7% of the lianas from the inventory were identified at the species level, 9.2% at the morphospecies level, 30.8% at the genus level, 0.5% at the family level, and we were unable to identify 1.8% of all lianas. Overall, vernacular names verified from these samples covered 98% of the liana stems measured during the 2017 inventory (64 of 82 vernacular names).

## 2.3 Liana functional traits

We measured functional leaf and stem traits that position species along the “fast-slow” plant-economic spectrum (Reich, 2014), for 44 liana taxa representing 95% of the liana stems measured in the inventory (Table 1). Leaf functional traits were measured on liana herbarium samples collected in May 2018, following the protocols and recommendations of Perez et al. (2020) for specific leaf area (SLA) and leaf thickness. These authors showed that values derived from herbarium measurements for SLA and thickness correlated strongly with values measured from fresh tissue, although values derived from herbarium SLA are slightly overestimated globally. SLA measurements were made with the petioles. After measuring mass and scanning all samples, we used ImageJ software (Abràmoff et al., 2004) and a semi-automated method developed by Borianne & Brunel (2012) to measure leaf area. For leaf thickness measurements, we rehydrated leaves in a 1:50 solution of neutral household detergent and water for 20 min before measurements. Measurements were then taken at 3 points in the center of the leaf using a digital micrometer (Mitutoyo QuantuMike with a 0.001 mm of resolution), avoiding the leaf veins. In addition, we performed elemental analyses of carbon, nitrogen, phosphorus, and potassium of the herbarium liana leaves. We collected 100 mg of dry leaves per sample and ground them into a powder. For the elemental analyses of carbon and nitrogen (%C and %N, respectively), we used the Flash Smart AE 2000 elemental analyser, which performs adsorption chromatography based on the Dumas method (Dumas, 1831). For phosphorus and potassium, we first mineralized the samples and then determined the total phosphorus (%PO<sub>4</sub>) by colorimetric determination using molybdenum blue with the HNO<sub>3</sub> gallery and the potassium concentration (%K) using a Thermo ICE 3000 Series atomic absorption spectrometer in flame mode.

We additionally measured liana wood infra-densities on liana stem samples. In May 2018 and October 2021, we collected 211 stem cylinders above 2 cm in diameter (range 2 to 10 cm) at 1.3 m from the stem root using an opportunistic sampling method outside the permanent plots to avoid destructive measurements within the plots. Stem samples were debarked and saturated with water

under pressure for 48 h before measuring Archimedes thrust according to the protocol described by Birouste et al. (2014). The samples were then first dried in an oven at 40°C for 10 days to avoid damaging the water-saturated materials with extreme temperatures. We then increased the oven temperature to 103°C for 48 hours to remove all water residues. Finally, the anhydrous masses of the wood samples were measured to determine the wood infra-density, hereafter referred to as stem tissue density (TD) because the stems of lianas, even when debarked, are not simple wood cylinders like trees, but most species have a mixture of different tissues consisting of both secondary xylem (wood) and other soft and lignified primary and secondary tissues.

**Table 1.** Description of leaf and stem liana functional traits used for 44 species.

Trait	abb.	Range	Unit	Mean ind/taxa	Ecological Role
Leaf thickness	Thick	[0.04-0.2]	mm	5	Leaf structure mechanical support and defense, longevity and resistance against herbivory
Specific leaf area	SLA	[13.0-64.7]	mm <sup>2</sup> .m g <sup>-1</sup>	5	Light capture and growth: leaf longevity, photosynthetic rate
Leaf Carbon	%C	[38.9-48.2]	%	5	Leaf investment on structures
Leaf Nitrogen	%N	[2.1-5.8]	%	5	Light capture and growth: carbon fixation (photosynthesis and respiration)
Leaf Phosphorus	%PO <sub>4</sub>	[0.07-0.27]	%	5	Light capture and growth: enzyme function
Leaf Potassium	%K	[0.3-2.2]	%	5	Maintenance metabolism: membrane function
Stem Tissue density	TD	[0.16-0.59]	No unit	4	Stem transport, mechanical structure, longevity and defense against herbivory

## 2.4 Forest structure and topography

To characterize the environment, we considered four groups of variables: ground-based tree variables, drone-based forest variables, ground-based giant herb variables and drone-based topography variables. First, we assigned four forest structure variables to each 20x20m liana quadrat with a 10-meter buffer on each side (40x40m subplots) because trees in close proximity to the liana quadrats may also influence liana structure and composition. We used the 2017 tree inventory dataset

to calculate four stand-level measures: tree stem density ( $N_T$ ), tree quadratic mean diameter ( $QMD_T$ ), tree total basal area ( $BA_T$ ), and tree mean wood density ( $WD_T$ ). Tree wood density values were extracted from the global wood density database (Chave et al., 2009; Zanne, 2009) through a procedure implemented in the BIOMASS package (Réjou-Méchain et al., 2017). Finally, we coupled the 2017 inventory with the 2015 inventory to determine the difference in tree basal area between the two censuses ( $\Delta BA_T = BA_{T2017} - BA_{T2015}$ ), translating the rate of tree basal area increment.

Second, we measured canopy-level variables using drone imagery (see details on the acquisitions in Kaçamak et al. (2022)). Briefly, red-green-blue (RGB) images were acquired in June 2018 and used to create a digital surface model ( $DSM_{2018}$ ) at 1 m resolution using a stereophotogrammetry approach. Thanks to a LiDAR-derived digital elevation model acquired in February 2020 ( $DEM_{2020}$ ), we created a canopy height model ( $CHM_{2018}$ ) by subtracting  $DEM_{2020}$  from  $DSM_{2018}$ . Finally, we used  $CHM_{2018}$  to calculate the mean of the top of the canopy height (meanTCH) at the quadrat level with a 10-meter buffer on each side ( $40 \times 40 m^2$  subplots). A high meanTCH typically represents a dense and high canopy, while a low meanTCH represents an open canopy, e.g. due to tree gaps.

Third, because lianas can interact with life forms other than trees, giant herbs from the orders Commelinales and Zingiberales were inventoried in the four 9-ha plots. These giant herbs are widespread in lowland forests of central and western Africa (Pouteau et al., under review), particularly at our study site where *Haumania danckelmaniana* (J. Brun et K. Schum.) Miln. Redh, a climber, dominates. The inventory was conducted on a systematic 10-m grid, resulting in 100 sampling points per hectare. At each sampling point, we quantified the projected leaf cover of giant herbs on the ground using a semicontinuous index from 1 to 3, where 1 represents low leaf cover (< 20%), 2 represents leaf cover between 20 and 70%, and 3 represents high leaf cover (> 70%). Therefore, we calculated the mean leaf cover of giant herbs over liana quadrats (GHFC) as the mean of the nine sampling points within the quadrat.

Finally, as the topography of the study area is homogeneous with no clear elevation or hydrologic gradients (Fig. 1), we measured only local topographic variation, because of the presence of numerous large termite mounds that may have an impact on water and nutrient availability (1.5 to 3 large mounds per ha with a radius of  $9.9 \pm 3.3$  m and a height of  $4.1 \pm 1.5$  m; see Appendix 2; Freycon et al., 2018; Penel et al., 2022). We used  $DEM_{2020}$  and the SAGA module of QGIS version 3.10 to derive the relative slope position index (RSP; see Appendix 3) to characterize termite mounds at the quadrat level. The RSP is measured as follows:

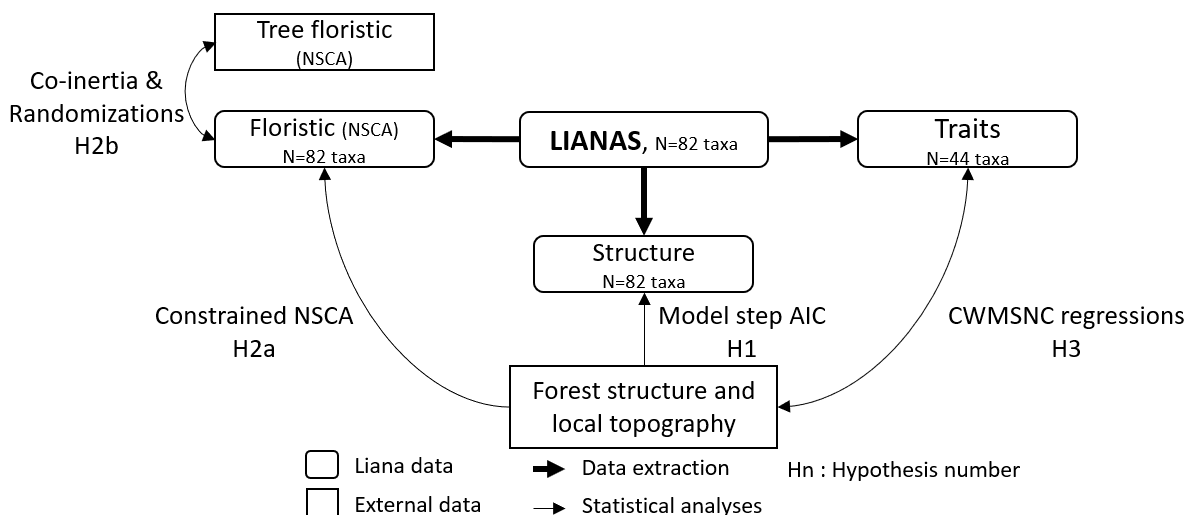
$$RSP = \frac{AACL}{AACL + ABRL}$$

with AACL the altitude above channel lines and ABRL the altitude below ridges (Bock et al., 1996). Hence, high RSP values ( $RSP=1$ ) represent the top of the termite mounds (see Appendix 3).

All the studied environmental variables displayed correlation  $<0.7$  with each other.

## 2.5 Statistical analyses

The analyses performed on the structure and floristic composition of liana communities were based on the entire liana inventory dataset, whereas the analyses of the functional composition were conducted with the subset of 44 liana taxa for which functional traits were measured (95% of individuals in the liana inventory). All analyses described below are summarized in Fig. 2 and were performed using the statistical software R 4.2.1 (R Core Team, 2022).



**Figure 2.** Diagram illustrating the different statistical analyses used to test the study hypotheses (Hn, see the last paragraph of the introduction). AIC: Akaike Information Criterion; CWMSNC: Community Weighted Mean Species Niche Centroid; NSCA: Non-Symmetric Correspondence Analysis; PCA: Principal Component Analysis.

### 2.5.1 Drivers of liana community structure

To test the relationship between the structure of liana communities and environmental gradients, we first calculated three liana metrics at the 20-m quadrat level: the number of stems ( $N_L$ ), mean quadratic diameter ( $QMD_L$ ) and total basal area ( $BA_L$ ) of lianas. We then used linear models and

a model selection procedure to identify the main environmental factors affecting liana structure. Because lianas were inventoried in a nested sampling design (quadrats in 1-ha subplots and 1-ha subplots in 9-ha plots), our observations were not independent. Therefore, to test for a possible pseudo-replication effect in our dataset, we used linear mixed-effects models in which the effect of the 9-ha plots was subsequently accounted for as a random effect. Likelihood ratio tests (LR; Bolker et al., 2009) were performed to test the statistical significance of the random term. Because the random effect was not significant in all models (results not shown), we performed all analyses considering only the fixed effects (our predictors) after scaling all explanatory variables. To select the best-fitting model, we used the Akaike information criterion (AIC). We finally selected the model with the lowest AIC for each liana structure variable using a stepwise forward and backward selection approach.

### 2.5.2 Drivers of liana floristic composition

To characterize the floristic composition of the liana community, we performed a non-symmetric correspondence analysis (NSCA) with species abundance data per quadrat. NSCA is similar to a correspondence analysis, but gives more weights to abundant species (Pélissier et al., 2003). We used an NSCA instead of a correspondence analysis because the correspondence analysis was too influenced by some very rare species. We first tested whether the floristic composition of lianas at our study scale was spatially structured by performing permutation tests for spatial variograms ( $n=9999$  random distributions; Dibiasi & Bowman, 2001), using the site scores on the first two NSCA axes. This test indicates whether the spatial variogram deviates significantly from a random structure at a given distance class.

To assess the effect of the environment on the floristic composition of lianas, we performed constrained ordinations (NSCAIV, i.e., nonsymmetric canonical correspondence analysis; Couteron et al., 2003) using the *diversity.R* package (Pelissier, 2014) with all environmental variables (H2a, Fig. 2). NSCAIV is similar to canonical correspondence analysis (CCA), but, again, gives more importance on abundant species (Pélissier et al., 2003). We used permutation tests ( $n=999$  randomizations) to assess whether the total explanatory variance was significant.

We also examined whether the floristic composition of the liana and tree communities significantly covary with each other by performing a Monte Carlo test on the sum of eigenvalues of a co-inertia analysis, based on the  $R_v$  coefficient (Dray et al., 2003; Heo & Gabriel, 1997; H2b). To test whether covariation between the floristic composition of the liana and tree communities arises only because of a common response to environmental gradients, we also performed this analysis on the



residuals of NSCAIVs applied to both liana and tree communities, i.e., assessing covariation between liana and tree floristic variations that are unexplained by the studied environmental variables.

Finally, we tested the existence of host species specificity using randomization tests of liana and tree associations. We restricted this analysis to lianas climbing into a tree (with an identified host tree,  $n=2737$  lianas) and kept the identity of the second host tree if present. At each randomization ( $n=999$ ), we randomly assigned a tree within the quadrat (including the 10-m buffer around each quadrat) to each liana individual that occurred in the same quadrat to create a null dataset corresponding to the expected number of infested trees per tree species for each liana taxa obtained by chance alone. Restricting this randomization process to the quadrat level allowed us to account for spatial autocorrelation in both the distribution of tree and liana taxa in the null expectations and thus to limit the potential influence of common environmental drivers. Finally, we compared the observed number of individual lianas infesting each tree species to the expected null distribution using the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles to detect significant repulsion or attraction between lianas and tree taxa. To ensure statistical power, we limited our analyses to the 10 most abundant liana taxa (> 60 individuals per taxa in the entire data set, for a total of 2110 liana individuals) and reported results only for tree species with more than 100 individuals in the entire data set ( $n=24$  species). We also recorded the climbing mechanisms of the 10 most abundant liana taxa to investigate whether climbing mechanisms play a role in host species specificity. We classified climbing mechanisms according to Sperotto et al. (2020). Twining lianas with tendrils, prehensile branches, or angular branches were classified as “active” climbing mechanisms, while scrambling lianas with hooks, spines, or adhesive roots were classified as “passive” climbing mechanisms.

### 2.5.3 Drivers of liana functional composition

We examined liana trait-environment relationships using an approach based on the combination of two parametric tests at the community and species level (CWM/SNC regressions), as recently introduced by ter Braak (2019, TraitEnvMLMWA package by ter Braak, 2022). This is a novel powerful regression-based analysis that account for the fourth-corner problem and allow to assess the influence of environmental gradients on community functional composition (i.e., CWM traits) in combination with how species distribution, parameterized by species niche centroids (SNC) in environmental space, relate to their traits. CWM and SNC regressions were weighted by Hill numbers of order 2 (i.e.  $N_2$ -weighted; ter Braak, 2019), which gives more importance to abundant species. In this method, p-values are obtained by permutation of sites in CWM-regression and species in SNC-regression, and the final p-value is equal to the maximum p-value of the two tests (ter Braak et al., 2018). Therefore, a significant trait-environmental relationship reflect not only changes in trait dominance across

communities, which could be driven by few dominant species, but rather a consistent response to environment across species with similar traits (Lepš & De Bello, 2023).

## 3 Results

### 3.1 Liana community structure

A total of 6 206 liana stems  $\geq 1$  cm in diameter were recorded, corresponding to a density of 1 077 stems per hectare. Overall, liana communities were dominated by small-size individuals, with 62% of stems between 1 and 2 cm DBH and 94% between 1 and 5 cm DBH, with a maximum diameter of 27 cm.

The best predictive models selected for each liana community structure variable are summarized in Table 2. Tree community structure appeared to have a strong influence on liana community structure, with the mean canopy height (meanTCH) having a predominantly negative effect on liana density and basal area. Liana abundance increased with increasing canopy opening and decreasing average tree size ( $QMD_t$ ), wood density, and biomass increment ( $\Delta BA_t$ ). Liana basal area decreased in tall, dense forests (meanTCH), but liana average size was larger ( $QMD_L$ ) in forests with fewer trees with increasing basal area and wood density. Giant herbs (GHFC) also significantly affected liana stand structure, with lower liana abundance and basal area in quadrats dominated by giant herbs. The topographic variable associated with termites (RSP) was not selected for and did not appear to affect liana stand structure. Overall, liana density was the best explained dependent variable (38%), followed by total basal area of lianas (25%) and liana mean quadratic diameter (23%).

**Table 2.** Estimates of predictors in the selected models predicting the structure of liana communities in response to the local environment, with confidence intervals in parenthesis. Parameters associated with variables that were not selected by the AIC step approach are not reported.  $\Delta BA_T$ =tree basal area increment, meanTCH=mean top of the canopy height, GHFC=giant herbs foliar cover, QMD<sub>T</sub>=tree quadratic mean diameter, BA<sub>T</sub>=tree total basal area, N<sub>T</sub>=tree stem density, and WD<sub>T</sub>=tree mean wood density.

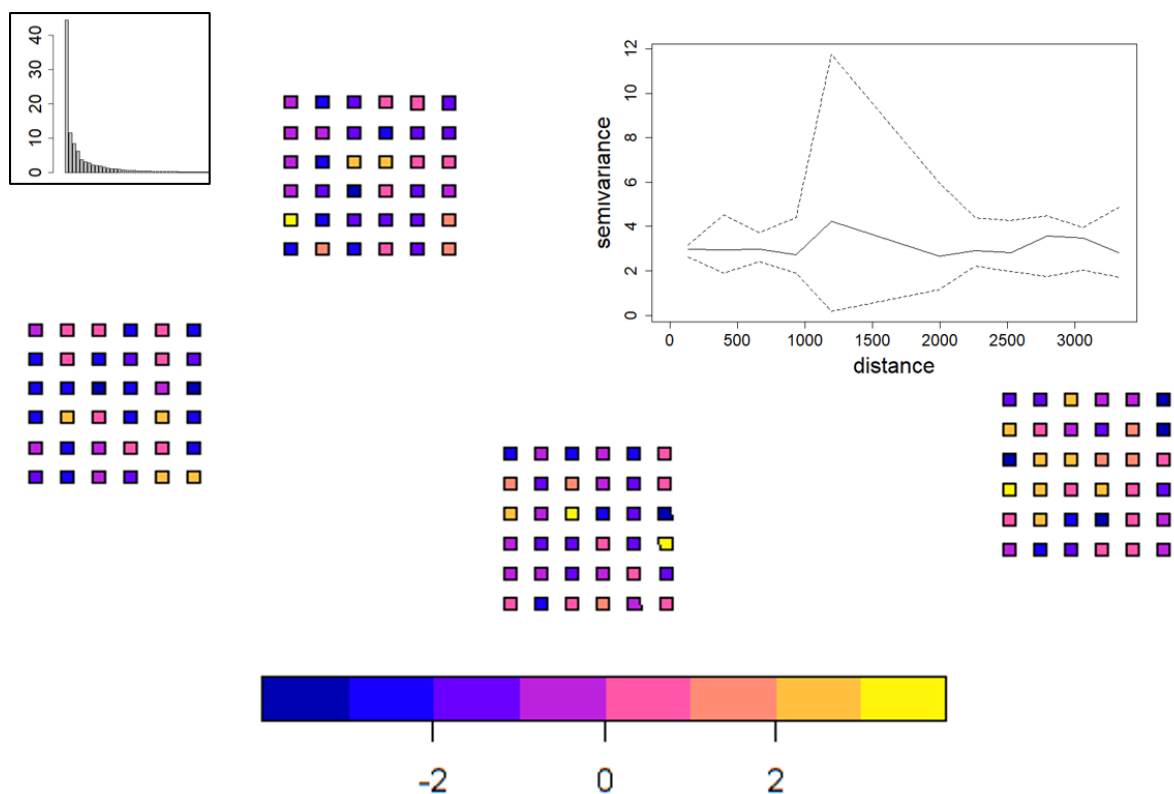
	<b>BA<sub>L</sub></b>	<b>N<sub>L</sub></b>	<b>QMD<sub>L</sub></b>
Intercept	0.62 (0.57, 0.67)	1077.4 (1011.0, 1143.9)	0.48 (0.46, 0.51)
<b><math>\Delta BA_T</math></b>	-0.103 (-0.155, -0.052)	-66.193 (-141.116, 8.729)	-
<b>meanTCH</b>	-0.140 (-0.193, -0.087)	-164.667 (-246.163, -88.467)	-
<b>GHFC</b>	-0.083 (-0.137, -0.030)	-81.271 (-158.978, -3.564)	-
<b>QMD<sub>T</sub></b>	-	-172.353 (-256.239, -88.467)	-
<b>BA<sub>T</sub></b>	-	-	0.078 (0.048, 0.109)
<b>N<sub>T</sub></b>	-	-	-0.061 (-0.090, -0.033)
<b>WD<sub>T</sub></b>	-0.080 (-0.133, -0.026)	-151.524 (-228.506, -74.542)	0.043 (0.013, 0.072)
R <sup>2</sup>	0.25	0.38	0.23
F Statistic	11.8	16.8	14.1

### 3.2 Liana floristic composition

The inventoried lianas belonged to 82 vernacular taxa and 22 families. The most abundant families were Euphorbiaceae (31%), Fabaceae (17%), Apocynaceae (13%), Loganiaceae (7%), and Connaraceae (5%). The liana communities were dominated by three hyperdominant taxa that

accounted for 54% of the liana stem abundance (*Manniophyton fulvum* Muell.Arg., 30%; *Dalhousiea africana* S. Moore, 12%; and *Agelaea spp.* Sol ex. Planch, 12 %).

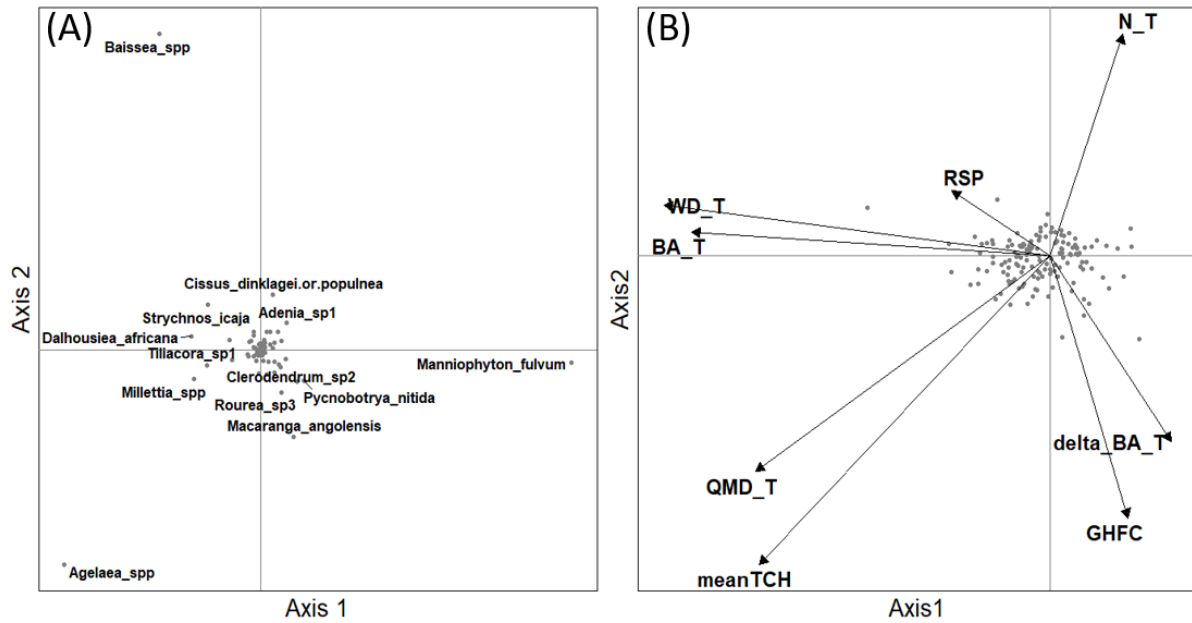
The first two axes of the NSCA were largely determined by the three most abundant taxa and captured 56% of the overall variation in the floristic composition of the lianas. As shown in Fig. 3, the floristic composition of the liana community was not spatially structured at our study scale. Permutation tests performed on spatial variograms of the first two axes confirmed the lack of spatial correlation in all distance classes (Fig. 3 for the first axis, see Appendix 4 for the second axis). Thus, floristic composition appeared to vary only at a local scale within our study area.



**Figure 3.** Spatial distribution of NSCA axis 1 scores of liana floristic composition on the 144 quadrats with eigenvalues (top left corner). The insert graph gives the variogram of NSCA axis 1 scores (See appendix 5 for the axis 2). The dotted lines on the variogram represent the confidence intervals at 95% and the solid lines the variogram.

Overall, environmental variables explained only 9.9% of the liana floristic variation ( $p$ -value=0.045). The first axis of the NSCAIV opposed forests with tall and dense canopies composed of large and hard-wooded trees to forests with large canopy openings. The second axis of the NSCAIV opposed forests with an abundance of small trees and forests dominated by giant herbs, where a large

deficit of small trees occurred and a high increase in tree basal area was observed (Fig. 4). Along the first axis, species such as *Manniophyton fulvum* and *Pycnobotrya nitida* were associated with open canopies, while *Agelaea spp.* tended to occur in tall and dense canopy forests. The second axis suggested that *Macaranga angolensis* preferentially co-occurred with giant herbs, while *Baissea spp.* tended to avoid them and to occur in areas with a greater number of small tree stems (Fig. 4).



**Figure 4.** NSCAIV on (A) liana species and (B) the associated environmental variables with liana quadrats in grey dots (B).  $\Delta$ BA\_T=tree basal area increment, meanTCH=mean top of the canopy height, GHFC=giant herbs foliar cover, QMD\_T=tree quadratic mean diameter, BA\_T=tree total basal area, N\_T=tree stem density, WD\_T=tree mean wood density, and RSP=relative slope position.

The floristic composition of lianas varied significantly with the floristic composition of the tree community (RV test observation = 0.11, p-value = 0.002), even after removing the effects of the environmental variables (RV test observation = 0.097, p-value = 0.037). The randomization procedure for tree infestation revealed that the 10 most abundant liana taxa had significant host specificity: 19% of pairwise associations with the 24 most abundant tree species were significant at the 5% level of risk, with 23 attraction and 22 avoidance relationships (Table 3). In most cases, liana species exhibited both attraction and repulsion patterns with tree species (e.g., *M. fulvum*), with obvious similarities among lianas: some tree species tend to either attract systematically (e.g. *Cleistanthus caudatus*, *Gilbertiodendron dewevrei*, *Lepalea thompsonii*, *Pentaclethra macrophylla*, *Petersianthus macrocarpus*) or escape liana infestation (e.g., *Celtis mildbraedii*, *Dichostemma glaucescens*, *Greenwayodendron suaveolens*, *Staudtia kamerunensis var. gabonensis*). Two tree species (*Diospyros*

*bipindensis* and *Manilkara mabokeensis*) tended to both attract and avoid some liana species, but without regard to their climbing mechanisms. Overall, there were no obvious relationships between liana climbing mechanisms and tree species preferences. Only one tree species, *Gilbertiodendron dewevrei*, tended to attract lianas with the same climbing mechanism (active mechanisms).

**Table 3.** Results from the host-species randomization test for the 10 most abundant liana species ( $N \geq 50$  individuals) and the 24 most abundant tree species ( $N \geq 100$  individuals). Liana taxa with (A) an active climbing mechanism and taxa with (B) a passive one. The observed number of lianas infesting the focal tree species is presented, with its confidence interval obtained from 999 simulations of liana-tree associations (in square parenthesis). Significant attraction and repulsion relationships are illustrated in blue and red, respectively.

		LIANA SPECIES									
		Agelaea spp (A)	Baijsea spp (A)	Dalhousiea africana (A)	Loeseneriella spp (A)	Manniophyton fulvum (P)	Pycnobotrya nitida (P)	Strychnos icaja (P)	Strychnos spp (P)	Tiliacora sp1 (A)	Triclisia macrophylla (A)
TREE SPECIES	<i>Angylocalyx pynaertii</i>	2 [0 ; 6]	2 [1 ; 9]	2 [2 ; 10]	2 [0 ; 3]	0 [3 ; 12]	0 [0 ; 2]	2 [0 ; 4]	0 [0 ; 4]	0 [0 ; 3]	1 [0 ; 3]
	<i>Carapa procera</i>	2 [1 ; 9]	2 [1 ; 9]	7 [5 ; 16]	1 [0 ; 4]	17 [9 ; 24]	0 [0 ; 4]	0 [0 ; 5]	2 [0 ; 6]	0 [0 ; 3]	1 [0 ; 4]
	<i>Celtis mildbraedii</i>	0 [0 ; 7]	4 [2 ; 11]	1 [3 ; 12]	0 [0 ; 3]	2 [5 ; 16]	0 [0 ; 2]	0 [0 ; 4]	0 [0 ; 5]	0 [0 ; 4]	1 [0 ; 4]
	<i>Cleistanthus caudatus</i>	23 [5 ; 15]	18 [7 ; 19]	36 [14 ; 29]	6 [0 ; 7]	36 [21 ; 37]	5 [1 ; 8]	11 [1 ; 8]	4 [1 ; 9]	1 [0 ; 6]	1 [0 ; 5]
	<i>Dichostemma glaucescens</i>	7 [5 ; 17]	12 [13 ; 28]	13 [16 ; 34]	2 [1 ; 9]	29 [39 ; 62]	4 [1 ; 7]	0 [1 ; 9]	6 [2 ; 12]	2 [0 ; 6]	4 [1 ; 8]
	<i>Diospyros bipindensis</i>	17 [4 ; 15]	17 [6 ; 19]	12 [13 ; 30]	1 [0 ; 6]	23 [19 ; 37]	0 [0 ; 4]	1 [0 ; 5]	4 [1 ; 9]	0 [0 ; 7]	1 [0 ; 6]
	<i>Diospyros iturensis</i>	3 [1 ; 8]	10 [2 ; 11]	10 [5 ; 16]	0 [0 ; 4]	4 [7 ; 20]	1 [0 ; 3]	0 [0 ; 5]	3 [0 ; 5]	0 [0 ; 5]	0 [0 ; 3]
	<i>Garcinia punctata</i>	6 [1 ; 10]	5 [3 ; 14]	13 [6 ; 18]	0 [0 ; 5]	17 [10 ; 24]	2 [0 ; 5]	3 [0 ; 6]	2 [0 ; 5]	0 [0 ; 4]	0 [0 ; 4]
	<i>Gilbertiodendron dewevrei</i>	9 [1 ; 9]	5 [1 ; 8]	28 [7 ; 19]	5 [0 ; 4]	19 [8 ; 21]	2 [0 ; 5]	5 [0 ; 6]	7 [1 ; 7]	11 [1 ; 8]	7 [0 ; 4]
	<i>Grossera macrantha</i>	1 [0 ; 7]	3 [2 ; 10]	8 [3 ; 13]	1 [0 ; 3]	20 [5 ; 16]	2 [0 ; 3]	0 [0 ; 5]	2 [0 ; 4]	0 [0 ; 4]	0 [0 ; 4]
	<i>Leplaea thompsonii</i>	13 [1 ; 8]	23 [3 ; 12]	33 [5 ; 16]	6 [0 ; 5]	39 [10 ; 24]	0 [0 ; 4]	0 [0 ; 4]	9 [0 ; 6]	1 [0 ; 3]	2 [0 ; 4]
	<i>Macaranga spinosa</i>	2 [0 ; 7]	6 [2 ; 10]	7 [4 ; 15]	1 [0 ; 4]	15 [13 ; 28]	4 [0 ; 4]	0 [0 ; 4]	4 [0 ; 6]	0 [0 ; 3]	2 [0 ; 5]
	<i>Manilkara maboensis</i>	5 [1 ; 9]	0 [3 ; 13]	5 [6 ; 18]	1 [0 ; 5]	4 [10 ; 23]	4 [0 ; 3]	3 [0 ; 7]	1 [0 ; 6]	2 [0 ; 4]	2 [0 ; 5]
	<i>Nesogordonia kabingaensis</i>	1 [0 ; 6]	3 [1 ; 9]	2 [2 ; 10]	0 [0 ; 3]	2 [5 ; 16]	0 [0 ; 2]	1 [0 ; 4]	1 [0 ; 5]	0 [0 ; 3]	0 [0 ; 3]
	<i>Pancovia harmsiana</i>	2 [1 ; 8]	3 [1 ; 9]	8 [3 ; 13]	0 [0 ; 3]	5 [6 ; 17]	0 [0 ; 3]	1 [0 ; 4]	1 [0 ; 4]	1 [0 ; 2]	0 [0 ; 3]
	<i>Pancovia laurentii</i>	1 [0 ; 6]	10 [1 ; 9]	5 [2 ; 12]	0 [0 ; 3]	12 [5 ; 15]	1 [0 ; 2]	0 [0 ; 3]	1 [0 ; 4]	1 [0 ; 2]	0 [0 ; 3]
	<i>Pentadethra macrophylla</i>	7 [1 ; 8]	4 [1 ; 9]	24 [4 ; 14]	3 [0 ; 4]	43 [7 ; 18]	1 [0 ; 3]	7 [0 ; 4]	2 [0 ; 5]	2 [0 ; 4]	4 [0 ; 4]
	<i>Petersianthus macrocarpus</i>	1 [1 ; 7]	12 [1 ; 10]	5 [3 ; 14]	0 [0 ; 4]	16 [6 ; 17]	1 [0 ; 4]	8 [0 ; 3]	1 [0 ; 5]	0 [0 ; 3]	2 [0 ; 4]
	<i>Greenwayodendron suaveolens</i>	2 [2 ; 12]	8 [5 ; 16]	6 [8 ; 21]	5 [0 ; 6]	3 [10 ; 24]	2 [0 ; 3]	1 [0 ; 6]	2 [0 ; 6]	1 [0 ; 5]	1 [0 ; 5]
	<i>Quassia silvestris</i>	1 [0 ; 6]	2 [1 ; 8]	3 [2 ; 12]	0 [0 ; 3]	1 [6 ; 17]	0 [0 ; 3]	0 [0 ; 4]	0 [0 ; 4]	0 [0 ; 3]	0 [0 ; 3]
	<i>Rinorea oblongifolia</i>	3 [0 ; 6]	1 [1 ; 9]	4 [3 ; 12]	0 [0 ; 3]	1 [5 ; 16]	1 [0 ; 4]	2 [0 ; 3]	1 [0 ; 4]	0 [0 ; 3]	1 [0 ; 3]
	<i>Santiria trimera</i>	7 [0 ; 6]	5 [0 ; 7]	9 [2 ; 10]	1 [0 ; 3]	13 [4 ; 13]	0 [0 ; 3]	1 [0 ; 3]	1 [0 ; 4]	3 [0 ; 3]	0 [0 ; 3]
	<i>Staudtia kamerunensis var. gabonensis</i>	1 [2 ; 10]	4 [3 ; 14]	5 [7 ; 20]	0 [0 ; 4]	11 [13 ; 27]	2 [0 ; 3]	1 [0 ; 6]	2 [0 ; 6]	1 [0 ; 5]	0 [0 ; 5]
	<i>Strombosia pustulata</i>	1 [1 ; 8]	5 [2 ; 11]	4 [2 ; 11]	1 [0 ; 4]	1 [4 ; 13]	0 [0 ; 2]	0 [0 ; 3]	1 [0 ; 5]	1 [0 ; 3]	0 [0 ; 3]

### 3.3 Liana functional composition

Overall, we found significant relationships between three liana functional traits and few environmental variables (Table 4). Only local forest structure variables influenced the functional composition of lianas. Liana species with high tissue density but low %PO<sub>4</sub> values tended to increase their relative abundance in tall, dense canopy forests with large basal area. We also found a weak but significant increase in abundance of liana species with high SLA values in areas dominated by small-size trees. Local topography (RSP) did not affect liana community functional composition.

**Table 4.** Fourth-corner correlations (N2w) between functional traits and environmental variables. Significant correlations, obtained with 999 permutations, are reported in red and blue for negative and positive correlations, respectively.  $\Delta$ BAT=tree basal area increment, meanTCH=mean top of the canopy height, GHFC=giant herbs foliar cover, QMDT=tree quadratic mean diameter, BAT=tree total basal area, NT=tree stem density, WDT=tree mean wood density, RSP=relative slope position, SLA=liana specific leaf area, Thick=liana leaf thickness and, and TD=liana tissue density.

	%C	%N	%PO <sub>4</sub>	%K	SLA	Thick	TD
<b>BA<sub>T</sub></b>	0,06	0,00	-0,07	-0,03	-0,04	0,00	0,10
Max p-value	0,25	0,95	0,05	0,71	0,14	0,41	0,05
<b>QMD<sub>T</sub></b>	0,02	-0,02	-0,05	-0,01	-0,06	0,03	0,07
Max p-value	0,65	0,67	0,12	0,91	0,04	0,58	0,31
<b>N<sub>T</sub></b>	0,03	0,00	0,00	0,00	0,04	-0,04	0,01
Max p-value	0,67	0,96	0,97	0,83	0,27	0,47	0,85
<b><math>\Delta</math>BA<sub>T</sub></b>	0,01	-0,03	0,00	0,00	-0,01	0,04	-0,01
Max p-value	0,85	0,45	0,97	0,83	0,75	0,33	0,83
<b>WD<sub>T</sub></b>	0,03	0,00	-0,08	-0,01	-0,06	0,00	0,06
Max p-value	0,74	0,95	0,08	0,94	0,05	0,67	0,48
<b>meanTCH</b>	0,07	-0,03	-0,10	-0,06	-0,05	0,02	0,14
Max p-value	0,12	0,67	0,04	0,22	0,06	0,69	0,03
<b>GHFC</b>	-0,05	0,00	0,05	0,00	0,01	0,01	-0,04
Max p-value	0,12	0,87	0,19	1,00	0,85	0,88	0,40
<b>RSP</b>	0,00	-0,02	0,00	0,01	-0,02	0,02	0,00
Max p-value	0,96	0,83	1,00	0,87	0,83	0,83	0,90



## 4 Discussion

In this study, we used a combination of ground inventories, functional traits, and high-resolution drone imagery to understand how local forest structure, tree composition and topography influence the structure, floristic, and functional composition of liana communities. Consistently with previous studies, mostly conducted in the Neotropics, forest structure was the primary factor affecting liana abundance. Higher liana abundances and total basal area, occurred in open canopies, where they appeared to compete with giant herbs. The floristic composition of lianas was not spatially structured but weakly influenced by environmental variables. Local topography had no discernible effect on liana structure nor functional composition. In contrast, tall and dense canopy forests appeared to be associated with a higher proportion of large lianas with more conservative traits (higher tissue density and lower %PO<sub>4</sub> and SLA values). After ruling out the environmental influences on liana and tree communities, we found significant covariation between their composition and a randomization approach confirmed a higher degree of host specificity than expected by chance. We discuss these results and their implications below.

### 4.1 Hyperdominance in the liana flora

Consistently with previous studies from central Africa (Ewango et al., 2015; Mumbanza et al., 2020), we found marked hyperdominance in the liana flora, with more than half of the individuals belonging to only three taxa. Our site had more or less the same abundant genera and families as distant African sites (Ewango et al., 2015; Mumbanza et al., 2020; Parren, 2003; Thomas et al., 2014), suggesting that these abundant taxa exhibit a regional hyperdominance. *Manniophyton fulvum* was by far the most abundant species, accounting for nearly one-third of the lianas at our study site. It is a geographically widespread species (Borsch et al., 2020) and found to be the most dominant species in two other studies in the Democratic Republic of Congo (DRC; Ewango et al., 2015; Mumbanza et al., 2020). Although these two studies considered this species to be a habitat generalist, we found that it was associated with open canopy and short-stature forests. Another example is the pantropical genus *Strychnos*, which was reported to be the most abundant genus in Korup National Park in Cameroon (Thomas et al., 2014) and was the third most abundant genus at our study site, where it appeared to be a habitat generalist. Taken together, these results suggest that both the local and regional central African liana flora are dominated by a few dominant and widespread taxa, even more than for tropical trees (Bastin et al., 2015; Ter Steege et al., 2013).

## 4.2 Gap-hypothesis and structure shifts along local forest structure

We demonstrated that the structure of tree communities and presence of giant herbs significantly influenced the structure of liana communities. In particular, liana stem density was found to be the most predictable metric (38% of the variance explained). We specifically found higher abundances in areas characterized by smaller and light-wooded trees and a low canopy height, corresponding to open canopy forests. These results are consistent with those of previous studies, mostly conducted in the Neotropics, which validated the so-called “gap hypothesis”, i.e., that disturbance and gaps in the canopy promote liana abundance (Ewango et al., 2015; Ledo & Schnitzer, 2014; Schnitzer et al., 2012, 2021; Schnitzer & Bongers, 2011; Villagra et al., 2021). However, the gap hypothesis may not be universal, as a recent study from Southeast Asia showed that liana abundance increased continuously along a successional gradient (Lomwong et al., 2023). In addition, we found that lianas tended to be significantly larger in areas characterized by a larger total tree basal area and a smaller number of trees belonging to hardwood species. Poulsen et al. (2017) found consistently in a forest in Gabon that the abundance of large lianas increased with the abundance of large trees and with the mean wood density of tree communities, both of which are characteristics of old growth forests. Letcher & Chazdon (2009) also showed that the highest values of liana biomass (estimated using diameter-based allometry) were at sites with old-growth trees in successional chronosequences in Costa Rica. The proportion of large-diameter liana stems may indeed indicate different stages of forest succession, as suggested by Dewalt et al. (2000), who demonstrated a decrease in liana abundance with stand age but an increase in total basal area. Interestingly, these findings are not consistent with our results, because we found an increase in the mean square diameter of lianas with tree wood density but a decrease in the total basal area of lianas. This suggests that the large number of small liana stems in open canopy areas compensates for their small individual basal area. Finally, Lomwong et al. (2023) found an additional pattern of variation in stem size and abundance in a forest in Thailand, with an increase in both liana abundance and basal area with ageing forest succession. Overall, these results suggest that patterns of changes in liana community structure along environmental gradients are not universal.

## 4.3 Competition with giant herbs

Our results suggest strong competition between woody lianas and giant herbs (Commelinales and Zingiberales) in open canopy areas. Among the dominant giant herbs in the study area was the climbing species *Haumania danckelmaniana* J.Braun & K.Schum. Milne-Redh. Giant herbs are known to be very light-demanding and to rapidly pre-empt above- and below-ground resources, drastically

limiting woody plant regeneration (Pouteau et al., under review). Our study suggests that giant herbs in central Africa, and perhaps elsewhere, constitute a fourth potential pathway for gap-phase regeneration, in addition to other life forms such as trees, palms, and lianas (Letcher, 2015; Schnitzer et al., 2000).

Facilitation between different climbing species is known to occur when lianas and other climbers use each other as support to reach the canopy (Putz, 1984aa). The reason why facilitation between woody and nonwoody climbers did not occur in our study area remains unclear. Two possible explanations for this remain to be examined. First, facilitation between lianas has been observed mainly in large lianas, which support smaller lianas (Campanello et al., 2007). At our study site, *H. danckelmaniana* barely reached 2 cm in diameter and rarely reached long distances (up to 15 m). However, while the size of the supporting species might limit the ultimate height that can be reached, most lianas climb small-sized supports to begin their upward growth (Lehnebach et al., 2022). Second, giant herbs are known to rapidly develop multi-shade leaf layers that drastically reduce light availability and thus seed germination (Brncic, 2002). Further detailed work should focus on understanding the conditions under which successional processes might branch toward a liana- or giant-herb-dominated pathway.

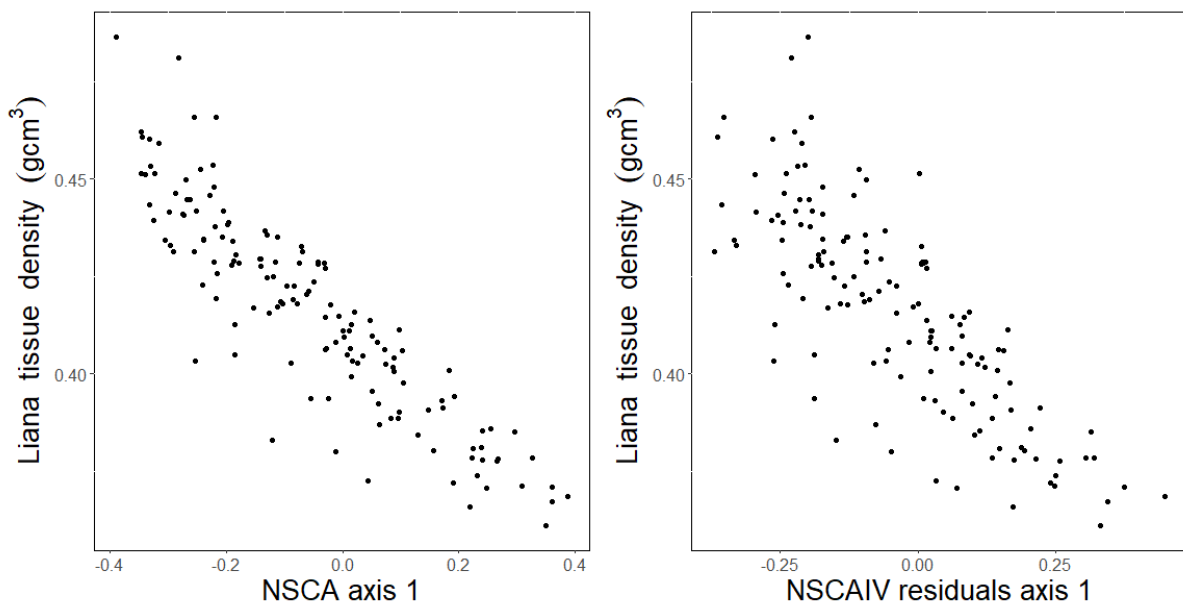
#### 4.4 Weak but significant floristic and functional shifts along local forest structure gradients

Our results suggested that the floristic composition of lianas do not vary at larger scale than the quadrat in our study site. We specifically found that the local environmental variables had only a weak but significant effect (9.8%) on liana floristic composition. Consistently, in DRC, weak floristic composition changes between regrowth and old growth mixed forests were reported (Mumbanza et al., 2020). By contrast, liana species composition differed strongly between forest succession stages in a landscape in Thailand (Lomwong et al., 2023).

We only found a few significant shifts in liana functional traits along environmental gradients in our study area. Liana stem tissue density increased, and leaf phosphorus concentration (%PO<sub>4</sub>) and SLA weakly decreased in taller and denser canopies. These results are consistent with those of other studies on liana traits along a forest successional gradient (Mumbanza et al., 2022; Villagra et al., 2021). SLA and %PO<sub>4</sub> are commonly measured leaf traits for which greater values indicate faster resource acquisition and growth (Baraloto et al., 2010; Reich, 2014; R ger et al., 2012; Wright et al., 2004), whereas higher wood density indicates higher investment in stem structure, shown to confer

greater resistance to disturbance in trees (Chave et al., 2009; Van Gelder et al., 2006). Therefore, as observed in trees, liana community composition shifts along the successional gradient from communities dominated by rapid resource acquisition strategies to conservative strategies, demonstrating that the liana flora exhibits, to an extent, a range of strategies adapted to different habitats (Letcher, 2015; Liu, Sterck, Zhang, et al., 2021; Rocha et al., 2022). Most other traits were not significantly related to the environmental variables studied, and we did not detect any trait shifts along the local topographical gradient (RSP).

Surprisingly, we found no significant variation of liana functional traits along the main liana floristic gradients, except for liana tissue density. Interestingly, the residuals of the NSCAIV for lianas, i.e., the variation in liana floristic composition that could not be explained by the studied environmental variables, was marginally significantly correlated with the mean liana tissue density after 999 randomizations on liana traits ( $p$ -value=0.057; Fig. 5), suggesting an undetected non-random variation in liana floristic composition along an ecological gradient that remains to be determined.



**Figure 5.** Relationship between the first axis of the NSCA or the first axis of the residuals of the NSCAIV (i.e. the part of the floristic composition of lianas not explained by environmental variables), and liana tissue density.

The traits commonly used to study plants (Werden et al., 2018) are not necessarily the most relevant to lianas. In fact, the relationships between liana traits and the environment appear to be much more indirect and not as straightforward as for trees (Liu, Sterck, Zhang, et al., 2021). Lianas are indeed mechanically very different from trees and known to experience different physiological

constrains. After an early self-supporting phase, they rely on physical supports to grow and develop, and show large changes in traits and tissue organization from young to old developmental stages (Rowe et al., 2004; Rowe et al., 2006). It is thus likely that functional traits used for tree and liana stems respond very differently to specific environmental conditions (Letcher, 2015). Stem traits could play important and possibly different roles relative to environmental constraints for lianas, particularly during their climbing (non-self-supporting) phase, depending on the life history of different species (Letcher & Chazdon, 2012). The tissue organization, mechanics, and density of lianas is much more complex than that of trees, exhibiting a wide diversity of tissue arrangements and vascular systems (Angyalossy et al., 2015). This diversity may translate into different functions and/or solutions for dealing with different environmental conditions (Rocha et al., 2022). Thus, considering macroanatomical wood characteristics seems to be a promising way to better understand the life history of liana species and decipher functional relationships with the environment.

## 4.5 Host-species specificity

The existence of host species-specific relationships between trees and lianas has been a long-standing question in liana ecology and, although relatively understudied, has led to conflicting results (Heymann et al., 2022; Song et al., 2023; Uwalaka et al., 2021; Vivek & Parthasarathy, 2016). Our co-inertia analysis revealed significant covariation between liana and tree community compositions, even after accounting for underlying environmental gradients. This result either suggests that (i) there is liana-host specificity or (ii) our analysis failed to account for environmental variables that influenced both liana and tree compositions. Our randomization procedure confirmed the first hypothesis, with 19% significant host-specific relationships between the most abundant liana and tree species. Although some studies have suggested that there were no species-specific relationships between trees and lianas (Vivek & Parthasarathy, 2016), others have found significant relationships (Heymann et al., 2022; Song et al., 2023; Uwalaka et al., 2021). In addition, some studies examining liana infestation from the point of view of trees have found that tree species identity is an important factor explaining liana species distributions, significantly more so than environmental variables (Nesheim & Økland, 2007). Nesheim & Økland (2007) found that environmental variables, such as canopy openness and light availability, played an important role in the early life stages of lianas prior to their attachment to host trees, while host tree characteristics played a greater role after initial attachment. The morphological and architectural characteristics of host trees, such as bark type, tree size, or length of branch-free trunks, were shown to affect liana colonization, probably through specific liana life history traits, such as reaching support, attachment, and climbing mechanisms (Campanello et al., 2007; Carsten et al., 2002; Heijden et al., 2008; Nesheim & Økland, 2007; Uwalaka et al., 2021). For example,

in our study, *Staudtia kamerunensis* var. *gabonensis*, which is characterized by exfoliating bark, tend to repel all the studied liana species, even if Song et al. (2023) did not provide sufficient support for the role of tree bark type in liana infestation prevalence. Regarding liana morphology, a recent study showed that tendril climbers tended to have short reach distances to find host trees, species with hooks and prehensile branches had longer reaches, and twining species displayed the largest range of reach distances (Hattermann et al., 2022). The abundance of twining liana species has been found to decrease with forest succession (Dewalt et al., 2000; Letcher & Chazdon, 2012), and shifts in tree composition have been found to influence liana species distribution in relation with their climbing mechanisms (Bongers et al., 2020). However, we found no apparent relationship between the climbing mechanisms of the most abundant liana species and tree species identity. Further studies are needed to better determine and understand how liana and tree characteristics interact to create host-specific relationships.

## 5 Conclusion

Our results showed that liana community structure was mainly determined by local forest structure but that its floristic and functional composition varied weakly along these gradients, with, however, faster acquisition strategies that tended to occur in open-canopy areas. This study thus provided further evidence for the neotropical gap hypothesis in a central African forest, but showed that the increase of lianas in canopy openings is only weakly associated with functional changes. We also provided the first evidence for a marked competition between lianas and giant herbs and revealed that species composition of trees and lianas exhibited significant species-specific associations for the most common lianas and trees.

In this study, we have shown that liana abundance and, to a lesser extent, composition both depend on the local structural organization of trees. From a practical and analytical perspective, some of the universally applied plant traits that are informative for studying the ecological patterns of tree life history may not be well suited for understanding those of vines and lianas, even if they share the same geographic space. We recommend further studies on more liana-specific functional traits, notably based on stem traits due to the apparent ecological impact of liana tissue density found in this study, to better understand their spatial distribution in local environments.

## 6 Acknowledgments

We thank the CIB-Olam logging company that host and greatly facilitates the work conducted in this site. Last but not least, we are specifically thankful to Marien Fongo his invaluable help during the field mission to collect leaf and stem samples.

## 7 Author contributions

Conceptualization: B.K., M.R.-M. and S.G.-F.; ground data collection: B.K., M.R.-M., E.F., I.Z. and S.G.-F.; drone data collection and pre-processing: N.B. and E.F.; formal analysis: B.K., M.R.-M. and B.X.P.; botanical identifications: B.K., S.B. and D.H.; wood trait measurements: B.K. and D.G.; writing (original draft): B.K., M.R.-M and N.R.; writing (review and editing): all authors.

## 5 Chapter III: Liana cambial variants, macro-anatomy and ecological strategies

In this chapter, I investigate the diversity of ecological strategies of lianas using combinations and associations of macro-anatomical and leaf functional traits at the species level. Functional traits associated with liana structure emerge as key features that provide a potential mechanistic understanding of liana growth strategies and success in several different environments. However, at the community level, macro-anatomical traits do not appear to contribute to a better understanding of changes in liana composition in local environments. Most importantly, this chapter demonstrates the complexity of lianas' ecological strategies and their relationship to the local environment and points out the need for further studies using anatomical functional traits across different environments.



Keywords: ecological strategies, leaf and wood economic spectrum, early-life, resilience to disturbance, Central Africa, DynAfFor, plant performance.



## Liana traits and macro-anatomy from the Republic of Congo: linking cambial variants and life history strategies

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### Abstract

Lianas are emblematic growth forms of tropical forests; however, their original and unique diversity of anatomical structures and associated functions are rarely included in community-level studies. Here, we examined how functional traits specific to liana life habits, such as cambial variants and juvenile wood, are related to liana ecological strategies and vary among species and local forest structure. We collected 164 adult liana stems ranging in diameter from 2 to 6.4 cm near permanent liana monitoring plots in northern Congo. We functionally sorted all stems into cambial variants, ranging from simple to complex degrees of compartmentalization, and derived functional traits associated with early life, resilience to disturbance, and hydraulic safety strategies. We used multivariate and bivariate analyses at the species and community-levels to reveal key liana ecological strategies and their evolution along the liana phylogeny and local forest structure gradients. Cambial variants were generally taxon-specific, but possessed plasticity among types depending on the ontogeny, environment, and life-history of each liana individual. Cambial variants were distributed from simple forms with juvenile stiffness and rigidity to find hosts to complex forms with adult flexibility and resilience to disturbances. We found evidence of a trade-off for hydraulic efficiency-safety that differed only slightly among cambial variants. Wood density reflected hydraulic safety but not survival. Two main axes for ecological strategies were identified: a leaf-based axis related to nutrient acquisition and a wood-based axis related to water-use and resilience. In contrast to other studies, liana species exhibited coupled leaf and wood strategies. Along the phylogeny, the leaf and wood strategies of liana species showed significant evolution in related species. However, at the community-level, only leaf acquisition-conservation strategies were influenced by local forest structure, with more conservative species occurring in tall, close-canopy forests with large and hardwooded trees. The diversity of liana wood strategies appears to exist independently of local forest structure shifts. Overall, lianas exhibit diverse strategies to balance efficiency, safety, and survival, which may allow them to thrive in various environments. The coordination between leaf and wood traits reveals the complexity of the functional diversity of lianas and their adaptation to different ecological niches.

# 1 Introduction

Lianas are an emblematic growth form of tropical forests, but also one of the most diverse plant forms (Chery, Pace, et al. 2020). It is particularly difficult to study them at the ecological level and to understand their functional biology, distribution, and responses to different environments (Schnitzer and Bongers 2002). Lianoid species have evolved in more than 130 angiosperm families (Gentry 1991). Many of them possess some of the most complex vascular organisations in plants. It is generally believed that this complex organisation is related to the particular physiological, mechanical, and ecological constraints that characterise their climbing lifestyle. Lianas and vines are terrestrial plants that germinate on the ground and go through a self-supporting phase in the early stages of development. Many species then change their ability to support themselves and become flexible as they begin to climb supports such as trees (G. Caballé 1998; Darwin 1875; F.E. Putz and Holbrook 1991). This profound change in growth form and associated functional traits is difficult to study. Liana stems are accessible near ground level for large-scale studies, but are nonetheless ontogenetically complex and vary from self-supporting (standing) to non-self-supporting (climbing). Trait-based approaches based on leaves can also be complicated in lianas from a routine sampling perspective because they are often inaccessible in the canopy.

During the early self-supporting phase of their development and their initial secondary growth, lianas may show similarities to young trees or shrubs by producing self-supporting upright stems. During wood development, the secondary xylem (wood) is produced centripetally and the secondary phloem centrifugally. In lianas, this first-produced wood is hereafter referred to as “juvenile wood” because it is produced during the early stages of liana development; it is characterised by narrow, sparse, or absent vessels, thick-walled fibrous cells, and limited, often lignified axial parenchyma (Angyalossy et al. 2012; G. Caballé 1998). As a result, juvenile wood of lianas generally has relatively high wood density and stiffness, as its main function is to provide mechanical stability to the self-supporting stem (Fisher & Ewers, 1991; Rowe et al., 2004; Rowe & Speck, 2005). Many liana species exit the juvenile, self-supporting growth phase when they attach to a support and begin to climb (Soffiatti et al. 2022). At this point, mechanical conditions change fundamentally, and the more mature stems require flexible and resistant stems to climb host trees in search of light (Obaton, 1960; Putz & Holbrook, 1991; Rowe & Speck, 2005). Climbers are thought to save structural costs by climbing up supports and developing only relatively narrow stems. However, the downside is that tree sway, wind, and falling branches and trees can break small-diameter stems (Ménard et al. 2013). As a result, many liana species have evolved complex woody forms at mature growth stages, termed “anomalous secondary growth” (Fahn 1982), “vascular cambial variants” (S. Carlquist 1991), and more recently

“vascular variants” (Cunha Neto 2023). It is generally believed that the likely functional advantage of many of these complex stem organisations is to enhance and optimise stem integrity in the face of mechanical perturbations and generally to favour flexibility and toughness over mechanical stiffness and brittleness (Caballé, 1998; Ménard et al., 2013; Rowe et al., 2004).

Cambial variants in lianas are found in circular to non-circular stems and often include different configurations of wood and secondary phloem produced by a single or multiple bifacial vascular cambia. They result in a huge diversity of structures with combinations of lignified tissues, xylem, and/or fibres alternating with much softer tissues, including unlignified parenchyma and tissues comprising secondary phloem (Angyalossy et al. 2012; Angyalossy, Pace, and Lima 2015; G. Caballé 1998; Chery, Pace, et al. 2020; Philipson, Ward, and Butterfield 1971). Cambial variants are thought to resist mechanical disturbance, particularly by preventing and limiting catastrophic failure of conduction of the long, slender stems through flexibility (J. B. Fisher and Ewers 1991). Observations and experiments on some complex stem organisations suggest that protection from disturbance goes beyond mere flexibility, and that stem protection is likely enhanced by preformed stem compartmentalization. In such cases, vital tissue functions are protected from damage by mechanically benign stem splitting and separation of the stem rather than a disastrous cross-sectional rupture (Angyalossy et al. 2012; David R. Dobbins and Fisher 1986; J. B. Fisher and Ewers 1991). Such mechanisms likely release violent mechanical stresses and limit the main structural damage from tension, twisting, or bending (J. B. Fisher and Ewers 1991; F.E. Putz and Holbrook 1991). Thus, the ability of lianas to endure significant stem deformation without losing functionality depends largely on the complex, often heterogeneous anatomy of their stems (F.E. Putz and Holbrook 1991).

The phylogenetic diversity of cambial variants has been described, often in great detail, in several studies since the 19th century. First by the work of Schenck (1892) and since then strengthened by others such as Obaton (1960), Carlquist (1991), Pace et al. (2009) and most recently Angyalossy et al. (2015). However, many studies on the diversity of cambial variants have been conducted at the botanical family, genus, or species level, such as Bignoniaceae (Angyalossy et al. 2012; Pace, Lohmann, and Angyalossy 2009) or Paullinia L. (Chery, da Cunha Neto, et al. 2020).

Similarly, functional and biomechanical analyses of lianas have been conducted with the goal of determining how mechanical properties such as stiffness and flexibility of a plant evolve during its development and life history from younger to older stages, in numerous species from different phylogenetic groups, including observations on adult wood and cambial variants (Putz & Mooney, 1991; Rowe et al., 2006; Rowe & Speck, 1996). However, with few exceptions (two articles by Gallenmüller et al. (2001, 2004) and one article by Ménard et al. (2013)) such variations have not

usually been analysed at the community level. Similarly, the influence of cambial variant diversity on hydraulic conductivity, resistance and resilience to damage, and repair mechanisms is considered extremely important for liana survival and has been studied at the individual level (J. B. Fisher and Ewers 1991; F.E. Putz and Holbrook 1991) but not at the community level. Such studies are needed to better understand which tissue combinations provide stiffness or flexibility, maintain water conduction, and repair damage, and would undoubtedly provide important information about the survival and preferences of different species at the community level. Mechanical and anatomical studies have also been applied to evolutionary contexts to understand how tissues and associated mechanical properties change during ontogeny and potentially respond to ecological factors. Indeed, the high phylogenetic and functional diversity, as well as the high degree of convergent anatomical plans underlying adult stem mechanics and hydraulics in lianas, have been suggested to explain the generally high degree of adaptive success to perturbed and changing environmental conditions (Angyalossy et al., 2015; Rowe & Speck, 2015).

Despite the rich background of the phylogenetic and functional diversity of liana stems, there are surprisingly few studies linking the anatomical diversity of lianas and their associated functions at the community level. Thus, there is a gap in our understanding between the individual level and how detailed traits associated with secondary cambial growth influence the ecological dynamics of lianas, as well as for understanding: (i) how this structural diversity varies within a given community, (ii) how an individual species can vary its structure within a community, (iii) how stem structures of different species and different ecological strategies are linked, and finally (iv) how stem organisation and responses to environmental factors change along environmental gradients.

While it is generally true that there is a lack of community-level studies to understand how cambial variants influence ecological patterns, to our knowledge there are only two pioneering quantitative studies, one by Caballé (1986) in Gabon, where he examined 225 liana species from 35 families, and a more recent one by Yang et al. (2022) in Taiwan, where they examined 287 liana species from 52 families. While these studies analysed the anatomical variations observed within specific communities, they did not address how the putative functional diversity and anatomical diversity might explain patterns within the community.

One of the problems facing anatomical and functional studies at the community level is the inherent destructive methods required for mechanical, hydraulic, and anatomical analyses. Most community-level study sites are permanent plots which are studied continuously in time and space and destructive methods are not allowed. Destructive methods must be conducted “around” or adjacent to the permanent plots in order to provide functional information on the ecological patterns

of the permanent plots (van der Sande et al. 2019). In addition, detailed functional and anatomical studies can be very time consuming and cannot be carried out with high levels of replication, and may depend on very specific local effects of the individual rather than reflecting broadly comparable effects over a large number of samples and replicates (Rowe & Speck, 2015). In addition to these difficulties, botanical identification of lianas from ground level is difficult. As a result, there is a general lack of studies in the scientific community on the functional characteristics of lianas based on their anatomy and cambial variants, which is arguably their most specific and emblematic feature that sets them apart from typical trees or shrubs.

Perhaps because of the challenges presented above, many studies in community ecology of lianas have considered them as a “single functional group” to understand their distribution and dynamics in space and time. Some studies that have tackled lianas as a truly heterogenous group have, however, investigated patterns of functional traits as used for trees and in analyses exploring the wood and leaf economic spectra (such as SLA, leaf thickness, wood density...). Up to now, recent studies have suggested that (i) lianas are as functionally diverse as trees (Medina-Vega et al. 2021; Meunier et al. 2020; Sun et al. 2022), (ii) their patterns of functional traits may vary along environmental gradients (Rocha et al. 2022) , and (iii) classically circumscribed functional traits may not uncover the changes in liana life histories and connections to the environment as strongly as they do for trees (Liu et al. 2021).

In this paper, we explore how the addition of cambial variants and wood traits (juvenile and adult wood) to classical functional traits contributes to a deeper understanding of the functional ecological strategies of lianas. We aim to show how different cambial variants and putative strategies vary among species and in terms of phylogeny. We then attempt to link individual observations and measurements of liana species to the diversity of strategies observed in a neighbouring liana community. We then explore the distribution of traits along local environmental gradients within a humid tropical forest in northern Republic of Congo. One of the main goals of this study is to incorporate the up-to-now underexplored functional trait the cambial variant in liana functional ecological strategies. We aim to find out how cambial variant characteristics vary with other anatomical traits and how they are related to different liana life-habits, species and local forest structure. We therefore address the following questions:

- 1) What is the anatomical diversity of cambial variants in the liana species in Northern Congo?
- 2) Do functional anatomical traits highlight different liana functional strategies? Are different ecological strategies associated with cambial variants?
- 3) How do anatomical traits contribute to classical leaf strategies and how do they vary by cambial variants and among species and phylogeny?
- 4) Do functional anatomical traits explain liana distributions along environmental gradients?

## 2 Materials and methods

In this study, we collected liana stem samples adjacent to permanent plots, which best represented the ecology of the monitored liana communities. We characterized and simplified (by necessity) the functional types of cambial variants based on wood geometry, component tissues and degree of division of vascular tissues with the hypothesis that the more complex the wood forms and compartments of different tissues, the more resilient it is to injury of the stems. We found how cambial variants were distributed in our liana community and explored the boundaries of cambial variant identification for community-scale studies. We derived functional anatomical traits that translate the self-supporting and non-self-supporting phases of liana growth habits, as well as early life, resilience to disturbance, and hydraulic safety strategies. We used these traits to reveal different liana ecological trends. We then combined these new functional anatomical traits in analyses with classical leaf traits and examined how they contribute to the description of liana ecological strategies from the point of view of both functional and phylogenetic diversity. Finally, we examined how these new anatomical traits vary along environmental gradients – the local forest structure.

### 2.1 Study site and liana stem collection

Our study was conducted in a semi deciduous forest in the north of the Republic of Congo (2°27'11.87" N and 17°02'32.17" E). Sampling took place adjacent to an experimental site established in 2014 for monitoring tree and liana dynamics over space and time, in the Loundoungou-Toukoulaka forest management unit, managed by the logging company CIB-Olam. The location of the permanent plots was chosen to maximize the homogeneity of abiotic environmental variables. They are located on a plateau with elevations between 395 and 470 m a.s.l. (above sea level), sandy-clay to clay-sandy soils and no evidence of human activities in the last 100 years (Freycon 2014).

The permanent plots are composed of four plots of 9-ha in which all trees  $\geq 10$  cm DBH (diameter at breast height) are tagged, identified and measured annually. Within these four plots, liana permanent quadrats of 20x20 m<sup>2</sup> have been established at regularly spaced intervals in 2017, where all lianas  $\geq 1$  cm DBH were tagged, identified and measured. For more information about the permanent plots, please see Kacamak et al. (in prep, chapter 2 of my thesis).

Our sampling to investigate the ecological significance of cambial variants required destructive sampling of adult liana stems and could not be carried out in the permanent plots described above. To sample lianas that most closely mirrored the patterns observed on the permanent plots, we sampled liana stems in forested areas adjacent to, but separated from, the permanent plots by a 20 m buffer where destructive sampling was not conducted, with a maximum sampling distance from the permanent plots of 1 km. 8 samples were taken between 8 and 20 m from the permanent plots because they were rare species, after checking that none of the liana stems were growing towards the permanent plots. Because the site was generally selected for its spatial homogeneity, we felt that this approach meant that the adjacent areas beyond the 20m buffer could be considered reliably comparable to the area surrounding the permanent plots.

During fieldwork in September-October 2021, we conducted sampling— along transects radiating from the edge of the buffer zone of the permanent plots, searching for and collecting liana stems from climbing individuals (no juvenile self-supporting stems) that were at least 2 cm and up to 6.4 cm (average 3.5 cm) in diameter at 1.3 m from their basal rooting point on the ground. This was done according to established protocols for sampling liana stems (Gerwing et al. 2006; S. A. Schnitzer, Rutishauser, and Aguilar 2008). Despite the high variability of individual tree-liana situations and the wide range of ontogeny stages of attached lianas in the field, we ensured as much as possible that the sampled climbing adult liana stems had similar diameters at 1.3 m to allow comparisons between species and individuals that represented, as much as possible, the same or similar ontogenetic developmental stage.

For each liana stem collected, we recorded the location (Garmin gps), identified the species by bark characteristics and leaves if present or visible, measured the diameter at 1.3 m height, and noted the following observations when possible: Bark description, climbing mechanism, approximate height of first attachment, stage of development (whether the liana is still climbing or has already reached the canopy). We used a saw to cut a section about 10 cm long with the diameter measurement point in the middle perpendicular to the stem, and stored it moist in plastic bags. We described the cut directly in the field (color, presence of latex or other exudates, odor). We also measured the distance between the rooting point of the liana and the first host tree and recorded any tree species the liana

climbed after connecting with the first host tree. The following day, each liana sample was directly polished very roughly with sandpaper to photograph and document the cut in the field. They were then conditioned in 40° alcohol in plastic bottles during transport to the laboratory and prior to taking high quality images (as described below and in Section 2.3.1). In total, we collected 164 stem samples, belonging to 66 liana species, with an average of 2.5 individuals per species (minimum of 1 sample and maximum of 6 samples per species).

In the laboratory, each stem sample was divided into three parts. One was stored in 40° alcohol. The second was used to measure liana wood density (described in section 2.3.1). The third stem segment was first polished on one side with a water-assisted, rotary grinder using a decreasing series of sandpaper grades with 8 different grain sizes, from FEPA P60 (260  $\mu\text{m}$  grain sizes) to FEPA P1200 (14  $\mu\text{m}$  grain sizes). The entire cross-section of each stem was then scanned with an Epson Stylux Perfection V700 scanner at a resolution of 2400 ppp.

## 2.2 Functional categorization of cambial variants

Using the scans taken in the laboratory, we characterized each liana stem based on macroscopic and microscopic anatomical details. Macroscopic properties concerned principally the patterns of tissues resulting from the growth of the variant cambium. Faced with a large diversity of anatomical organizations, we decided to group the macroanatomical organizations provisionally according to (i) the geometry of the secondary xylem and (ii) the degree of subdivision of the vascular tissue produced by the bifacial vascular cambium. The latter is shown in Figures 1, 2, and 3. Both elastic mechanical properties, e.g., stiffness, and resistance to catastrophic failure, e.g., toughness (J. B. Fisher and Ewers 1991) of lianas may depend to a large extent on the degree of homogeneity and subdivision or alternation within the secondary vascular cylinder of “stiff” and compliant “soft, flexible” tissues. Mature liana stems that have alternating soft parenchyma tissue and stiffer mechanical tissue are known to have both relatively compliant and tough properties. For example, axial rays of phloem or xylem, allow the stem more flexibility to procure more resistance to twinning and twisting, more storage space, and better repair after injury (Angyalossy, Pace, and Lima 2015; S. Carlquist 1991; D. R. Dobbins 1990; F. W. Ewers and Fisher 1991; J. B. Fisher and Ewers 1991; Schenck 1892; Wagner et al. 2012). In particular, alternating segments of secondary xylem and soft parenchyma tissue can provide “fracture-stopping” heterogeneities, where energy present at the tip of a developing fracture or crack can be effectively dissipated as it travels through the wood cylinder when it encounters a patch of soft tissue. This type of mechanical compartmentalization is likely responsible for many of the resilient



properties of lianas (David R. Dobbins and Fisher 1986; J. B. Fisher and Ewers 1991; Ménard et al. 2013; Philipson, Ward, and Butterfield 1971; F.E. Putz and Holbrook 1991).

While the type of mechanical compartmentalization plays an important role in adult liana mechanical stiffness, juvenile wood takes up a different role in the early-life of lianas, providing young liana self-supporting stems with mechanical stiffness (Fisher & Ewers, 1991; Rowe et al., 2004; Rowe & Speck, 2005). We explored the role of juvenile wood and relationships with the development of cambial variants and anatomical characteristics related to different life-history strategies further in through functional traits described in section 2.3.

We sorted the sampled liana stems from simple, complete, and uncompartimentalized wood cylinders to more complex forms with some degree of compartmentalization and an alternation of stiff and soft tissue types (Isnard & Silk, 2009; Ménard et al., 2013; Rowe & Speck, 2005). All the forms described below come from a differential cambium activity producing phloem wedges or alternate activities of multiple cambia, created by the differentiation of pericyclic cells, producing phloem arcs embedded in wood or separations of wood parts (Philipson, Ward, and Butterfield 1971). We distinguished 3 different categories of wood structure that are further differentiates into 14 different cambial variants (cambial variant types) for the species collected from the northern Congo site, shown in Figure 1, 2 and 3 and defined below:

Uniform woods (Figure 1): In this category, secondary xylem (juvenile, inner (depicted in light brown) and adult, outer wood in dark brown) is undivided apart from narrow rays, but the circumference outline of the wood cylinder has different degrees of slight lobing due to variations in cambium activity (black line), creating variations of the outer perimeter. We identified:

- Regular (Figure 1, A): Cambial growth is regular (black lines) with homogeneous xylem. The outer perimeter of the wood is circular with a cylinder of secondary xylem (young and adult wood in light and dark brown) surrounded by a cylinder of secondary phloem. The latter is not always macroscopically separable from external cortical tissues and other non-conductive tissues, such as the periderm (orange). Where primary cortex secondary phloem and periderm cannot be distinguished macroscopically we refer to this as “bark.” Although this generalization concerning tissues exterior to the wood cylinder is sometimes difficult to apply microscopically, the main focus of identifying different vascular variants still holds.
- Lightly grooved (Figure 1, B): Cambial growth is regular but shows different degrees of growth around the perimeter, forming grooves. Lightly uneven cambial growth with differential

production of phloem and xylem, where the radial length of the grooves is shorter than half the wood radius.

- Crenellated (Figure 1, C): Cambial growth around the perimeter is more irregular, even ceasing xylem production in some parts of the perimeter, resulting in phloem wedges, furrowing the xylem.
- Grooved with phloem wedges (Figure 1, D): The phloem wedges created by irregular activity of the cambium have geometrical rectangular forms in the wood cylinder.
- Deeply grooved (Figure 1, E): Highly uneven cambial growth with differential production of phloem and xylem intensifies, creating deep grooves across the wood cylinder, where the radial length of the grooves is greater than half the wood radius.
- Radial (Figure 1, F): Axial elements of the vascular cylinder are radially separated by wide rays (greater than one cell wide) of axial parenchyma, sometimes with xylem and phloem tissue, which can extend from the margin of the pith to the outer margin of the secondary phloem. Ray tissues can be lignified or non-lignified (in white lines from the pith until the external phloem in the orange cortex and bark).

Internal phloem woods (Figure 2): In this category secondary xylem is still the main component of the wood cylinder but includes pockets (inclusions) of soft tissue (yellow), generally of phloem and/or parenchyma. Inclusions can appear from the alternate activity of a single cambium, or from the activity of intraxylary multiple cambia (light blue). Presence of inclusions leads to 3 different types of cambial variants:

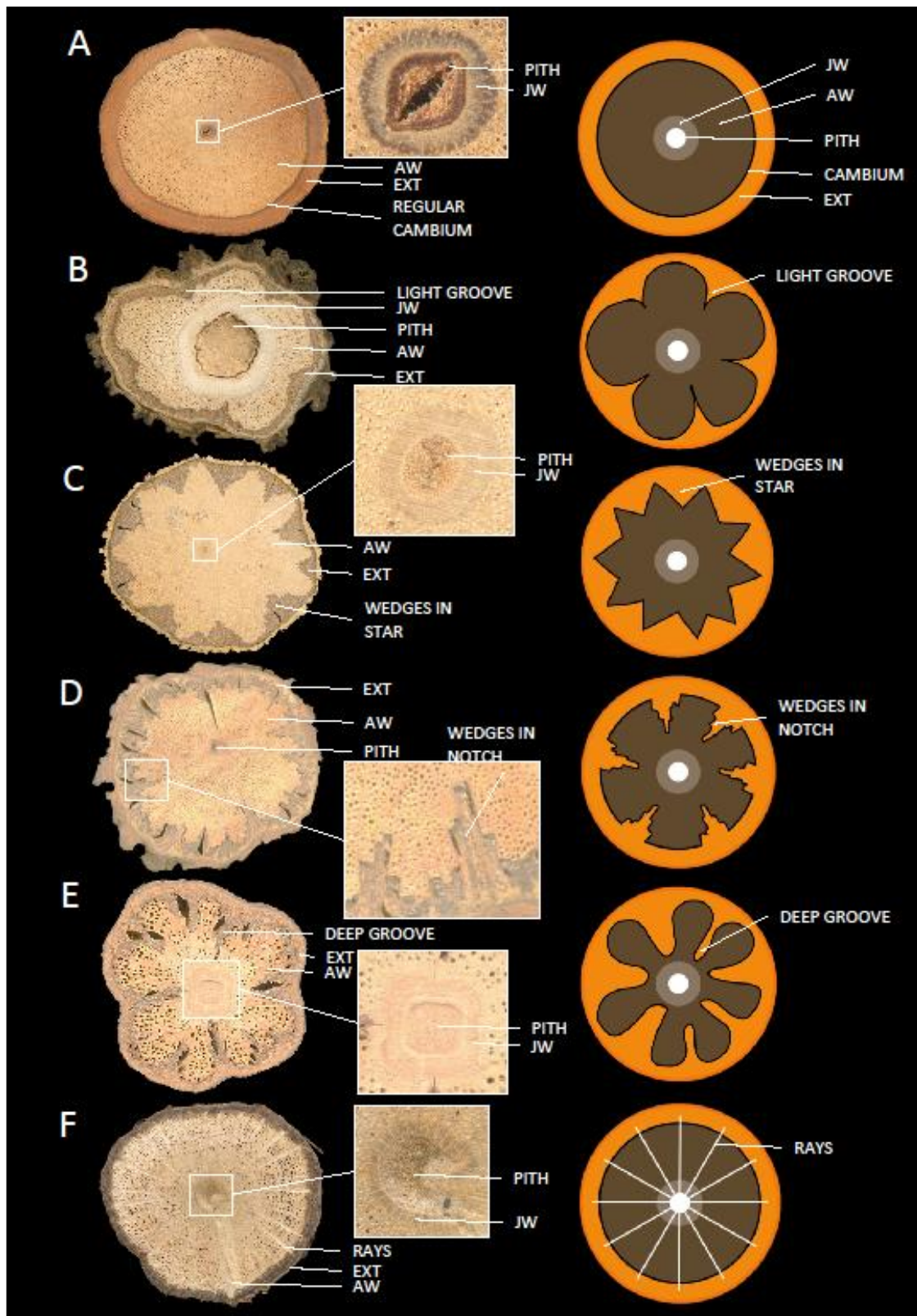
- Scattered islands (Figure 2, A): irregular cambium activity or alternate cambia activity (in light blue) produce phloem arcs that are included within the secondary xylem. This creates macroscopically visible intraxylary phloem islands within the wood (yellow).
- Fragmented circles (Figure 2, B): A high proportion of the cambium or cambia produce phloem arcs, which are subsequently embedded in the xylem cylinder and appear as fragmented circles within the wood cylinder.
- Flame-like phloem (Figure 2, C and D): Highly uneven cambial growth with differential production of phloem and xylem producing deep phloem wedges and a high production of phloem arcs embedded in the xylem cylinder confer a flame-like look to the phloem inclusions.

Compound woods (Figure 3): In this category, secondary xylem is divided into independent parts. Phloem soft tissues separate the secondary xylem, into multiple fragments which are either fragments of adult wood, adult and juvenile wood, or also pith fragments. These cambial variant types are generally derived from multiple cambia and a combination of irregular cambium activities:

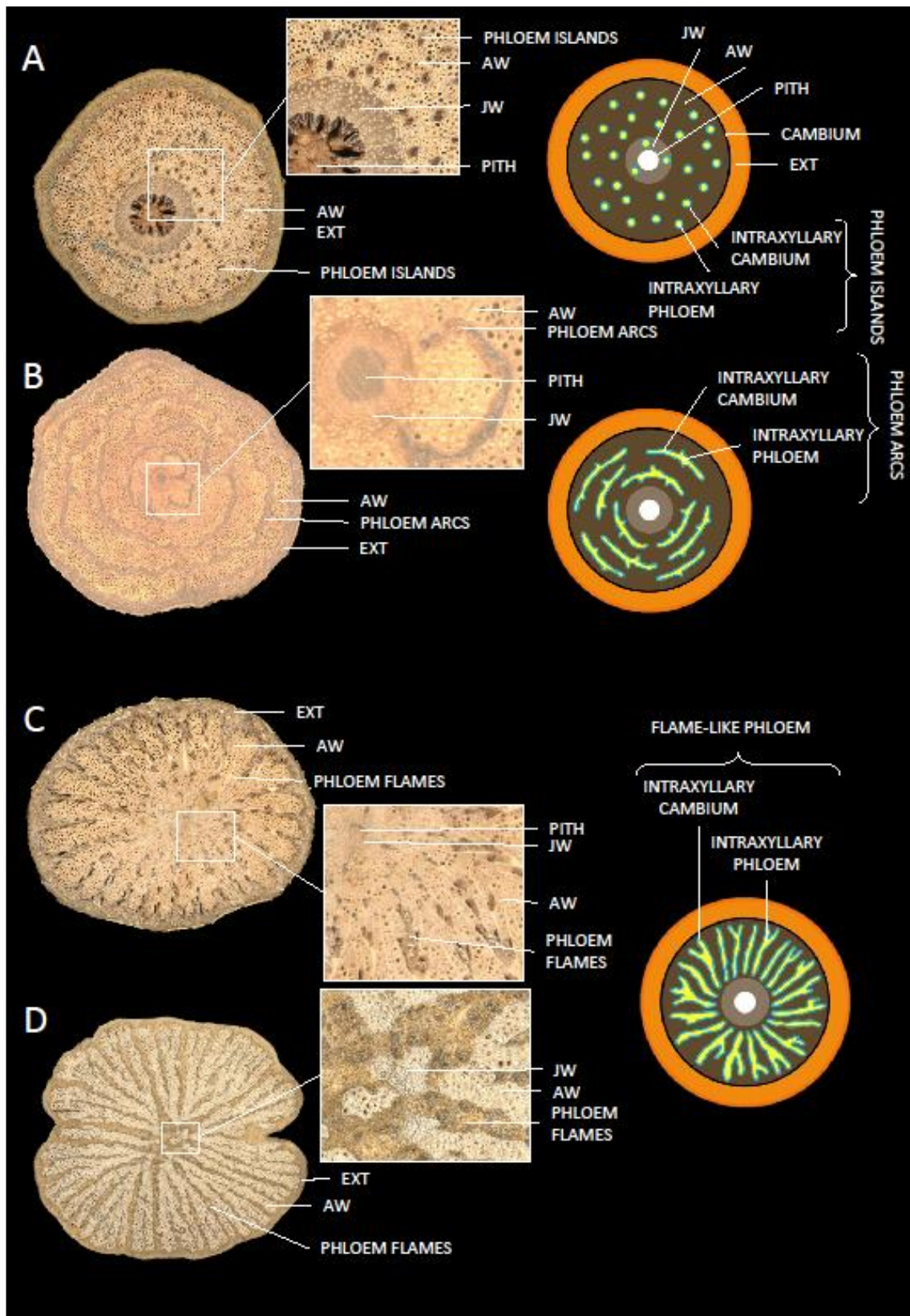
- Clusters (Figure 3, A): The wood cylinder is divided into multiple fragments of different but relatively equivalent sizes, with clusters of soft tissues created by the activity of multiple cambia (black lines), dividing completely the wood cylinder, including or not the pith. The divisions are centered on the pith. The activity of the cambia is nevertheless regular, creating an approximatively homogeneous outline of the clusters.
- Grooved clusters (Figure 3, B): The same mechanisms of clusters combined with an irregular activity of the most external cambia, combining clusters with irregular conformations, producing grooved outlines for the wood clusters, with uneven cambial growth.
- Successive bands (Figure 3, C): Cambia arises successively by cell divisions of external portions of the pericycle (secondary vascular system), producing xylem centripetally and phloem centrifugally regularly along the entire girth of the stem, dividing the wood by bands of successive phloem bands.
- Radial bands (Figure 3, D): The combination of successive cambia with the production of axial elements (rays, white lines) results in phloem head caps in bands and xylem elements wrapped in conjunctive tissue, looking like radial bands.
- Scattered (Figure 3, E): The stem is composed of multiple vascular cylinders, creating visually multiple wood fragments with multiple piths or young and adult woods, scattered in a common matrix. The independent wood parts are not centered on the pith.

After establishing different categorizations for the stems that were present at the site, we observed for all individuals of the same species, how cambial variants varied, from an ecological and developmental point of view.

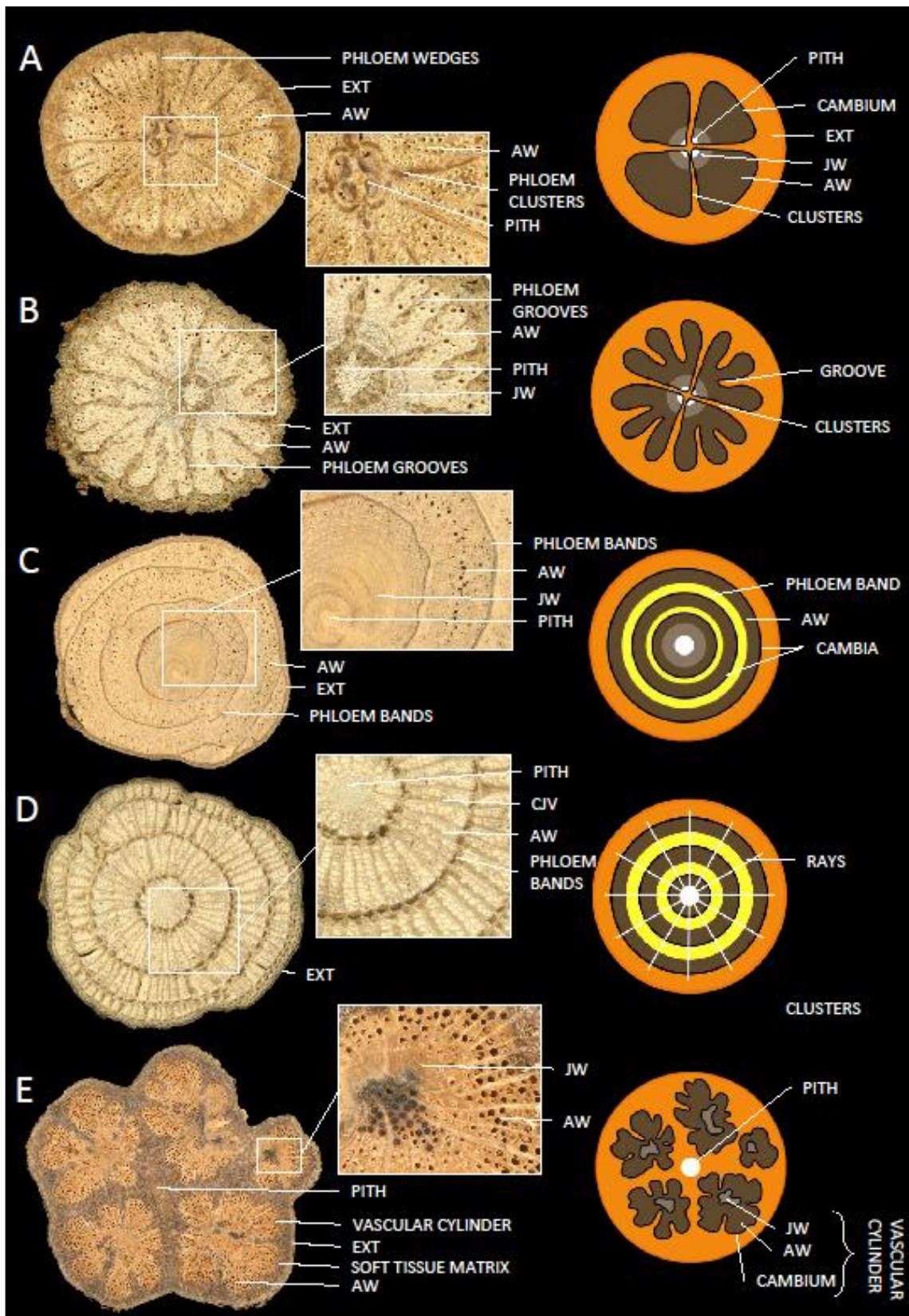
Finally, in order to explore how cambial variants were distributed in our liana community and to check the limits of cambial variant identification for community-scale studies, we expanded cambial variant types to the community level and the permanent liana inventory from 2017. We linked a wood category and a cambial variant type to each species. For species with multiple cambial variants, we assigned the most compartmentalized cambial variant type observed, considering that it likely represents the final (most developed compartmentalized) stage of development that can be achieved by the species. We then observed how cambial variants vary between the liana community or northern Congo, using the data from the 2017 liana inventory in the permanent plots.



**Figure 1.** Uniform wood and cambial variant types. (A) *Landolphia landolphioides*, regular (B) *Manniophyton fulvum*, lightly grooved (C) *Loeseneriella sp. 2*, crenellated (D) *Strophantus preussi*, grooved with phloem wedges (E) *Loeseneriella sp. 1*, deeply grooved (F) *Tetracera podotricha*, radial. JW: juvenile wood; AW: adult wood; EXT: external phloem, cortex, bark and all other non-conductive tissues.



**Figure 2.** Internal phloem, wood types and cambial variant types. (A) *Strychnos sp. 1*, scattered islands (B) *Celastraceae spp*, fragmented circles (C) *Loeseneriella sp. 2* and (D) *Mokasso* (vernacular sp), flame-like phloem. JW: juvenile wood; AW: adult wood; EXT: external phloem, cortex, bark and all other non-conductive tissues.



**Figure 3.** Compound wood and cambial variant types. (A) *Neuropeltis velutina*, clusters (B) *Turraea vogelii*, grooved clusters (C) *Agelaea pentagyna*, successive bands (D) *Triclisia macrophylla*, bands (E) *Loeseneriella sp1*, scattered. JW: juvenile wood; AW: adult wood; EXT: external phloem, cortex, bark and all other non-conductive tissues.

## 2.3 Functional traits

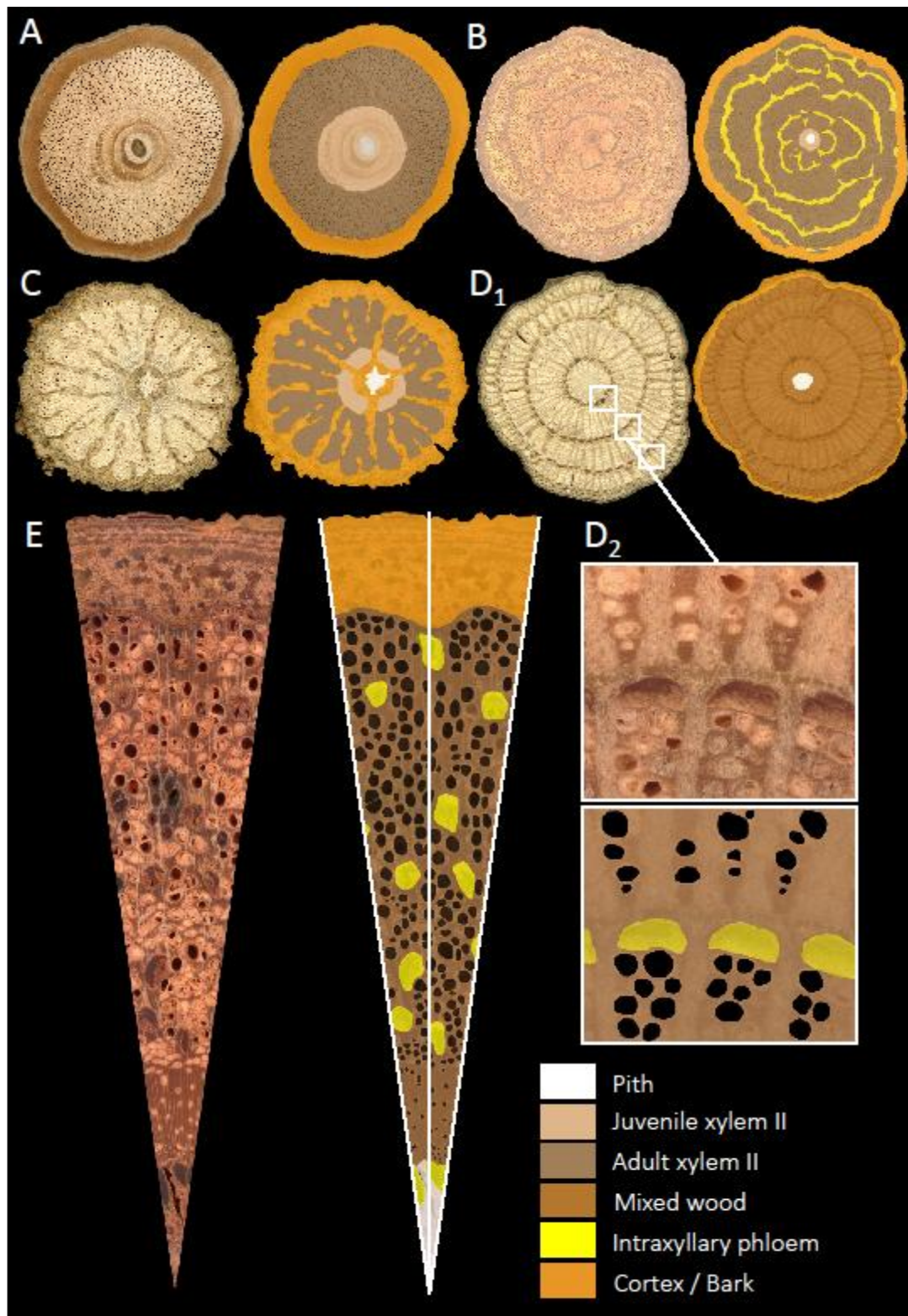
### 2.3.1 Anatomical functional traits

We selected eight functional anatomical stem traits to explore liana ecological trends, which are related to different life-history functions including early-life history strategies of lianas- the self-supporting phase, their resilience to disturbance and perturbation and their hydraulic safety (see plant traits studied in Table 1).

**Table 1.** Anatomical functional traits and their definitions for 136 liana individuals

Strategies	Traits	Abbreviation	Range	Unit	Ecological / functional role
<b>Early-life</b>	Pith area	Pith	[0-1.96]	mm <sup>2</sup>	Rigor of searching stems & mechanical spacer
	Juvenile wood area	JW	[0-2.33]	mm <sup>2</sup>	Cost of self-supporting phase, investment into stiff initial stem structure
	Adult, juvenile wood and intraxylary phloem area	Mix_Wood	[0-0.34]	mm <sup>2</sup>	Growth
<b>Resilience to disturbance</b>	External phloem, cortex and bark area	Ext	[0-13.49]	mm <sup>2</sup>	Protection of vital tissues and defense against herbivory
	Heterogeneity index	Hetero_index	[0.09-2.14]	No unit	Stress dissipation and fracture point stopping
	Cambial variants			No unit	Compliance and flexibility – escaping concentrations of mechanical stress
	Phloem/Xylem ratio	ratio_PX	[0-1.08]	No unit	Elasticity and stiffness of wood and fracture point stopping
<b>Hydraulic safety</b>	Tissue density	TD	[0.18-0.70]	No unit	Mechanical structure, transport, longevity and defense against herbivory
	Wood vessel density	vessel_density	[1.76-30.37]	No./ mm <sup>2</sup>	Conductance efficiency
	Wood vessel area	mean_vessel	[0.004-0.177]	mm <sup>2</sup>	Conductance safety

On scan images, stem tissues were delineated in Photoshop and numerically analyzed using ImageJ software (Figure 4). We measured the areas of the pith, juvenile secondary xylem (juvenile wood), adult secondary xylem (adult wood), intraxylary phloem (when possible, if not, it was included in the adult wood area and recorded as mixed wood) and external tissues (comprising the external phloem and all other non-conductive tissues such as parenchyma, cortex and bark), as presented in Figure 4, A, B, C and D<sub>1</sub>.



**Figure 4.** Anatomical tissue and vessel delineations. (A) *Landolphia robustior* with a regular form. (B) *Celastraceae spp* with internal phloem wood with fragmented circles. (C) *Turraea vogelii* with compound wood with grooved clusters. (D) *Triclisia macrophylla* with compound wood with radial bands. (E) *Strychnos sp. 1* with internal phloem wood with scattered islands.



For more fine-scale measurements, we took high-resolution images of a radial segment depending on the size and intactness of each segment, which was centered at the centroid of the pith and extended to include the outermost perimeter of the stem. For a given stem section, we selected the largest radial segment if the stem diameter was variable, as is often the case. Variable radial widths for a given liana stem can have a significant influence on not only the diameter, but also the complexity of the tissues produced by the cambial variant. Thus, the protocol ensured that we measured the “maximum” development for a given stem section. Anatomical details of the surfaces of the radial segments were captured using a Keyence VHX 7000 microscope with resolutions between 4850 and 19600 ppp.

We delineated and measured all vessel areas (entire vessels; Figure 4, E, black), the entire wood area, and the intraxylary phloem areas (Figure 4, E, yellow) for samples that could not be delineated on scans. From these measurements, we derived wood vessel density, mean wood vessel diameter, and phloem/xylem surface ratio. We also measured a value representing the macroscopic heterogeneity of each sample as the mean number of tissue types traversed along the three radial lines of the radial segment: the two lateral sides and the middle of each radial segment (Figure 4, E, white lines). This value was normalized to each radial line length to consider different stem diameters and size factors. The mixed wood area (Mix\_Wood in Table 1), comprising the juvenile and adult wood, and when present, the intraxylary phloem was also standardized by the diameter of each sample.

One type of liana organization comprised a striking organization of radially arranged bands, including pockets and bundles of secondary xylem and phloem vascular tissue, often with tangentially alternating bands of wide-ray tissue (Figure 4, D2). Because of the highly intricate organization of such species and the time required for manual vessel delineation, we measured the mean vessel areas, wood, and phloem cap areas for three sub-sections (Mennega 1982), regularly positioned along the middle radius for lianas (inner, middle, and outer positions on the vascular cylinder), with radial bands as a cambial variant structure (Figure 4, D1). The mean vessel density, diameter, and phloem/xylem ratio were computed as the mean values of the three sub-sections.

Vessel delineation of numerous different species with different tissue characteristics was compounded by the range of appearances and lumen -wall details visible with the fast throughput analysis necessary for handling large numbers of specimens. A common problem was the presence of occluded vessel lumens resulting from natural causes, tyloses, breakdown of wall material, or artifacts resulting from clogging of the lumens. In a single section, although some vessels might be clear, others were occluded or clogged. Blocked vessels can occur naturally, with the production of tyloses, gum, or deposits, if the vessels are no longer functional or because of a detached fragment of the plant cell

wall entering the lumen. It has been documented that wide liana vessels can be occluded with tylose or gum as an immediate response to cutting to seal the surface (J. B. Fisher and Ewers 1991). However, it can also be an artifact of polishing with clogging of the lumen owing to sawdust. We delineated all visible entire vessels, whether clogged or not, as we could not determine the cause of the clogging, whether it was natural or artificial. Moreover, some vessel elements were somewhat oblique in the transverse view and inclined from the horizontal plane of the cross-section. Although these technical problems could potentially lead to an overestimation of theoretical water conductance through vessels, we considered that such effects were not significant. Finally, in some cross-sections, parts of the vascular cylinder appeared to have decayed in otherwise healthy stems. Such areas were not used for vessel area and tissue delimitation, and the samples were excluded from trait analysis.

We performed liana wood density measurements using the Archimedes thrust technique. All samples were first debarked (removing the bark and external phloem layer) and saturated with water under pressure for 48 h, through several vacuum–negative pressure cycles (-1 – 0 bar). We then measured the Archimedes thrust according to the protocol described by Birouste et al. (2014). The debarked stems were then dried in an oven at 40°C for 10 days, to avoid damaging the water-saturated materials at extreme temperatures, and then at 103°C for 48 h to eliminate all water. Finally, we measured the mass of the dried stem samples to assess wood density. We named this measure the stem "tissue density" hereafter because even after debarking, many liana species still contain a mixture of stiff and soft tissues that might not include actual wood tissue in the stem samples used for measurements.

### 2.3.2 Leaf traits

In May 2018, we collected liana herbarium samples from in and around the permanent plots, in shaded locations where lianas had sprouted yielding leafy shoots. This collection was first carried out due to a lack of botanical expertise in the region. In order to determine botanical names of liana species and check the coherence of vernacular names (used for the liana inventory in the permanent plots), leaf material from each herbarium samples was dried with zeolite beads in ziplock bags for genetic analyses (described in 2.3.3). We maximized the number of samples for the most abundant lianas (up to 17 samples per vernacular name; average 4 samples per vernacular name).

For a total of 46 liana species, we measured leaf traits on the herbarium samples following the guidelines of Perez et al. (2020) for the measurements of the Specific Leaf Area (SLA) and leaf thickness (Thick). Perez et al. (2020) found that herbarium-based and fresh-tissue based trait measurements were significantly and strongly correlated. We measured the SLA with petioles, their mass and scanned

all samples with an Epson Stylux Perfection V700 scanner. We assessed leaf area using the ImageJ software (Abramoff et al, 2004) and a semi-automatic method developed by Borianne & Brunel (2012). We measured leaf thickness at 3 points: mid-leaf, avoiding veins, with a digital micrometer after rehydrating leaves in a 1:50 solution of neutral household detergent for 20 minutes, following (Perez et al. (2020).

We measured the carbon, nitrogen, phosphorus and potassium of 100 mg of dry liana herbarium leaves. After grinding the leaves to powder, we carried out an elemental analysis for carbon and nitrogen (%C and %N), with the elemental analyser Flash Smart AE 2000, by adsorption chromatography. We mineralized the rest of the leaf powder to determine the total phosphorus (%PO<sub>4</sub>) content by colorimetric determination with molybdenum blue and with the HNO<sub>3</sub> Gallery, and the potassium (%K) by absorption spectrometer in flame mode with the Thermo ICE 3000 Series atomic.

**Table 2.** Description of liana leaf and stem functional traits used for 46 species

Trait	Abr	Range	Unit	Ecological Role
Leaf thickness	Thick	[0.05-0.2]	mm	Leaf structure mechanical support and defense, longevity and resistance against herbivory
Specific leaf area	SLA	[13.0-49.9]	mm <sup>2</sup> .mg <sup>-1</sup>	Light capture and growth: leaf longevity, photosynthetic rate
Foliar Carbon	%C	[38.9-53.7]	%	Leaf investment in structural composition
Foliar Nitrogen	%N	[2.1-4.9]	%	Light capture and growth: carbon fixation (photosynthesis and respiration)
Foliar Phosphorus	%PO <sub>4</sub>	[0.07-0.2]	%	Light capture and growth: enzyme function
Foliar Potassium	%K	[0.3-2.2]	%	Maintenance metabolism: membrane function

### 2.3.3 Liana phylogenetic tree construction

We extracted successfully DNA from 192 dried liana leaf tissue samples collected in May 2018. We extracted at least one DNA sequence per vernacular name, focusing on samples from genera known to contain several lianescent species. We sequenced the two plastids identified for barcoding terrestrial land plants, *rbcl* and *matK* (CBOL Plant Working Group 1 et al., 2009). DNA extractions were carried out with a Qiagen Kit (QIAamp 2010) and then we performed the Polymerase Chain Reaction

(PCR) following the protocol for *matK* and *rbcl* by Dunning & Savolainen (2010). We finally sequenced all isolates in both directions (forward and reverse) with the Sanger method (Gonzalez et al. 2009) and built consensus sequences with the Geneious software (Geneious 2018). Sequences were aligned using the MEGA software (Kumar et al. 2018). We then concatenated both *rbcl* and *matK* sequences and used the MEGA software to first determine the best nucleotide substitution model *to generate pairwise evolutionary distances between samples* (the model with the lowest BIC; which was GTR+G+I) and to second build a maximum likelihood phylogenetic tree using the selected substitution model. We used the *chronos* function in R package *ape* (Paradis et al. 2019) to fit a chronogram to the phylogenetic tree to get an ultrametric tree and pruned the tree to only have liana species studied on the ecological strategies through leaf and wood functional traits described in section 2.4.2.

#### 2.3.4 Local environmental gradients

The local environment in which the liana inventory has been made has been characterized in Kacamak et al. (in prep, chapter 2). Briefly, three sets of variables were assessed: ground-based tree variables, drone-based forest variables and ground-based giant herbs variables. These were used to assess 8 environmental variables: tree stem density ( $N_T$ ), tree quadratic mean diameter ( $QMD_T$ ), tree total basal area ( $BA_T$ ), tree mean wood density ( $WD_T$ ), tree basal area increment ( $\Delta BA_T$ ), mean leaf cover of giant herbs (GHFC), mean of the top of the canopy height (meanTCH) and relative slope position index characterizing local termite mounds (RSP). For more details of the acquisitions of variables see Kacamak et al (in prep, chapter 2).

We reduced the local environment variable dimensionality using a PCA, and used the first two axes of the PCA as proxies of local environmental gradients to test their effects on liana ecological strategies. These first two axes represented two main gradients (Appendix 1). The first axis contrasted forests with large canopy openings to forests with tall and close canopies composed of large and hard wooded trees. We refer to this axis as the «forest successional gradient». The second axis contrasted forests with an abundance of small trees to forests dominated by giant herbs where a large deficit in small trees occurs and a high tree basal area increment is observed. We refer to this axis as the «giant herbs gradient».

## 2.4 Statistical analyses

All statistical analyses were made with the statistical program R, version 4.2.1 (R Core Team, 2022). We used the packages *ade4* for multivariate analysis (Dray and Dufour, 2007), *phylosignal* to test phylogenetic signals (Keck et al, 2016) and *ggplot2* for visualisations (Wickham, 2016).

### 2.4.1 Multivariate analysis of anatomical trends

To reveal the main ecological trends of liana functional strategies, we carried out a multivariate analysis with all anatomical traits using a PCA and described the main trends and their variations by wood category and cambial variant types. We then computed linear models between traits to explore in detail the different strategies related to early life history, resilience to disturbances, and hydraulic safety. This analysis was carried out on samples where all anatomical functional traits were measured and too damaged samples were excluded, for a total of 136 samples belonging to 59 liana species.

### 2.4.2 Ecological trends of stem and leaf traits across species and growth habits

To explore how functional anatomical traits were linked to leaf traits, we performed a PCA at the species level combining all anatomical and leaf traits. We explored how liana ecological strategies vary according to phylogeny and functional diversity (cambial variants). We investigated whether leaf and stem traits were coupled or not in liana communities and provided an overview of how they are associated. This analysis was carried out on samples where all anatomical and leaf functional traits were present, for a total of 46 liana species.

We then examined how the main ecological strategies highlighted by the association of leaf and stem traits were distributed across a liana phylogeny and tested if we detected a significant phylogenetic signal using Abouheif's Cmean (Abouheif, 1999; Munkemuller et al, 2012). The presence of a phylogenetic signal was tested for 44 liana species.

Finally, we examined how the ecological strategies (the scores of species on the first two PCA axis of leaf and wood trait associations) vary along environmental gradients – the local forest structure, at the community level using Community Weighted Mean's. We tested significant variations of ecological strategies along local forest structure gradients (forest successional and giant herbs gradients) with randomization tests (n=999) of the ecological strategies associated to each species. This analysis was carried out with common liana species with the liana inventory in the permanent plots, for a total of 37 liana taxa.

## 3 Results

### 3.1 Taxonomic and cambial variant diversity of lianas from northern Congo

Among the 164 samples collected, 73% had uniform wood, 24% had internal phloem wood, and 12% had compound wood. The categorization of cambial variant types in all samples is shown in Table 3. Most of the samples collected had a regular cambial variant type (48%; Figure 1, A). Among the other uniform woods, there were 7% lightly grooved (Figure 1, B), 1% crenellated (Figure 1, C), 1% grooved with phloem wedges (Figure 1, D), 3% deeply grooved (Figure 1, E), and 12% radial cambial variants (Figure 1, F). Within the internal phloem wood lianas, we found 11% scattered islands (Figure 2, A), 1% fragmented circles (Figure 2, B), and 2% flame-like phloem cambial variants (Figure 2, C and D). Within the compound wood lianas, we found 1% clusters (Figure 3, A), 1% grooved clusters (Figure 3, B), 1% successive bands (Figure 3, C), 7% radial bands (Figure 3, D), and 2% scattered cambial variants (Figure 3, E).

**Table 3.** Wood structure categories and cambial variants of the collected 164 liana stem samples

Uniform wood	Regular	Lightly grooved	Crenellated	Grooved with phloem wedges	Deeply grooved	Radial	TOTAL
	79	12	2	2	5	20	<b>120</b>
Internal phloem wood	Scattered islands	Fragmented circles	Flame-like phloem	-	-	-	
	18	2	4	-	-	-	<b>24</b>
Compound wood	Clusters	Grooved clusters	Successive bands	Radial bands	Scattered	-	
	2	2	2	11	3	-	<b>20</b>

We observed 12 species with individuals having different cambial variants within the same wood structure category (Table 4). They all have uniform wood, but exhibit different cambial variants, mostly between regular, lightly grooved, and radial variant types. In addition, four species, all belonging to the Celastraceae family, in the genus *Salacia* or *Loeseneriella*, included individuals with different cambial variants as well as different wood structure categories.

**Table 4.** Different cambial variant types and wood structure categories within species.

Family	Species scientific names	Vernacular names	Wood structure categories	Cambial variant types	Variant types observed ratio
Connaraceae	Agelaea sp3	Mopoupou	Uniform wood	Regular / Lightly grooved	3 / 2
Apocynaceae	Baijsea multiflora	Ewouwa 1	Uniform wood	Regular / Lightly grooved	2 / 1
Apocynaceae	Baijsea subrufa	Ewouwa 2	Uniform wood	Regular / Lightly grooved	4 / 1
Connaraceae	Cnestis corniculata	Kpayo	Uniform wood	Regular / Lightly grooved	2 / 1
Euphorbiaceae	Manniophyton fulvum	Mokossa	Uniform wood	Regular / Lightly grooved	2 / 4
Apocynaceae	Strophanthus preussi	Ndemele	Uniform wood	Regular / Grooved in nutch	1 / 2
Lamiaceae	Clerodendrum sp2	Moungenzou	Uniform wood	Regular / Radial	1 / 1
Combretaceae	Combretaceae spp	Combretum	Uniform wood	Regular / Radial	1 / 1
Passifloraceae	Passifloraceae spp	Moundikipomba 2	Uniform wood	Regular / Radial	1 / 1
Dilleniaceae	Tetracera podotricha	Nsoue	Uniform wood	Regular / Radial	1 / 2
Fabaceae	Dalhousiea africana	Mbizo 1	Uniform wood	Lightly grooved / Radial	2 / 3
Fabaceae	Leucomphalos brachycarpus	Mbizo 2	Uniform wood	Regular / Deeply grooved / Radial	2 / 1 / 2
Celastraceae	Salacia or Loeseneriella sp1	Digbiya	Uniform wood / Internal phloem / Compound wood	Deeply grooved / Flames / Clusters	1 / 1 / 1
Celastraceae	Loeseneriella sp1	Mountendo rouge	Uniform wood / Compound wood	Deeply grooved / Grooved in nutch / Scattered	2 / 1 / 1
Celastraceae	Loeseneriella sp2	Mountendo blanc grande feuilles	Uniform wood / Internal phloem	Crenellated / Scattered islands	2 / 2
Celastraceae	Salacia laurentii or zenkeri	Mombe	Uniform wood / Internal phloem	Regular / Fragmented circles	1 / 1

At the scale of the liana community monitored in the permanent plots, we assigned a wood category and cambial variant type to 95% of all individuals monitored in the liana inventory (5926 individuals out of a total of 6206), representing 45 taxonomic species (Table 5). Of the 5926 individuals, 85.5% were uniform wood lianas, 8% had internal phloem wood, and 6.5% had compound wood. The five most abundant cambial variants were the lightly grooved type (53.2% of all individuals), followed by the radial (17.0% of all individuals), regular (13.9% of all individuals), scattered islands (7.3% of all individuals), and radial bands (3.5% of all individuals) types.

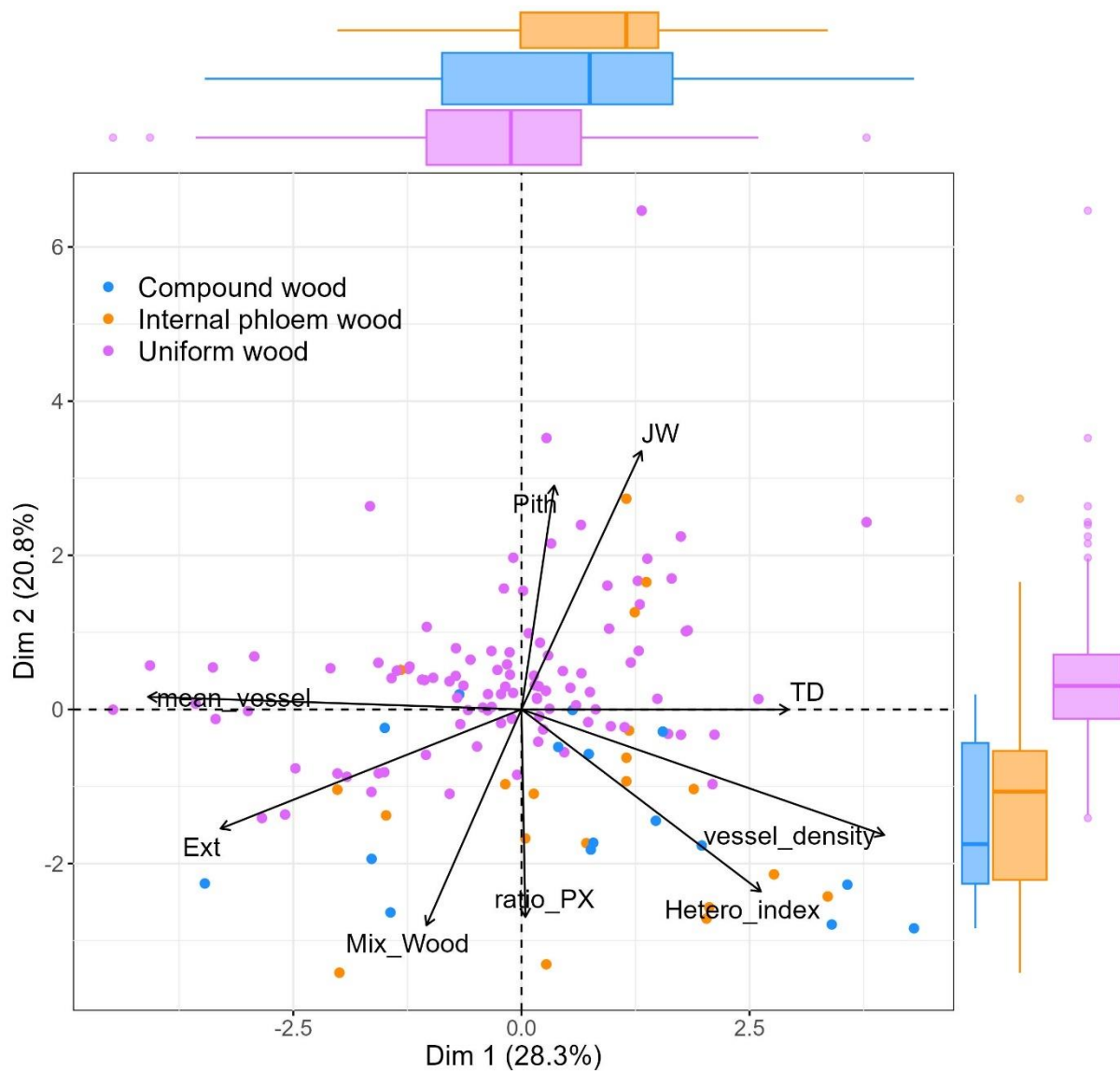
**Table 5.** 45 liana taxa representing 95% of all liana individuals of Northern Congo liana community, their wood structure category and cambial variants.

Family	Species scientific names	Vernacular names	Wood structure category	Cambial variant type	Number inventory	Number collected	% in inventory
Fabaceae	<i>Acacia kamerunensis</i>	Empele	Uniform wood	Deeply grooved	39	2	0,63
Passifloraceae	<i>Adenia</i> spp	Moundikipomba	Uniform wood	Radial	37	3	0,60
Connaraceae	<i>Ageleae poggeana</i>	Bemba	Uniform wood	Regular	36	2	0,58
Connaraceae	<i>Ageleae</i> sp1	Nsongue	Uniform wood	Regular	14	2	0,23
Connaraceae	<i>Ageleae</i> sp2	Mboko	Uniform wood	Regular	30	2	0,48
Connaraceae	<i>Ageleae</i> spp	Ageleae	Uniform wood	Lightly grooved	751	7	12,10
Apocynaceae	<i>Ancylbothrys robusta</i>	Elongou	Uniform wood	Lightly grooved	69	1	1,11
Annonaceae	<i>Artabotrys</i> sp1	Mbeko	Uniform wood	Radial	38	3	0,61
Apocynaceae	<i>Baissea</i> spp	Ewouwa	Uniform wood	Lightly grooved	459	8	7,40
Vitaceae	<i>Cissus dinklagei</i> or <i>populnea</i>	Mossembe	Uniform wood	Radial	47	4	0,76
Lamiaceae	<i>Clerodendrum</i> sp2	Moungenzou	Uniform wood	Radial	70	3	1,13
Connaraceae	<i>Cnestis corniculata</i>	Kpayo	Uniform wood	Lightly grooved	30	3	0,48
Combretaceae	<i>Combretum</i> sp1	Dissessengue	Uniform wood	Regular	36	1	0,58
Combretaceae	<i>Combretum</i> spp	Combretum	Uniform wood	Radial	32	2	0,52
Fabaceae	<i>Dalbergiella welwitschii</i>	Kpayo ngai	Uniform wood	Regular	62	2	1,00
Fabaceae	<i>Dalhousiea africana</i>	Mbizo	Uniform wood	Radial	741	10	11,94
Fabaceae	<i>Dewevrea bilabiata</i>	Kombe	Uniform wood	Regular	76	3	1,22
Cucurbitaceae	<i>Friesodielsia enghiana</i>	Dipembegne	Uniform wood	Radial	7	1	0,11
Apocynaceae	<i>Landolphia landolphioides</i>	Touba	Uniform wood	Regular	11	1	0,18
Apocynaceae	<i>Landolphia owariensis</i>	Sendja	Uniform wood	Regular	18	3	0,29
Apocynaceae	<i>Landolphia robustior</i>	Bogne	Uniform wood	Regular	21	3	0,34
Celastraceae	<i>Loeseneriella</i> spp	Mountendo	Compound wood	Scattered	115	9	1,85
Euphorbiaceae	<i>Macaranga angolensis</i>	Loka	Uniform wood	Regular	73	4	1,18
Euphorbiaceae	<i>Manniophyton fulvum</i>	Mokossa	Uniform wood	Lightly grooved	1843	6	29,70
Fabaceae	<i>Millettia</i> spp	Epougne	Uniform wood	Regular	214	9	3,45
Convolvulaceae	<i>Neuropeltis velutina</i>	Ngougola	Compound wood	Clusters	2	1	0,03
Pentadiplandraceae	<i>Pentadiplandra brazzeana</i>	Enkama	Compound wood	Successive bands	15	1	0,24
Apocynaceae	<i>Pycnobotrya nitida</i>	Dinguenzo	Uniform wood	Regular	107	4	1,72
Connaraceae	<i>Rourea obliquifoliolata</i>	Elendi matei	Uniform wood	Regular	38	2	0,61
Connaraceae	<i>Rourea</i> sp3	Elendi 2	Uniform wood	Regular	72	5	1,16
Celastraceae	<i>Salacia</i> or <i>Loeseneriella</i> sp1	Digbiya	Compound wood	Clusters	28	3	0,45
Celastraceae	<i>Salacia laurentii</i> or <i>zenkeri</i>	Mombe	Internal phloem wood	Fragmented circles	41	2	0,66
Apocynaceae	<i>Strophanthus preussi</i>	Ndemele	Uniform wood	Grooved in notch	45	4	0,73
Loganiaceae	<i>Strychnos aculeata</i>	Boboukou	Internal phloem wood	Scattered islands	10	1	0,16
Loganiaceae	<i>Strychnos icaia</i>	Mbondo	Internal phloem wood	Scattered islands	139	1	2,24
Loganiaceae	<i>Strychnos</i> spp	Komba	Internal phloem wood	Scattered islands	282	12	4,54
Dilleniaceae	<i>Tetracera podotricha</i>	Nsoue	Uniform wood	Radial	34	3	0,55
Menispermaceae	<i>Tiliacora</i> sp1	Mbenga	Compound wood	Radial bands	95	5	1,53
Menispermaceae	<i>Triclisia macrophylla</i>	Ditokobola	Compound wood	Radial bands	115	6	1,85
Meliaceae	<i>Turraea vogelii</i>	Dzola	Compound wood	Grooved clusters	14	1	0,23
Urticaceae	Unk 11	Madzembe	Uniform wood	Regular	8	2	0,13
Unknown	Unk 12	Mokasso	Internal phloem wood	Flames	2	2	0,03
Loganiaceae	Unk 21	Nganda	Internal phloem wood	Scattered islands	1	2	0,02
Apocynaceae	Unk 24	Pembe	Uniform wood	Regular	6	1	0,10
Unknown	Unk 6	Dzaboudzabou	Uniform wood	Regular	3	1	0,05



## 3.2 Multivariate and bivariate anatomical trait associations

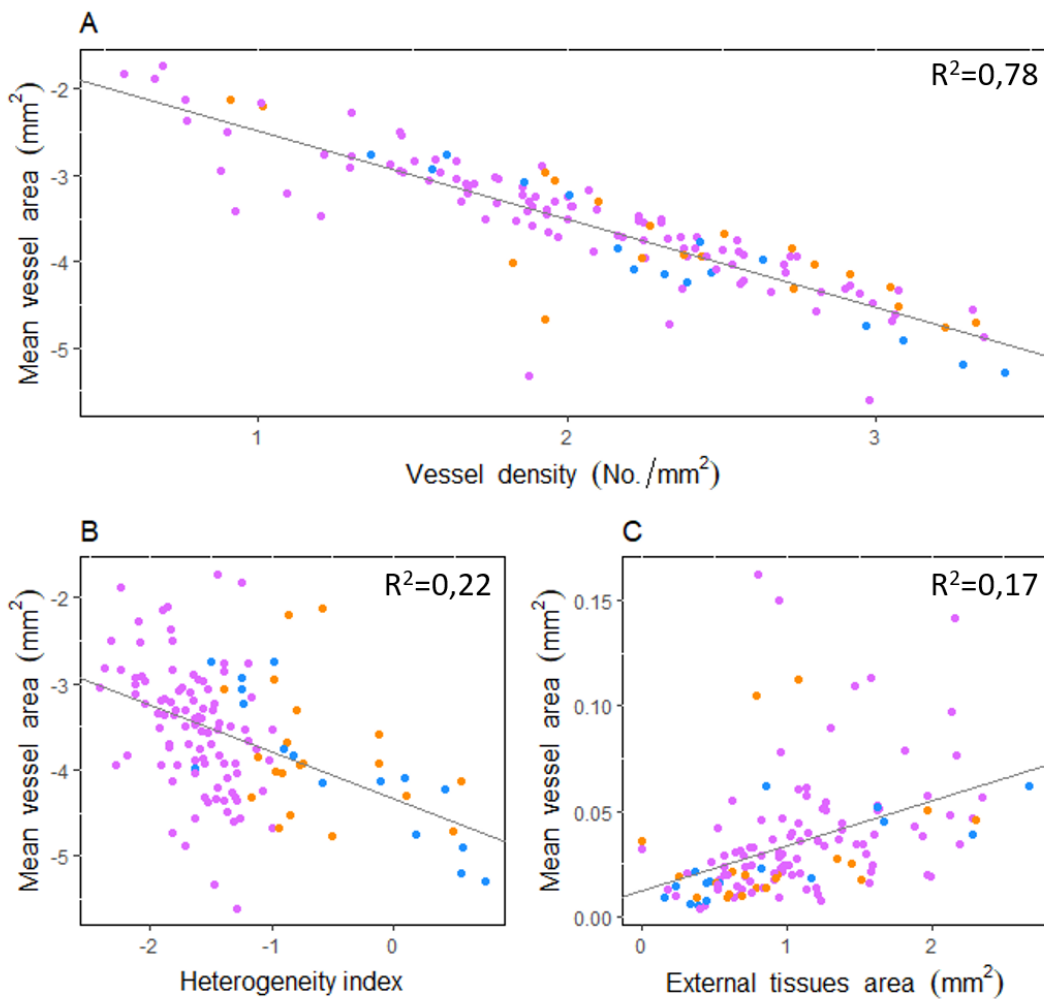
PCA performed on functional anatomical traits presented two dominant axes, with 49.1% of the variation, on which all variables were well represented (Figure 5). The first two axes represent two ecological strategies. The first axis opposed lianas with a low density of large vessels, low tissue densities, and thick external tissues to lianas with a high density of small vessels, high tissue densities, and thin external tissues. The second opposed lianas with simple forms characterized by large piths and producing large juvenile wood cylinders to lianas with more complex forms (with successions of different tissue types) characterized by small piths and small to no juvenile wood. On the first axis, we found that lianas with different cambial variants and wood structures exhibited slight to no significant differences (only the scores between uniform woods and internal phloem woods had a marginally significant Wilcoxon's  $W=650$ ,  $p\text{-value}=0.014$ ). However, along the second axis, the scores of lianas with uniform wood were significantly different from those of lianas with internal phloem wood ( $W=1614$ ,  $p\text{-value}=1.5 \times 10^{-5}$ ) and with lianas with compound wood ( $W=1466$ ,  $p\text{-value}=9.7 \times 10^{-8}$ ).



**Figure 5.** Plan 1-2 of a Principal Coordinate Analysis performed on anatomical functional traits. Wood structure categories; uniform, internal phloem and compound woods; are represented in pink, orange and blue, respectively. Boxplots illustrate the differences between the scores of wood structure categories along the two first PCA axes.

Among functional traits shaping the first axis, we found a strong linear relationship between mean vessel area, vessel density, heterogeneity index, and external tissue area (Figure 6). The strongest relationship was a negative one between liana vessel density and mean vessel area ( $R^2=0.78$ ; Figure 6, A), with smaller vessels observed as vessel density increased. Moreover, we found that lianas with larger vessels tended to have thicker external tissues, which surrounded the vascular cylinder ( $R^2=0.17$ ; Figure 6, C). Neither of these two significant relationships depended on the liana wood

structure category. Nevertheless, uniform wood appeared to have larger vessels than more heterogeneous internal phloem and compound woods ( $R^2=0.22$ ; Figure 6, C).



**Figure 6.** Relationship between the vessel density (A), the heterogeneity index (B), or the external tissues area (C), and the mean vessel area. The grey line illustrates the predicted linear log-log model and the  $R^2$  of the model is displayed on each graph. Wood structure categories; uniform, internal phloem and compound woods; are represented in pink, orange and blue, respectively.

Among the functional traits shaping the second PCA axis, we found the strongest positive relationship between juvenile wood and the pith area ( $R^2=0.32$ ; Figure 7, A). Lianas with larger piths tend to produce thicker juvenile wood. Most of the lianas with uniform wood tended to produce juvenile wood, while most lianas with compound wood either produced or did not produce any juvenile wood. We also found that lianas tended to have thicker external tissues with larger mixed wood areas, regardless of their wood structure categories ( $R^2=0.20$ ; Figure 7, B).

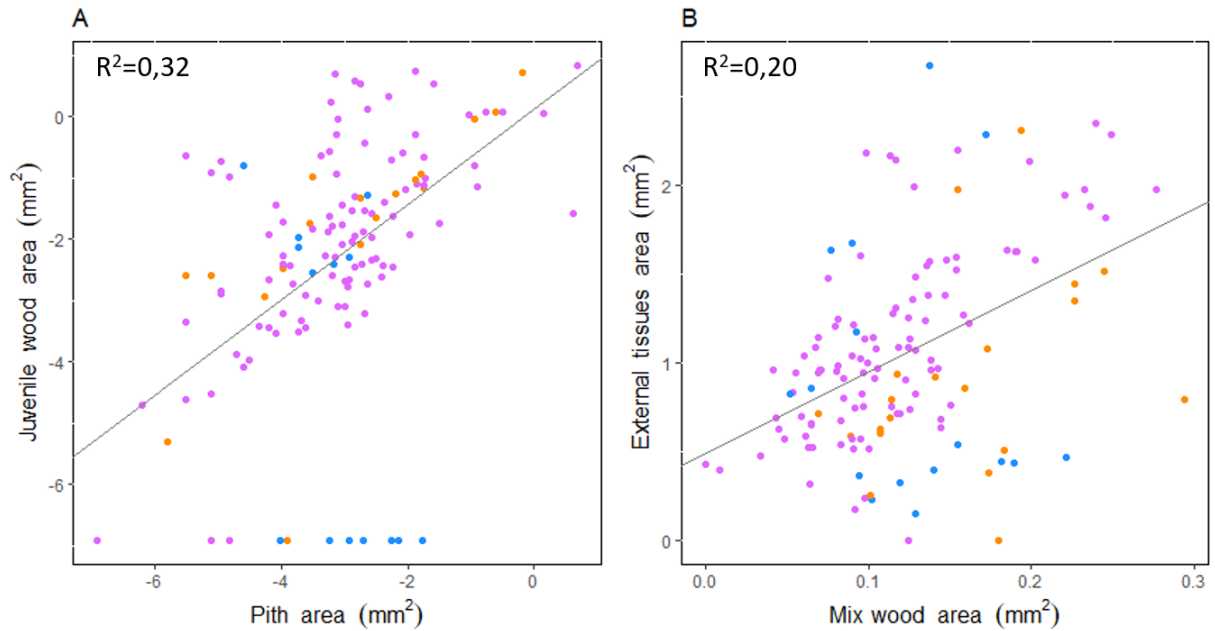
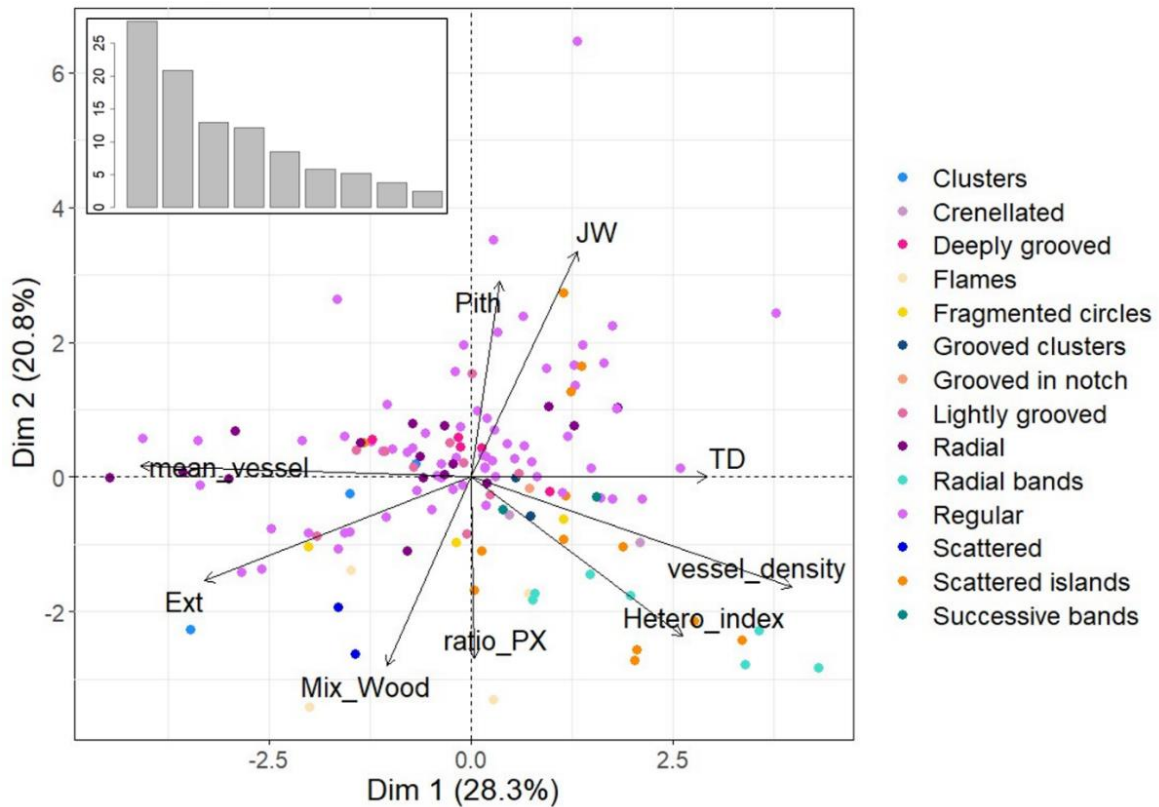


Figure 7. Relationships between the pith and juvenile wood area (A) and the mix wood and external tissues area (B). The grey line illustrates the predicted linear log-log model and the  $R^2$  of the model is displayed on each graph. Wood structure categories; uniform, internal phloem and compound woods; are represented in pink, orange and blue, respectively.

Visually, it was very difficult to observe tendencies between cambial variant types (as there were 14 types) within the space of the first two axes of the PCA performed on the functional anatomical traits (Figure 8). Nevertheless, all radial bands seemed to have a large density of small vessels, high tissue densities, and thin external tissues, and were characterized by small piths and close to no juvenile wood (on the lower right of the graph in Figure 8).

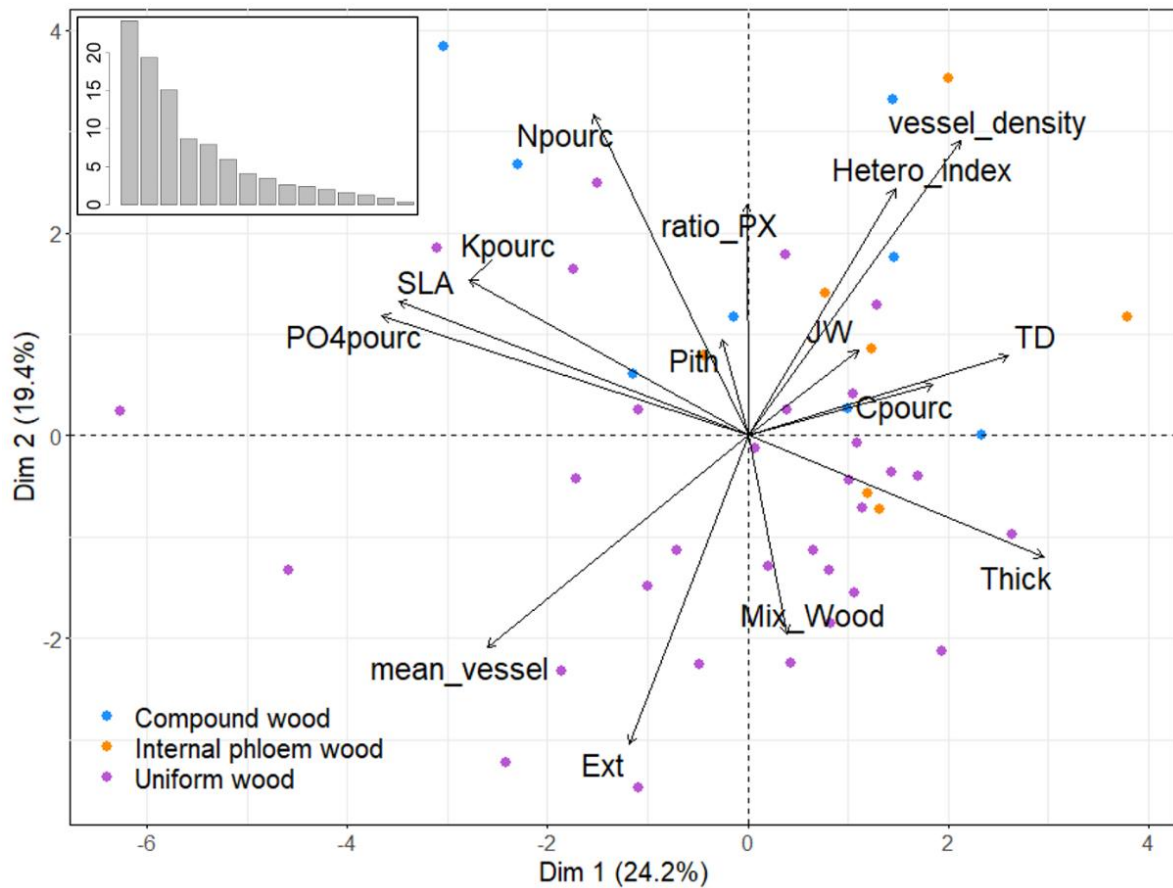


**Figure 8.** Plan 1-2 of a Principal Coordinate Analysis performed on anatomical functional traits. Cambial variant types are represented in different colors. Eigenvalues (%) are represented in the top left corner.

### 3.3 Multivariate leaf and wood trait associations

The analysis of all leaf and stem anatomical functional traits, indicated that 44% of the total variability was explained by the PCA (Figure 9). The first axis is mainly driven by leaf functional traits (%PO<sub>4</sub>, SLA, Thick, %K), liana tissue density (TD), and mean vessel area. It contrasts lianas with more light acquisitive strategies, high %PO<sub>4</sub>, SLA, and %K and large vessels, against lianas investing more in mechanical structure and longevity with thicker leaves and higher tissue densities, but smaller vessels. The second axis was mainly driven by leaf %N, stem external tissue area, vessel density, heterogeneity index, phloem/xylem ratio, and mean vessel area. It contrasts lianas having complex anatomical structures, high density of small vessels, thin external tissues and high leaf photosynthetic rates to lianas with simpler forms, lower vessel densities but larger vessels, surrounded by thicker external tissues, and low %N in the leaves. While leaf traits mainly contribute to the first axis and wood traits to the second, they are not uncoupled. We found significant bivariate associations between most leaf and wood traits. Nevertheless, pith and juvenile wood were poorly represented in the first two axes.

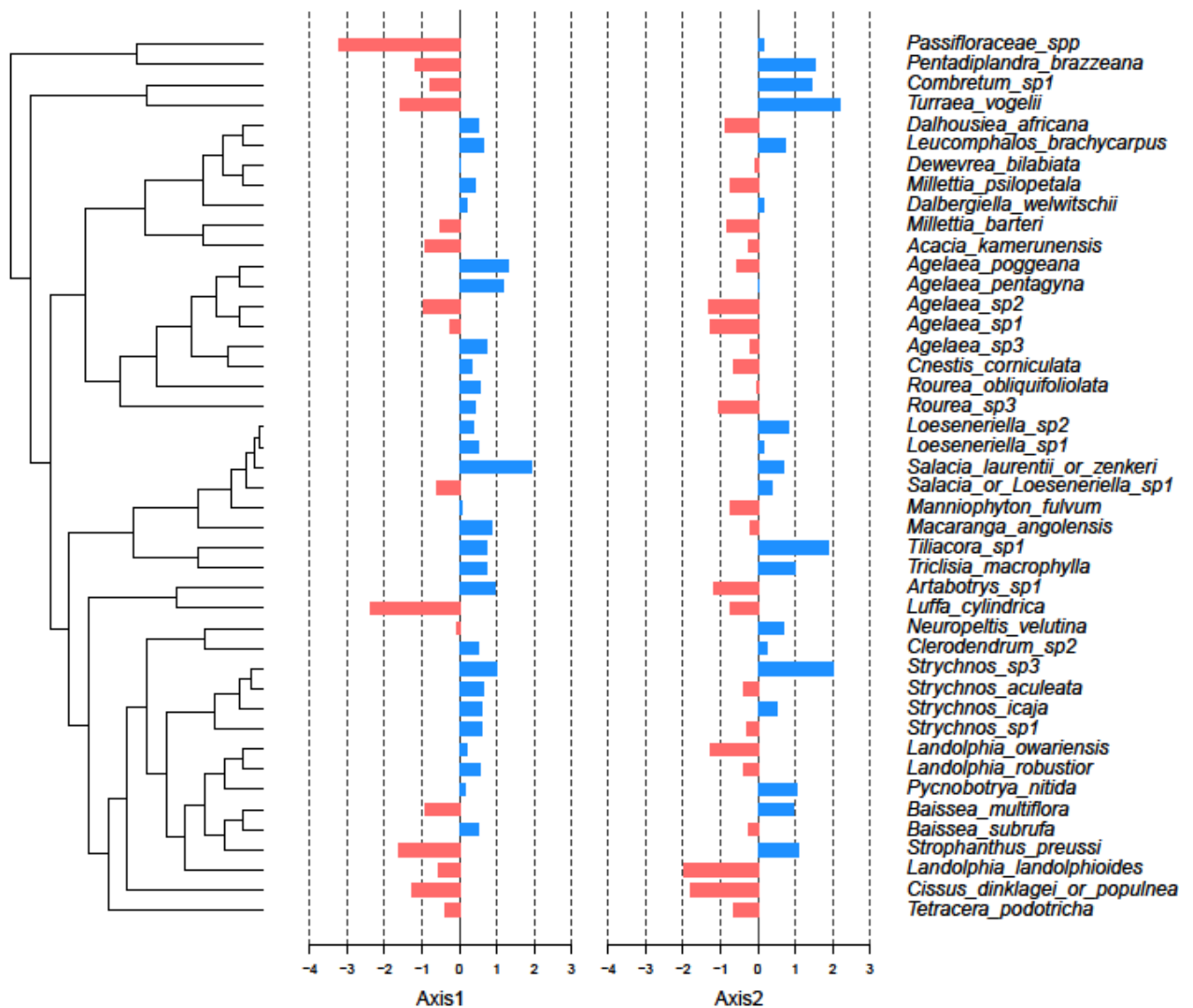
Species with the most leaf acquisitive strategies included *Passifloraceae spp* and *Luffa cylindrica*. Species investing more in wood and leaf structure and longevity over light capture included *Salacia laurentii or zenkeri* and *Agelaea poggeana* (Appendix 2). In contrast, species with simpler forms and large but few vessels included *Landolphia landolphioides* and *Cissus dinklagei or populnea* while more complex forms with higher vessel densities but small vessels were *Turraea vogelii* and *Strychnos sp3*. Along the first PCA axis strategy gradient, there were no significant distributional differences between wood structure categories, apart from between lianas with uniform and internal phloem wood (Wilcoxon's  $W=45$ ,  $p\text{-value}=0.017$ ). However, along the second PCA axis strategy gradient, the internal phloem and compound wood liana distributions were significantly different from those of lianas with uniform wood ( $W=50$ ,  $p\text{-value}=0.028$  and  $W=28$ ,  $p\text{-value}=8.41 \times 10^{-4}$ ).



**Figure 9.** Plan 1-2 of a Principal Coordinate Analysis performed on leaf and stem functional traits of 46 liana species with wood structure categories; uniform, internal phloem and compound woods; are represented in pink, orange and blue, respectively.

### 3.4 Phylogenetic signal of trait associations

We found significant phylogenetic signals for both axis scores of liana species in the PCA exploring leaf and wood traits associations. Related liana species had the tendency to share more similar strategies along leaf (C<sub>mean</sub>=0.25, p-value=0.01; Figure 10, axis 1) and wood strategy axis (C<sub>mean</sub>=0.2, p-value=0.02; Figure 10, axis 2) than with liana species randomly drawn in the phylogeny. Interestingly, phylogenetically distant species, the nodes containing *Passifloraceae spp*, *Pentadiplandra brazzeana*, *Combretum sp1*, and *Turrea vogelii* and the nodes containing *Tetracera podotricha* and *Cissus dinklagei or populnea*, resembled each other along the first axis of the PCA more related to leaf traits, while differed on the second axis, more related to wood traits. Liana species seem to display wood hydraulic efficiency or resilience to disturbance strategies regardless of leaf strategies, but still exhibited similar wood strategies between related species.



**Figure 10.** Scores of the first two axis of the PCA on leaf and wood functional traits of 46 liana species distributed along the phylogenetic tree.

### 3.5 Variation of ecological strategies along local environmental gradients

Overall, we found only one significant association between liana ecological strategies and local environmental gradients. Only the local successional gradient influenced liana leaf strategies (Table 6). Liana species with leaf acquisitive strategies (Figure 9) were significantly more associated with open and short canopy forests characterized by light-wooded trees with small basal areas (Appendix 1). The local giant herbs gradients did not influence any liana leaf or wood strategies. In general, liana wood



strategies remained neutral and were not influenced by any local environmental gradients. The diversity of liana wood strategies seemed to co-exist regardless of local forest structure shifts.

**Table 6.** Correlations between the first two axis of the PCA on liana ecological strategies (leaf and wood traits associations) and the local forest structure variables. P-values, obtained with 999 randomizations are reported below each variable. Significant correlations are in bold.

	Axis 1 Leaf strategies	Axis 2 Wood strategies
Local successional gradient	<b>0.45</b>	0.13
p-value	<b>0.004</b>	0.641
Local giant herbs gradient	0.10	-0.03
p-value	0.376	0.822

## 4 Discussion

In this study, we collected samples of mature liana stems from nearby permanent liana community plots to explore the functional anatomical diversity of lianas and their putative strategies. The main objectives were to investigate patterns of traits as well as cambial variants and understand how they are associated with functional leaf traits, how they vary across phylogeny, and how they are distributed along local forest structure gradients. The cambial variants analyzed were mostly species-specific, but showed some plasticity depending on ontogeny, local environment, and different life histories of liana individuals. Wood structure categories associated to cambial variant types did not differ significantly among water-use strategies—based on the traits analyzed dealing hydraulic efficiency and safety—but they did exhibit differences particularly in terms of early life strategies with longer/shorter expressions of juvenile traits, with differences between uniform or non-uniform wood structures in terms of extent of juvenile wood thickness and size of the pith. The tissue density of lianas was associated with hydraulic efficiency strategies but not with safety and other resilience traits (hetero\_index and P/X ratio). Consistent with trees, liana leaf and wood trait associations revealed first, a leaf acquisitive – conservative trade-off, along which all cambial variants (through wood structure types) appeared to be distributed randomly. In contrast to trees, the second strategy gradient consisted of contrasting hydraulic safety, wood resilience, and photosynthesis rates against hydraulic efficiency, along which wood structure categories appeared to be differentially distributed. Lianas with compound and internal phloem in wood tended to have more resilient characteristics than water-use efficient strategies. Both leaf and wood strategies showed significant signals along the liana

phylogeny, with clear similarities among the related liana species. Only the leaf acquisitive-conservative trade-off was influenced by the local forest successional gradient, whereas liana wood strategies appeared to be neutral to local forest structure shifts. We discuss these results and their implications below.

## 4.1 Functional strategies of lianas

### 4.1.1 Hydraulic safety versus efficiency trade-off and potential adjustment strategies

The first axis of the PCA exploring stem anatomical trait associations was related to the trade-off between the number and size of vessels, from liana species with a low density of large vessels to those with a high density of small vessels. As vessel and lumen sizes increase, water flow and hydraulic conductivity exponentially increase (Sperry, Hacke, and Pittermann 2006; Aloni and Zimmermann 1983; Ewers 1991). However, wider vessels are more susceptible to failure due to embolism (Ewers, Fisher, and Chiu 1990). This trade-off between hydraulic conductivity, safety and efficiency is well documented for tree species (Poorter et al. 2010; Sperry et al. 2008; Baas 1986), and is important for a better understanding of their functioning, performance, and distribution in the environment (van der Sande et al. 2019; Zhang et al. 2023). Compared to tree vessel dimensions, lianas have consistently been found to have wider vessels, presumably to compensate for their slender stem form (Ewers, Fisher, and Chiu 1990; Zhu and Cao 2009), regardless of the vegetation type (Zhang et al. 2023). This trade-off has been shown for co-occurring lianas and trees (Zhu and Cao 2009) but has been less documented among liana species (shown in a seasonally dry forest by De Guzman et al. 2016). On the other hand, some studies have found a decoupled relationship between liana hydraulic efficiency and safety (van der Sande et al. 2019; Zhang et al. 2019), although lianas appear to have comparable variability in vessel size to that of trees (Meunier et al. 2020).

Plants have evolved several strategies to efficiently transport water upward while avoiding embolisms (Zhang et al. 2023). They can (i) adjust their vessel structure by changing the size and density of the vessels, which has not always been proven to correlate with lianas (van der Sande et al. 2019; Zhang et al. 2019). Alternatively, they can (ii) adjust their vascular design. One documented adjustment is xylem vessel dimorphism (Carlquist 1981). Vessel dimorphism is the combination of wide vessels and small narrow vessels adjacent to the wide vessels to create hydraulic bridges between the wide vessels to prevent embolism (Angyalossy, Pace, and Lima 2015). Vessel dimorphism allows lianas

to maintain high hydraulic conductivity, while providing safety measures against embolism and avoiding cavitation under extreme conditions (Zhang et al. 2023; van der Sande et al. 2019).

Another less-documented adaptation towards safety is cambial variants. Although lianas that coexist with trees have wider vessels (Zhang et al. 2023; Zhu and Cao 2009), their hydraulic conductivity is less affected by twining and twisting than trees, and they are also able to maintain water flow in the last thread between two fractured stem segments (Putz and Holbrook 1991). This ability to resist constraints without losing function and hydraulic conductivity is directly related to stem anatomy. We found that the distribution of lianas with internal phloem wood was significantly different along the vessel number-size gradient compared to that of lianas with uniform wood structures. Lianas with internal phloem wood appear to favor hydraulic conductivity safety over efficiency. However, it has been suggested that they may maintain efficient hydraulic conductivity through the intraxylary phloem, which performs the function of conduction, while the regular external phloem specializes in storage (Pace, Lohmann, and Angyalossy 2011; Angyalossy et al. 2012; Sherwin Carlquist 2013). In addition, we found thicker external tissues in the lianas, with wider vessels. The role of these outer tissues, from the external phloem to the cortex and the bark, is primarily to protect against constraints. Cambial variants may play a role in helping lianas maintain high hydraulic efficiency while still being safe against embolism through the intraxylary phloem, taking up conductance, or external tissues to protect vital functions. Further research is needed to better understand how water-use strategies are combined with cambial variants. Vessel dimorphism in lianas appears to be taxon-specific, with *Paullinia* (Chery et al. 2020) or *Bauhinia* (F. W. Ewers, Fisher, and Chiu 1990). Cambial variants also seemed to be taxon-specific, but they appeared to show a large plasticity of cambial variants within the genus (Chery et al. 2020). While we found little evidence that cambial variants condition vessel size-number trade-offs, they may be responsible for alternative strategies for hydraulic efficiency and safety.

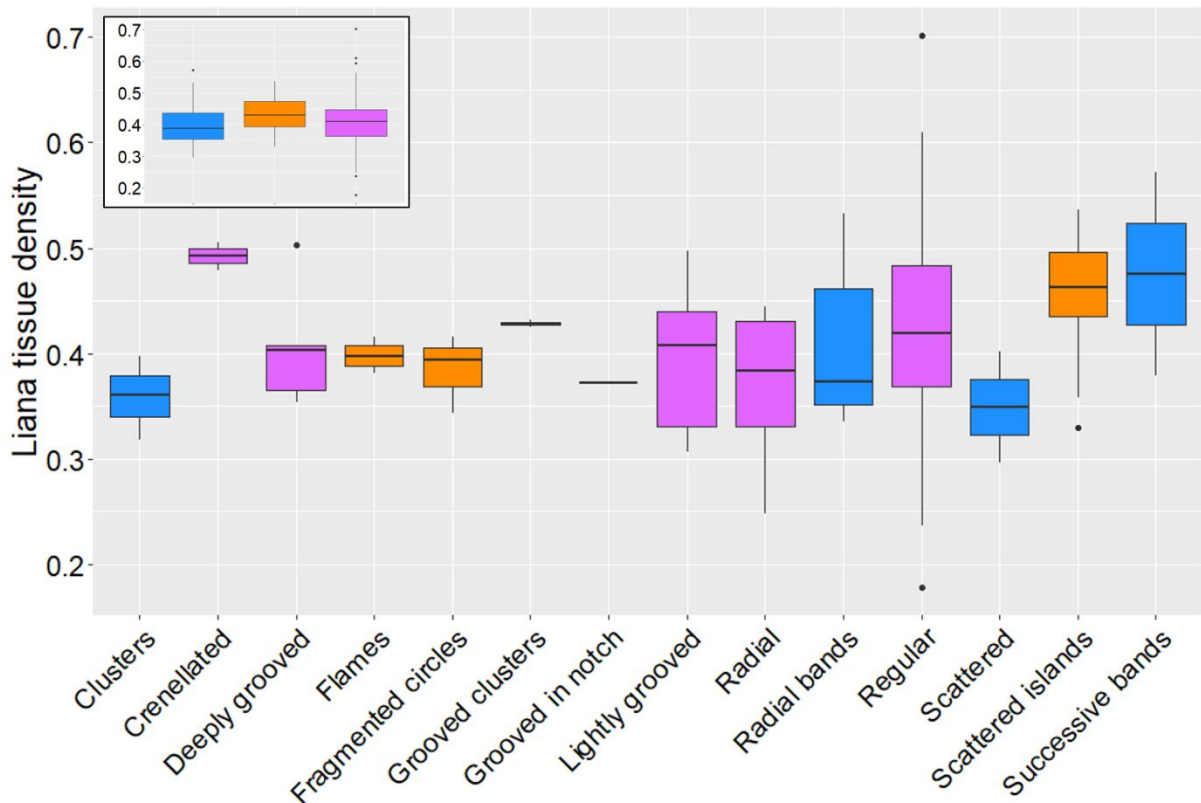
#### 4.1.2 Revisiting the notion of resilience through different growth – survival trade offs

In tree species, wood density is often used as a proxy for the trade-off between growth and survival (Poorter et al. 2010). Light-wooded tree species are characterized by rapid growth with high hydraulic conductivity efficiency (low vessel density and wide vessels), whereas hard-wooded tree species generally have smaller vessels but higher survival and resistance to disturbance through high resilience to embolism and mechanical strength (Poorter et al. 2010; Van Gelder, Poorter, and Sterck 2006; Putz et al. 1983). Concerning the “growth proxy” part through associations of wood density and

hydraulic traits, we found similar significant relationships with lianas. Consistent with other studies, liana wood density was significantly related to water flow (De Guzman et al. 2021; Ewers, Fisher, and Chiu 1990; Meunier et al. 2020). Light-wooded liana species had significantly lower densities ( $cor=0.36$ ,  $p\text{-value} < 0.001$ ) and wider vessels ( $cor=-0.5$ ,  $p\text{-value} < 0.001$ ). However, this negative relationship between wood density and hydraulic efficiency (van der Sande et al. 2019) was not systematic for all liana species, e.g., Zhang et al. (2023) found one species with extremely wide vessels but not light wood. In addition, some studies have found no relationship between wood density and stem vulnerability to cavitation (De Guzman et al. 2021). Wood density appears to be related to “growth” through hydraulic efficiency, but perhaps not to hydraulic safety or mechanical strength. The concepts of vulnerability and resilience are not the same in lianas as they are in trees.

Mature and adult non-self-supporting lianas, which rely primarily on flexibility, have different mechanical properties than mature and adult self-supporting trees that rely on stability and strength (Rowe and Speck 2005). Lianas and trees have been found to have the same range of wood density values (Putz and Holbrook 1991; Meunier et al. 2020), but they exhibit significant differences in bending, torsion modulus, and rotation-to-break characteristics (Putz and Holbrook 1991). The ability of lianas to resist disturbances and constraints and to survive depends on their complex and heterogeneous stem anatomy, which favors flexibility over stiffness and toughness over strength (Rowe, Isnard, and Speck 2004; Caballé 1998; Putz and Holbrook 1991). We found no relationship between liana tissue density and the phloem/xylem ratio or heterogeneity index. We found that liana tissue density was similar among cambial variants, regardless of whether they had a uniform, internal phloem, or compound wood structures (Figure 11). Flexibility and a higher proportion of “soft” tissue with more complex anatomical stem configurations appear to be the primary mechanisms by which lianas, unlike trees, avoid the effects of disturbance. Therefore, wood density should be used with caution when studying lianas, as it can reflect hydraulic efficiency, but is not fully related to survival. Thus, for lianas, wood density might also not be related entirely to longevity as it is for trees, where they are positively related (Laurance et al. 2004).

Nevertheless, we found a significant positive relationship between juvenile wood of liana species and the tissue density of lianas ( $cor=0.17$ ,  $p\text{-value}=0.048$ ). Indeed, tissue density may play a more important role in the early life strategies of lianas during their self-supporting phase, than in the resilience of mature and adult lianas, by providing rigidity and stability to standing young stems before their attachment and shift in growth form.



**Figure 11.** Distribution of liana tissue density values across liana cambial variants. Uniform, internal phloem and compound wood lianas are in pink, orange and blue respectively.

#### 4.1.3 Early life strategies

We found a strong significant relationship between the liana pith and juvenile wood proportions ( $R^2=0.32$ ). Though pith is usually a parenchymatous tissue with little mechanical stiffness, it has been found in some studies to stiffen and rigidify stems indirectly by acting as a geometrical spacer for stiff tissues and thus increasing the rigidity efficiency of the wood cylinder (Mahley et al. 2018; Olson et al. 2018). This feature has recently been shown to be a key trait describing the reach of liana searchers (the maximum distance of self-supporting stems before attaching to a host or losing their self-supporting habit; Hattermann et al. 2022). They found that lianas with larger piths tended to have longer reaches of searchers. Juvenile wood has also been found to increase the maximum length of searchers before finding a support to climb on (Ewers and Fisher 1991) including higher proportions of juvenile wood when there is a scarcity of hosts (Rocha et al. 2022). We found that larger areas of pith and juvenile wood were contrasted against high heterogeneity and mixed wood proportions associated with decreasing stiffness, likely providing elasticity to allow twisting and bending (Rowe, Isnard, and Speck 2004; Angyalossy, Pace, and Lima 2015). Those lianas, which are composed of complex cambial variants (internal wood and compound wood structure lianas), are potentially less

vulnerable to disturbance, with thicker external tissues ( $R^2=0.20$ ) and a high strength of recovery after injury (Fisher and Ewers 1989, 1991).

Overall, we show that lianas can have two different early life strategies: either a long self-supporting phase with high juvenile growth with long reach and stiff searcher stems, or small or no self-supporting phase and short searcher stems, enhancing their flexibility through mixed wood and heterogeneous tissue configurations, and are less vulnerable to disturbance. Liana species expressing more juvenile characteristics might therefore be more inclined to thrive in environments with a scarcity of hosts or large trees and closed-canopy forests, where they will need long and stiff searcher stems to climb and will be spared from frequent disturbances as large trees are less exposed to natural disturbances. In contrast, liana species that prefer to express their adult properties more quickly and choose flexibility over stiffness in their early life might be more adapted to disturbed environments with an abundance of hosts of multiple sizes and forms in open-canopy forests (Rowe and Speck 2005).

#### 4.1.4 The main ecological strategies of lianas, in phylogeny, and their distribution along local forest structure gradients

The association of leaf and wood anatomical traits of lianas revealed two principal strategy axes, along which liana species and cambial variants were distributed. The first strategy axis was mostly related to the leaf acquisitive-conservative trade-off, similar to trees, known as the leaf economic spectrum (LES; Wright et al. 2004; Baraloto et al. 2010). Consistent with other liana trait studies (Liu et al. 2023; 2021), liana species varied in their strategy of carbon and nutrient use from high nutrient acquisition rates (high SLA and %PO<sub>4</sub>) to expensive structures (high leaf carbon rate and tissue density). Except for internal phloem wood lianas, which generally appear to have more conservative strategies, liana wood structure types and cambial variants seemed to be randomly distributed along the carbon-nutrient acquisition rate gradient. The second strategy axis was mostly related to liana wood resilience to disturbance and the hydraulic efficiency-safety trade-off, similar to the known wood economic spectrum for trees (WES; Baraloto et al. 2010; Chave et al. 2009). Interestingly, this gradient contrasted species with high water-flow efficiency (high mean vessel area) to species with high mechanical and hydraulic safety (high vessel density, heterogeneity index, and P/X ratio), but both ends of the efficiency-safety trade-off were coupled with other acquisition or resilience strategies. Species relying on survival were positively associated with high leaf photosynthesis rates through high leaf nitrogen concentrations, and species relying on growth were positively associated with thick external tissues likely offering protection to vital tissues. This illustrates the potential capacity of liana species to preserve high efficiency as well as a safety strategy through different mechanisms.

Both strategy axes exhibited significant phylogenetic signals along the liana species phylogeny, suggesting that the existence of these strategies was partly related to phylogenetic constraints. However, only the variation of strategies associated with the LES was significantly influenced by the local forest structure gradient. Tall and closed canopy forests with large and hard-wooded trees tended to be significantly more associated with liana species with more conservative strategies favoring leaf longevity and investment in leaf and stem structures. However, the diversity of strategies associated with WES, water use, and resilience to disturbance appeared neutral to local environmental gradients. Other studies have found significant variations in liana wood functional strategies along hydrological gradients (Rocha et al. 2022), but we used different anatomical traits related to liana cambial variants, and our study area is abiotically homogeneous. Our results suggest the coexistence of a diversity of liana wood strategies that are not influenced by local forest structure shifts. Further research with traits more related to liana life histories such as ours and along more contrasting abiotic gradients, and comparison of liana trait space between different study sites might help us better understand whether the environment truly shapes liana functional composition and their dynamics over time.

#### 4.1.5 Coordination between leaf and wood traits

Contrary to other studies on liana traits, we found significant coordination between leaf, stem, and hydraulic traits (Medina-Vega et al. 2021; van der Sande et al. 2019; Liu et al. 2021; Rocha et al. 2022). The first axis of the multivariate leaf and wood PCA was mostly associated with LES, whereas the second axis was associated with WES, but both included wood hydraulic and leaf photosynthetic rate traits, respectively. Moreover, there were significant bivariate associations between leaf and wood traits related to water use and mechanical strength strategies. The leaf trait mainly associated with almost all wood traits was leaf nitrogen content (%N), which was positively associated with hydraulic safety (high vessel density) and resilience to disturbance (high heterogeneity index and phloem/xylem ratio). This is inconsistent with previous studies that have found leaf nitrogen content to be mostly related to efficient water flow (Zhu and Cao 2009; De Guzman et al. 2016). However, other leaf gas exchange traits (%PO<sub>4</sub>, SLA) were positively associated with hydraulic efficiency (high mean vessel area) and negatively associated with tissue density, consistent with van der Sande et al. (2019), who found a positive relationship between hydraulic efficiency and gas exchange rates, but a negative relationship with wood density. Nevertheless, they found no significant relationships between hydraulic safety and any other liana traits and suggested unknown mechanisms for lianas to determine hydraulic safety and local-scale abundance (van der Sande et al. 2019). As discussed in Section 4.2.2, we believe that for lianas, safety is more related to stem flexibility and resilience to injury through mechanical strength as well as hydraulic safety. We found that liana wood density, commonly

used as a proxy of “safety and survival” in most studies (van der Sande et al. 2019; Rocha et al. 2022; Medina-Vega et al. 2021), is only related to water-use efficiency and leaf nutrient acquisition traits. The divergent results between our studies might be related to the choice of appropriate traits used to describe the different liana life strategies.

Overall, our results suggest that liana species express a large diversity of strategies using different methods to maintain high nutrient acquisition, as well as safety measures to survive. This gives lianas a relative advantage over trees who cut heavier compromises between efficiency and safety (Fortunel, Fine, and Baraloto 2012; Zhang et al. 2023; Medina-Vega et al. 2021). Interestingly, we found no significant associations between liana self-supporting early life strategy traits (pith and juvenile wood) and other liana traits. One explanation is that the early life strategies of lianas are less taxon-specific and more dependent on the direct local environment of the liana during its self-supporting host-searching phase (as observed for *Salacia laurentii* or *zenkeri*, where two stems of the same diameter have completely different early tissue expressions; see below section 4.2.2). The plasticity of the expression of early life strategies by liana species and the co-existence of diverse liana wood strategies might explain their abundance, dynamics, and survival in a multitude of different environments worldwide.

## 4.2 Functional categorization of wood structures and cambial variants

### 4.2.1 Ontogenetic conservation and plasticity

After removing species for which only a single specimen was collected (24 out of 66 species), we found that 26 out of 42 species (i.e., 62% of species with more than one specimen collected) had the same type of cambial variants as categorized in this study. Cambial variants are generally taxon-specific, and some families are known to display a specific cambial variant (G. Caballé 1986), such as the Menispermaceae, in which all species appear to have a compound wood with successive cambia and wide rays (Angyalossy et al. 2012; Carlquist 1996; Mennega 1982; Ortiz, Kellogg, and Van Der Werff 2007). We also found that species belonging to the Menispermaceae family (*Tiliacora sp1* and *Triclisia macrophylla*) within our sample show the same cambial variant (“radial bands”). Indeed, the first study that was able to reconstruct the evolution of stem ontogeny of the genus *Paullinia* found that, with the exception of successive cambia (pertaining to the successive and radial band cambial variants), all other cambial variants of *Paullinia* had evolved multiple times, suggesting an evolutionarily labile process generating cambial variant origins for all other species (Chery, da Cunha Neto, et al. 2020).

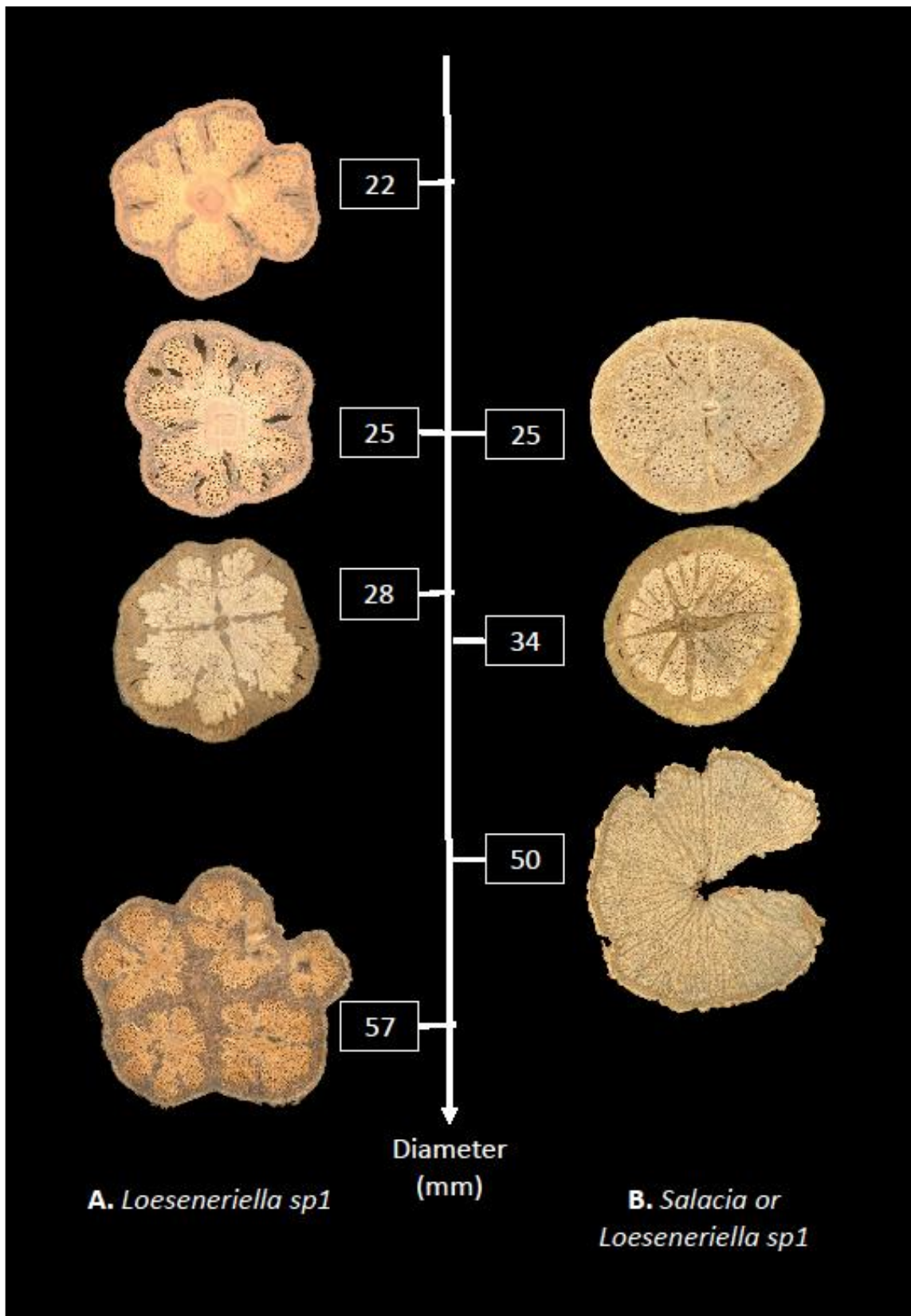


Out of the total of 42 species, we found that 16 species had different cambial variants (none with successive or radial bands), with all forms belonging to the labile forms identified by Chery et al. (2020). In particular, we noted that only Celastraceae species had cambial variants from different wood structure categories (Figure 12 and 13), whereas the other 12 species had different forms, but all had a uniform wood structure. During evolution, the cambium appears to maintain the plasticity potential of species' growth forms (Rowe and Speck 2005), varying depending on cambium type and development (Angyalossy, Pace, and Lima 2015). While the initial developmental steps are common to almost all forms (Chery, Pace, et al. 2020) —uniform and regular activity of the cambium around the entire stem circumference during the juvenile phase—the subsequent anatomical development may differ profoundly.

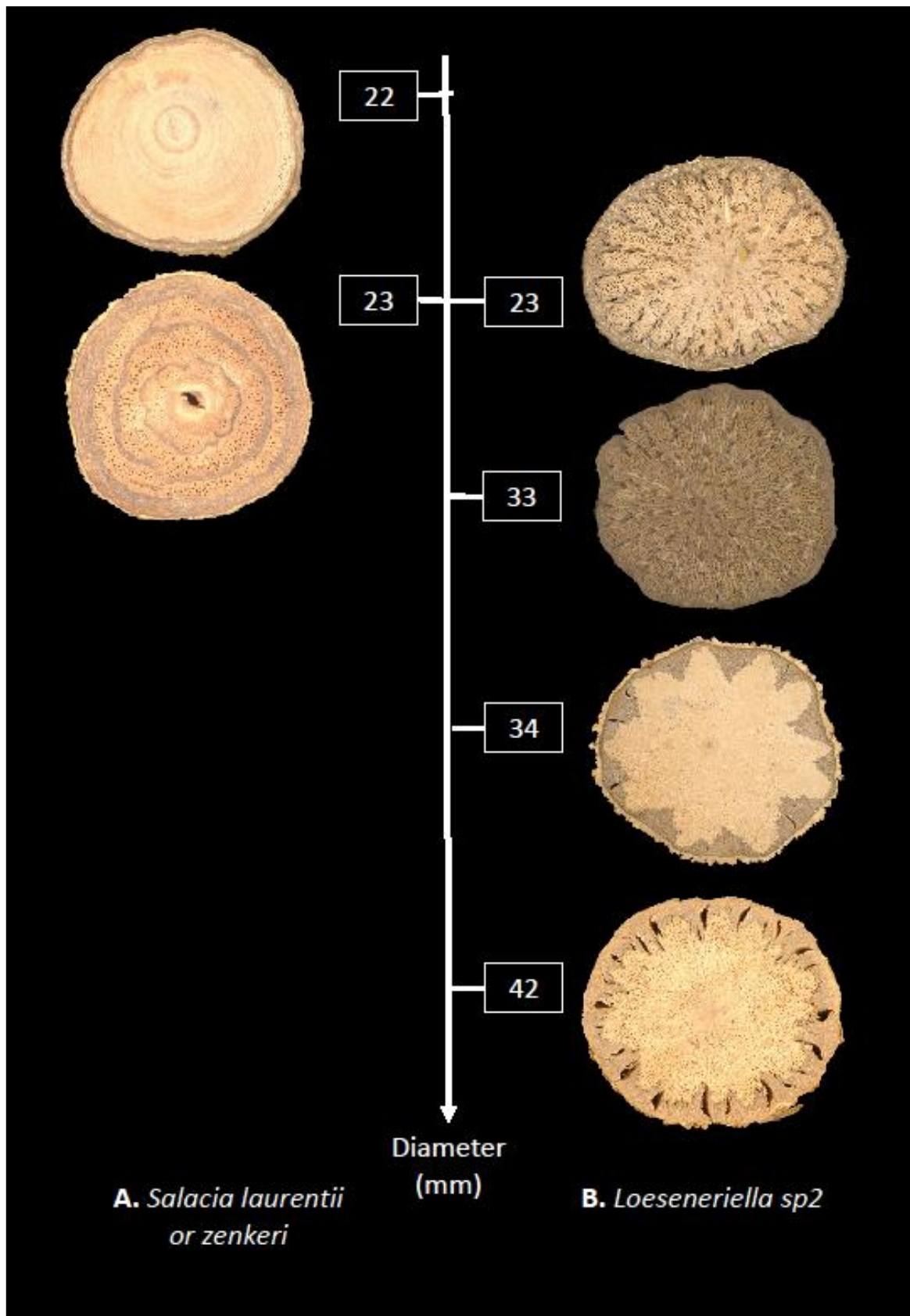
We found a tendency that species with a continuous cambium (uniform wood structure) might be capable of developing phloem wedges and rays, but maximum anatomical development in terms of stem size and complexity is less extensive compared with species that develop discontinuous or multiple cambia (Angyalossy, Pace, and Lima 2015; Chery, Pace, et al. 2020). Species that develop discontinuous or multiple cambia (internal phloem and compound wood structures) have the tendency to anatomically develop more “compartmentalized” mature stems.

#### 4.2.2 Variability modified by the environment

Looking more closely at the variability of the cambial variants of the four Celastraceae species, we noted that in two of them the level of compartmentalization increased with diameter (Figure 12) *Loeseneriella sp1* showed a uniform wood with deep grooves, a compound wood with clusters, and finally a scattered cambial variant. However, the other two Celastraceae did not increase in complexity with diameter (Figure 13) but showed different cambial variants regardless of diameter. In *Salacia laurentii or zenkeri*, there were two individuals with approximately the same diameter but with completely different anatomical stages of development. The first specimen with a diameter of 22 mm had almost only juvenile wood and no expression of cambial variants, whereas the second specimen with a diameter of 23 mm had a very small juvenile wood and displayed an internal phloem wood with fragmented circles. While the existence of a juvenile phase seems to be ontogenetically similar to all lianas (G. Caballé 1998), the timing of its expression is likely dependent on the spatial contingencies and time required to find support (Rowe and Speck 2005) in the surrounding environment (Soffiatti et al. 2022) as well as the maximum diameter of juvenile wood a given species is able to develop.



**Figure 12.** Different cambial variant development in stems of the same species with increasing compartmentalization with diameter. (A) *Loeseneriella sp1* (B) *Salacia or Loeseneriella sp1*.



**Figure 13.** Different cambial variant development in stems of the same species with different compartmentalization levels with (A) similar diameters, *Salacia laurentii* or *zenkeri* and (B) with increasing diameters, *Loeseneriella* sp2.

In addition, cambial variants that result in greater flexibility in the mature and older parts of the liana stem may be a mechanical strategy for the liana to adapt to unstable environments, favoring resilience and survival (Rowe and Speck 2005). In the field, for example, we observed that damaged *Loeseneriella sp.1* exhibited a compound, scattered form that split into several separate strands at the site of injury and subsequently reformed as a single stem (personal observation; Appendix 3), which was also observed by Caballé (1986) on *Loeseneriella* and demonstrated by Fisher and Ewers (1991) with experimentally induced injuries. Few studies, such as Fisher and Ewers (1991), have reported the different repair mechanisms and damage shown by cambial variants. For example, lianas with “radial” microanatomy as characterized here tend to rupture along the rays and then autorepair by parenchymal proliferation until the separated xylem tissues are united (Fisher and Ewers 1989).

In our study area, we found that 86.2% of the liana community showed development of cambial variants, but only 14.5% showed compartmentalized forms with internal phloem or compound wood structures. In contrast, a rather different proportion was observed by Caballé in a northeastern forest in Gabon where 42% of lianas showed internal phloem or compound wood structures, and only 56% of the lianas had cambial variants (G. Caballé 1986). However, one very real factor influencing efforts to “characterize” representative cambial variants is the role that the environment plays in changes made to stem development making it even more difficult to determine the originally distinct cambial variant and the life history of lianas.

Our results indicate that when mature liana stems are collected at a community scale from a given natural setting, differential responses and resistance and repairs to damage associated with each cambial variant occurs readily. This suggests that any interpretation of macro-anatomical organization at the community level must take into account (1) evolutionary diversity of cambial variants as well as interspecific variation and (2) the fact that both ontogeny and environment significantly influence the expression of cambial variants. These potentially might influence the values of all anatomical based trait measurements on liana stems.

#### 4.2.3 Identification and collection

Our collection of mature liana stems at 1.3 m following recent protocols (Gerwing et al. 2006; Schnitzer, Rutishauser, and Aguilar 2008) also aimed to *a priori* minimize ontogenetic variability and standardize developmental stage between individuals. In practice, however, because of the complex life histories of lianas we were not always able to distinguish forms due to life history events in the past —self-repaired organizations, branch nodes interrupting normal anatomy, or significantly different ontogenies and life histories, such as a long expression of juvenile wood to find a suitable

host against relatively early expression of cambial variant organization. We believe it is important to keep in mind when categorizing liana cambial variants, especially uniform wood structure variants, that different types are possibly labile and may differ slightly depending on the immediate environment and different physical conditions. These concerns can be addressed in well-documented species whose cambial variants such as *Menispermaceae* are more evolutionarily conserved.

Finally, while proving difficult to sample and interpret in terms of functional organization, the anatomical structures of liana stems can also serve as a tool for species identification when leaves are not present or visible and when flowers are not present (Caballé 1993). Although cambial variants are directly dependent on ontogenetic and environmental variability, they are key descriptive features of liana stem functionality because they provide different flexibilities to avoid breakage and repair mechanisms in the event of injury. Inferring functional anatomical traits from cambial variants to study ecological trends is a first step toward extending this approach to community ecology and, more precisely, exploring ecological strategies of lianas along environmental gradients.

## 5 Conclusion

This is the first study to link functional strategies with cambial variants and quantify their diversity within a forest community in North Congo. We have shown that in an abiotically homogeneous area, there is a co-existence and large diversity of liana cambial variants. Most stem and cambial variant diversity are associated with contrasting juvenile phase life histories and strategies relating to resilience, and hydraulic safety and security. Moreover, we found evidence that lianas had (1) coupled leaf and wood strategies to an extent and (2) the capacity to exhibit multiple strategies to maintain a relatively high growth as well as a strong survival capacity. At the species level, different ecological strategies were significantly associated with phylogenetic proximity. At the community level, local forest structure filtered liana species based on their leaf acquisition-conservation trade-offs, whereas there was a co-existence of all wood strategies, independent of shifts in local forest structure. We believe this study is a first step to make the link between individual and community scale studies. We also hope that it will help future studies to better understand how liana species are distributed through time and space and predict shifts under large-scale and drastic environmental constraints.

## 6 Acknowledgments

We thank the CIB-Olam logging company that host and greatly facilitates the work conducted in this site. Last but not least, we are specifically thankful to Patchely Mbondo and Cyril Dzebou for their invaluable help during the field missions. We additionally like to thank everyone who helped for the realization of this work. Sylvie Gourlet-Fleury for her guidance. Romain Lehnebach for his previous work on cambial variants. David Harris for his help with botanical identifications.

## 7 Author contributions

Conceptualization: B.K., M.R.-M. and N.R. ground data collection: B.K.; pre-processing: B.K., M.G.; formal analysis: B.K., M.R.M, V.R. and N.R.; leaf trait measurements: B.K., S.B.; wood trait measurements: B.K., M.G. and D.G.; writing (original draft): B.K. and N.R.; writing (review and editing): all authors.





## 6 General discussion and perspectives

An important challenge of my thesis was to explore and expand our knowledge of the ecology of lianas in northern Republic of Congo at different scales. At the individual/species scale, I studied different leaf and wood traits to better understand liana functioning. At the forest stand scale, I used cutting-edge drone technologies to understand how lianas spread over tree crowns and how it related to classical ground measurements. Finally, I combined trait measurements with field community-level data to understand the ecological drivers of liana assemblages. Here below, I summarize the main results associated with these approaches and discuss them in the context of the current literature.

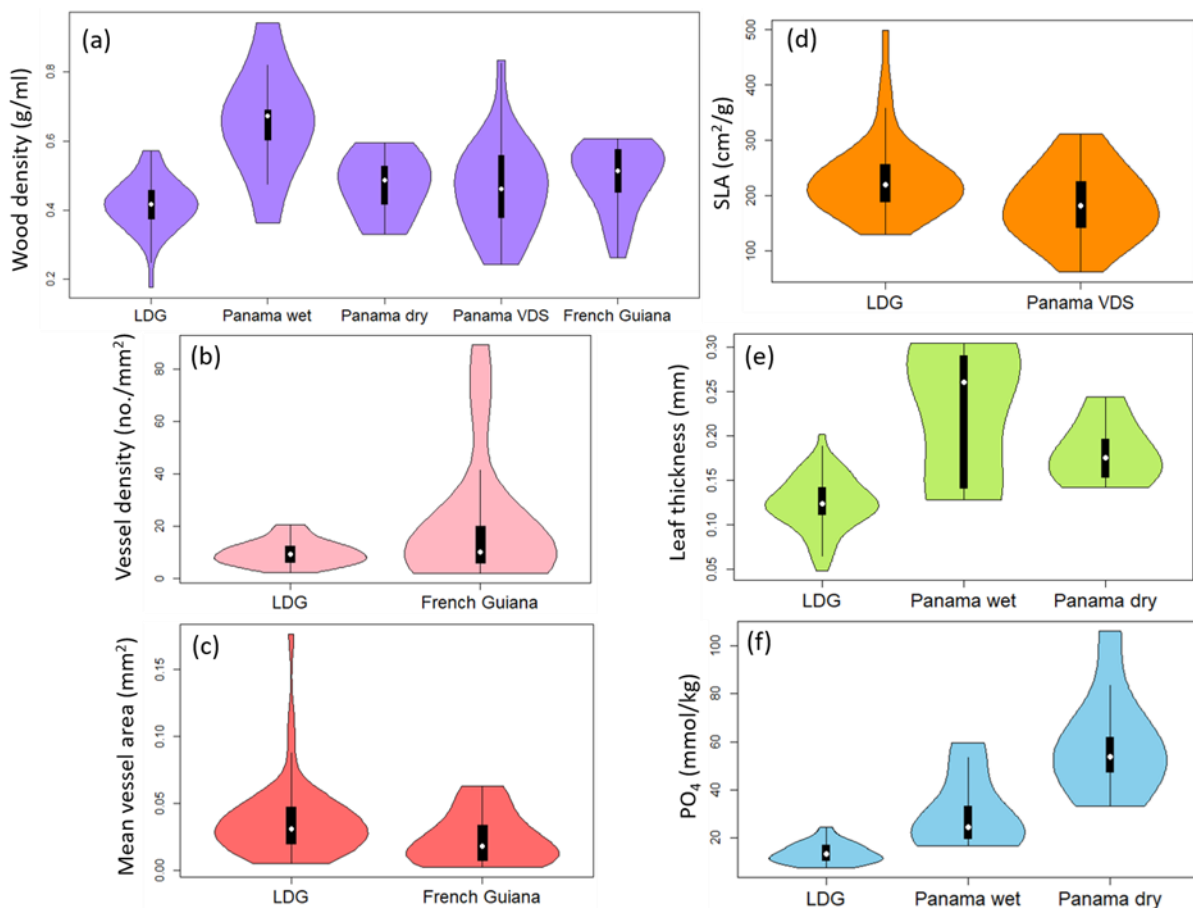
### 6.1 Understanding the role of functional traits and ecological strategies in liana species distribution

At the species level, my work has led to a better understanding of the potential of lianas to balance efficiency, safety, and resilience through different trade-offs among traits. There appeared to be three dimensions of strategies that liana species seemed to deal with: strategies organized along the classical leaf economics spectrum (related to resource acquisition), and two independent strategies that are more related to their woody structure with two apparent economic spectrums (chapter 3). Lianas can thus develop a wide array of functional adaptations linked to water-use strategies, mechanical resilience and flexibility in their juvenile and adult stages. Overall, more complex anatomical structures (cambial variants) tended to express a likely lower juvenile stiffness and not a particularly developed early-life strategy (self-supporting phase). Nevertheless, they tended to acquire a more likely flexibility and resilience to disturbance in their climbing phase through a higher combination of soft and stiff tissues in their wood cylinder. The characterization of this wide range of ecological strategies provided promising avenues for understanding the spatial distribution of liana species and their success in environments.

The environmental gradients studied (chapters 2 and 3) had only a weak influence on liana assemblage and functions, suggesting that the diversification of ecological strategies, especially wood-related liana strategies, occurred independently of forest structure, for instance. Leaf-related strategies were, to an extent, influenced by local forest structure. Functional shifts occurred along local forest structure gradients, favoring liana species with conservative strategies (higher wood density, lower SLA and %PO<sub>4</sub> values) in tall and dense forests. Floristic composition was, however, weakly related to changes in forest structure but the unexplained floristic variation was still associated



with functional changes, especially with the wood density community average. Lianas also showed a significant host specificity with tree species even if the mechanisms of specificity remained unclear. One hypothesis for the weak effect of the environment on liana species composition could be due to the highly homogeneous abiotic environment in our study area that was specifically designed to minimize environmental effects on silvicultural treatments (Figure 15). It is also possible that variation in forest structure is too local to observe environmental filters on liana strategies, notably due to the mass effect. This effect consists on the establishment of species in adjacent unfavorable habitats to their original habitat (Shmida 1984; Shmida and Wilson 1985), attenuating the effect of environmental filters on species composition when the environment is weakly aggregated in space (Réjou-Méchain and Hardy 2011; Zelený, Li, and Chytrý 2010).

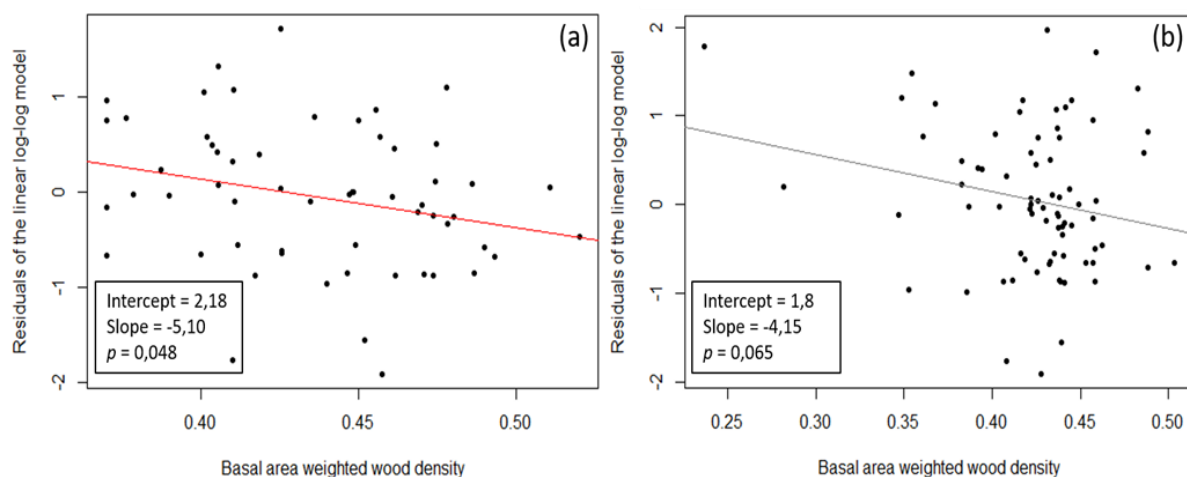


**Figure 15.** Additional preliminary analyses, comparing open-access liana traits from different studies, reveal that mainly liana wood density, leaf thickness and leaf phosphorus content differed between our study site (LDG) and others, suggesting either biogeographical or environmental effects on these traits. Wood density (a), wood vessel density (b) and mean vessel area (c) for stem traits, and SLA (d) leaf thickness (e) and %PO<sub>4</sub> (f) for leaf traits are illustrated. LDG (Loundoungou) is our study site in northern Congo; Panama wet and dry are trait values from Medina-Vega et al., (2021) in a wet and

dry forest respectively; Panama VDS is trait values from van der Sande et al., (2019); and French Guiana is trait values from Meunier et al., (2020).

Another hypothesis for the weak relationship between environmental gradients and liana composition is the potentially important role of intraspecific variation in species traits (Violle et al. 2012). Indeed, contrasting intraspecific trait responses can occur along environmental gradients, with sometimes contrasting responses between and within species, potentially blurring the link between environment and plant functional composition (Kichenin et al. 2013). Considering intraspecific variability could even better reveal habitat filtering to detect mechanisms underlying niche differentiation (Jung et al. 2010). According to Albert et al. (2011) who reviewed under which conditions intraspecific trait variability should be considered, local scale studies with a homogeneous environment and a focus on response traits should account for the intraspecific variability of traits. Under local environmental gradients, species turnover might be lower than intraspecific variability, which can be greater because of both phenotypic variability (genetic adaptation) and/or phenotypic plasticity (environmental acclimation). However, the extent to which lianas exhibit functional plasticity along environmental gradients is unclear and would require a much larger amount of trait measurements than were made in my work (see below discussion section 6.3.), although I observed that shifts in functional strategies likely occur during ontogeny and contribute to individual intraspecific trait variations (chapter 3). Indeed, the values of stem traits measured for a given liana stem depend largely on the extent of development of the juvenile phase of that liana (Rowe and Speck 2015). In lianas, the transition from the juvenile to the adult stage results in changes in wood density, vascular characteristics, and tissue configurations to adapt to the new mechanical demands of the lianescent habit (Fisher and Ewers 1991; Rowe and Speck 2005). Because most liana species exit their juvenile stage when they attach to a host and begin climbing (Soffiatti et al. 2022), their time of expression, i.e., the extent of the juvenile phase, could depend on local environmental variables and influence the complex plasticity and intraspecific variation of traits within liana species, and within individuals depending on the ontogenetic stage (Nesheim and Økland 2007; Obaton 1960; Putz and Holbrook 1991; Rowe and Speck 2005). Also, as observed in my study, not all liana species tend to exhibit or even develop a juvenile, self-supporting phase, suggesting varying degrees of plasticity within and between liana species (Rowe and Speck 2015). Further studies in more heterogeneous environments and considering intraspecific variability in species traits along stronger environmental gradients are needed to better highlight the mechanisms responsible for the spatial distribution of liana species (see below discussion section 6.3.).

At the forest stand level, combining ground and drone-based data helped reveal that, while liana infestation of tree crowns depended on tree height and the amount of lianas climbing on them, liana leaves spread over crowns was also influenced by the functional identity of lianas, especially by their tissue (wood) density (chapter 1). Liana species with lower wood density for a given diameter tended to allocate more biomass to leaves, resulting in greater leaf coverage than expected over tree crowns. However, it still appears to be quite difficult to uncover strong ecological patterns at the community level, as a reanalysis of this relationship with an extended wood density database, considering additional liana species (as described in Chapter 3), highlights that a larger amount of trait data is needed to draw robust inferences (Figure 16).



**Figure 16.** Relationship between the basal area weighted liana wood density measured and collected (a) in 2018 for 20 liana taxa and 57 trees, and (b) in 2021 for 33 liana taxa and 76 trees, with the residuals of the selected linear model predicting liana leaf coverage over tree crowns from total liana basal area climbing on a tree (see details of the method in chapter 1). The red (significant slope) or grey (non-significant slope) lines illustrate the predicted linear model between the two variables. This additional analysis highlights the difficulty of identifying community patterns without a high sampling effort of liana traits, suggesting either a considerable intravariability of liana species wood density or/and much greater complexity of liana functioning system and ecological strategies.

## 6.2 Better interpreting the meaning of traits

Community ecology has evolved over decades through the lens of functional ecology, and trees were by far the most studied group in tropical forests. As a result, there is a tendency to take the “easy way out” when considering liana communities, and to apply terms and shortcuts developed

for trees, hypothesizing that trees function in the same way as lianas. Therefore, the main traits used to understand the functioning, coexistence, and distribution of trees were mainly used to study the functioning and distribution of lianas as well (Poorter et al. 2010; Van Gelder, Poorter, and Sterck 2006). However, compared to trees, lianas have not been studied as much, and there is a gap in data and knowledge about the shortcuts and proxies between plant traits and performance that already exist in trees (King et al. 2005; Curran et al. 2008; Falster 2006). In addition, lianas are physiologically different from trees due to their climbing habit and therefore could have a relatively different functioning. In my thesis I have tried to use new traits related to liana physiology, such as for instance the heterogeneity index, phloem/xylem ratio in the wood cylinder, or juvenile wood area (see details in chapter 3). However, these macro-anatomical traits are still considered as shortcuts, as they represent proxies for a mechanical property of the liana stem that is not directly measured. For instance, the heterogeneity index is hypothesized to represent the stress dissipation and fracture point stopping ability of the stem; the phloem/xylem ratio likely translates the elasticity/stiffness of wood and also fracture point stopping (Dobbins and Fisher 1986; Fisher and Ewers 1989; Fisher and Ewers 1991); whereas juvenile wood is expected to reflect the cost of the self-supporting phase and the investment into a stiff initial stem structure (Fisher and Ewers 1991; Rowe, Isnard, and Speck 2004; Rowe and Speck 2005). While I used these traits to study different liana life strategies, such as the resilience to disturbance through the heterogeneity index and phloem/xylem ratio, I did not test if these functional traits were actually related to the ability of lianas to survive or recover after disturbances (the same analogy can be said for vessel area and density and direct measurements of water conductance and xylem cavitation, related to hydraulic efficiency and safety).

To establish and improve our understanding of the relationships between “more accessible” functional traits of interest for lianas (such as done in my thesis) and their actual biological function within the plant, there is a need for further studies investigating the mechanical and hydraulic properties associated with trait variations. Although studies like this exists at the species level for lianas, they are still rare, especially at the community level (Gallenmüller et al. 2001; Gallenmüller, Rowe, and Speck 2004; Ménard et al. 2013). To move forward, I would suggest simple mechanical approaches, such as the three-point bending measurements, to acquire a quantitative measure of the elasticity and toughness properties of liana species stems in a community (Ménard, McKey, and Rowe 2009). Measures such as Young’s elasticity modulus (translating the flexibility of the stem, with stiffer stems with increasing modulus) can thus be used at the community level (i) as a functional trait, attributing a mean elasticity value to liana species and study spatio-temporal composition variations, (ii) to create proxies between elasticity and the development of different stem tissues and cambial variants using cross-sections, and (iii) to explore the role of ontogenetic variations, especially during

the transition from juvenile to climbing stage of lianas and the importance of intra-individual specific variations, by measuring the elasticity modulus of different segment of an individual (from the searching stem tips not yet attached to the more mature climbing stem). Especially for lianas, intra-individual specific variability of mechanical properties during ontogeny needs further attention considering that there might be significant differences in stiffness and elasticity between the self-supporting searcher stem and the climbing stem, as revealed by Soffiatti et al. (2022) and shown by Ménard et al (2009) for climbing stems above 1 cm in diameter after anchorage. Moreover, the role of these mechanical properties and other anatomical functional traits in the resistance and resilience of liana stems to disturbances could be tested through (i) simulations of controlled disturbances such as the experiments by Fisher et al. (Dobbins and Fisher 1986; Fisher and Ewers 1989; Fisher and Ewers 1991) to test how much of the liana stem is functional after damage by their degree of heterogeneity for instance, and (ii) field observations and measures in different disturbance field situations (see perspectives, section 6.4.2.).

### 6.3 Bridging scales, limits and suggestions

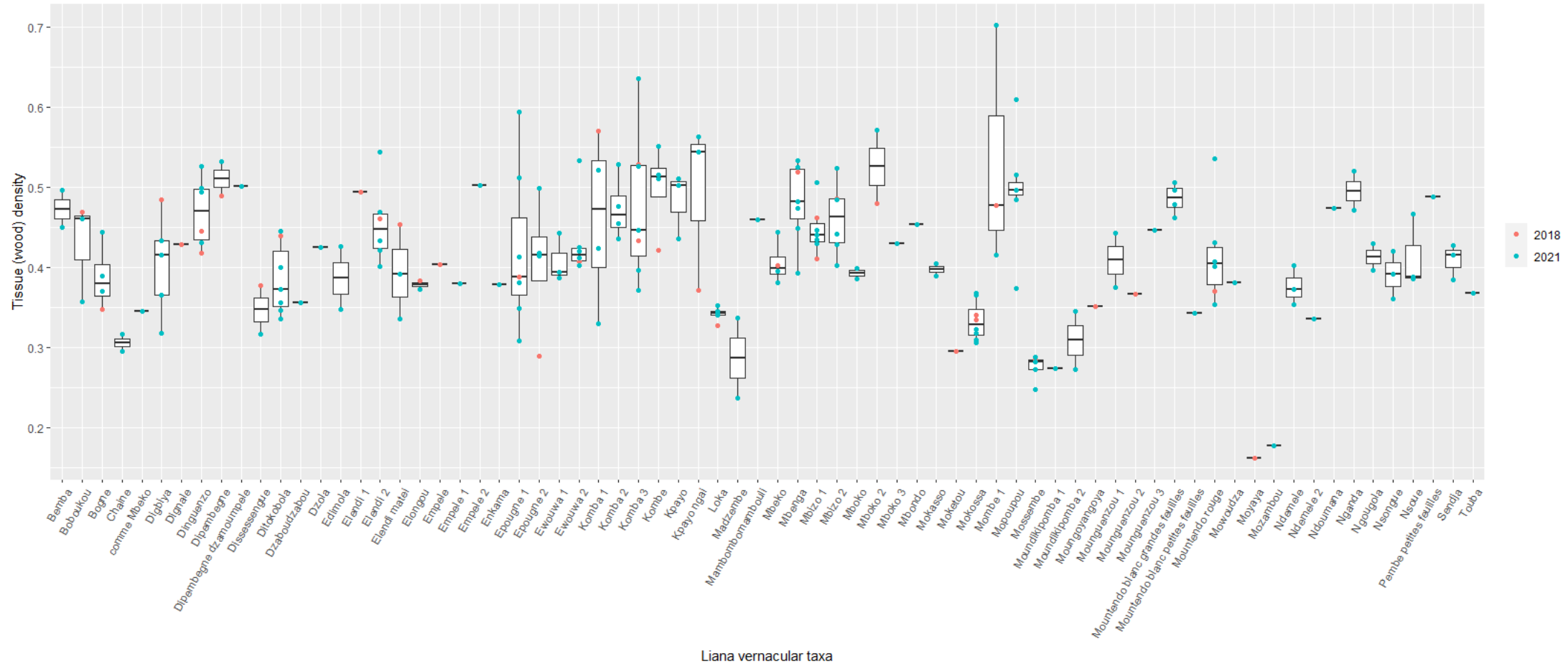
We need a better mechanistic understanding of the functioning and ecology of lianas to make progress in understanding their spatial and temporal distribution in different environments. Previous studies revealed inconsistent results at the community-scale, whether in the factors that influence their structure or composition patterns in different environments (Ledo and Schnitzer 2014; Dalling et al. 2012; Gerolamo et al. 2018; Liu et al. 2021; Lomwong et al. 2023; DeWalt et al. 2006; Rocha et al. 2022), or in their dynamics over time (Ingwell et al. 2010; Laurance et al. 2014; Phillips et al. 2002; Bongers et al. 2020; Thomas et al. 2014; Caballé and Martin 2001). For instance, whether liana abundance is actually increasing globally due to increasing CO<sub>2</sub> and rising temperatures is still subjected to debate (Stefan A. Schnitzer and Bongers 2011). These inconsistencies have led to a need to deepen our understanding of the ecology of lianas at the species level and to link it with community level patterns, increasing the use of different approaches, in particular through the lens of functional ecology and with emerging remote sensing technologies.

Bridging scales between species-level and community-level studies are necessary to fully understand the life history of lianas and to provide a more accurate idea of the role of individual functional traits and the mechanisms underlying community patterns (Levin 1992; Swenson 2013). For instance, at the community level, liana tissue (wood) density indicated more resource conservative strategies as the forest matured, with increasing wood density values associated mainly with tall and dense forests, characteristic of late successional stages (see chapter 2). At the species level, we were

able to confirm that hypothesis through the significant associations between wood density and water-use and nutrient acquisition strategies, especially with vessel area (see chapter 3). Bridging scales helped us better understand the physiological characteristics underlying liana performance along forest structure gradients. Through different trait relationships, we were also able to reveal that wood density did not tend to be related to anatomical heterogeneity traits, standing for the flexibility ability and resistance/resilience to disturbances of liana stems. Individual approaches such as trait measurements are needed to first create a database of liana species ecology and explore traits relationships and variations within and between species (for environmental plasticity or ontogenic variations), as has been done for trees in recent decades (Jung et al. 2010; Kichenin et al. 2013; Garcia et al. 2022; Maracahipes-Santos et al. 2023; Falcon-Lang 2005; Laforest-Lapointe, Martínez-Vilalta, and Retana 2014), and then help explore key variations and movements in liana composition at the community level, using some key traits as proxies for specific liana life strategies and functions (Kneitel and Chase 2004). However, the difficulty remains in reaching the community level. At large scales, such as in my thesis, it still seems difficult to fully account for liana functional strategies and traits and to capture finer variations in functional composition (see discussion, section 6.1.).

During my thesis I used functional traits to link individual functional and anatomical characteristics with community assembly patterns, but still encountered many limitations. Even if I was able to collect at least one individual per liana species, representing more than 95% of liana stem individuals at the community level, sampling replications for each species was very difficult, and led to low replications of traits for each species. For instance, for stem traits, I collected in total 207 stem samples (2018 and 2021) belonging to 72 liana taxa but with only 2.9 samples per species on average, for minimum 1 sample and maximum 8 sample per species. The coefficient of variation (CV) of wood density measures by species varied between 2.0 to 28.3% (11.2% in average), with very contrasting variations for species with high replication rates (7.1% of CV with 8 samples of Mokossa, *Manniphyton fulvum*; and 23.5% of CV with 7 samples of Epougne 1, *Millettia psilopetala*). The effect and role of intraspecific variations of traits and their potential plasticity cannot be assessed accurately with low replication rates per species (Figure 17). It has been suggested by multiple studies that at least 10 individuals per species are necessary to consider intraspecific variability and detect species based on their traits (for trees; Baraloto et al. 2010; Hulshof and Swenson 2010). However, selecting random individuals with a high replication rate per species as recommended (Albert et al. 2011), selecting climbing individuals (not in their juvenile phase) to minimize ontogenetic variation (trait variation within individuals), and limiting the search for species outside of permanent observation plots due to the destructive aspect of the method are extremely difficult and time consuming as we are completely dependent on what is available in the field. Moreover, the botanical identification problems at the

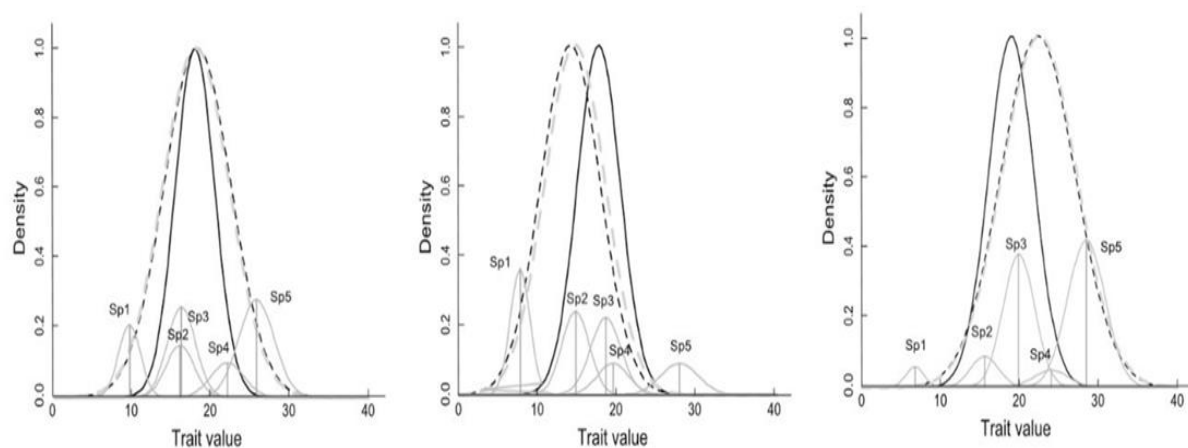
community level forced me to take mean values for several liana vernacular taxa representing different species, which might have also emphasized the effects of species-specific variability of trait values. Lastly, because of the difficulty of identifying liana leaf coverage over tree crowns by species (with drones), the link between functional traits or structure measures such as basal area (see chapter 1) and liana distribution in canopies was based on community weighted means, translating tendencies more than actual relationships.



**Figure 17.** Intraspecific variability of wood density measures of liana species from stems collected in 2018 and 2021 (see details in chapter 2). The figure illustrates the lack of replications for multiple species and the large variability that can occur within some species (such as “Komba 1” or “Mombe 1”) and between vernacular taxa belonging to different botanical species (such as “Epougne 1” and “Epougne 2”). It highlights the need to i) improve botanical identifications and ii) increase the number of trait measurements per taxa as to better consider the role of intraspecific variation in community level processes.



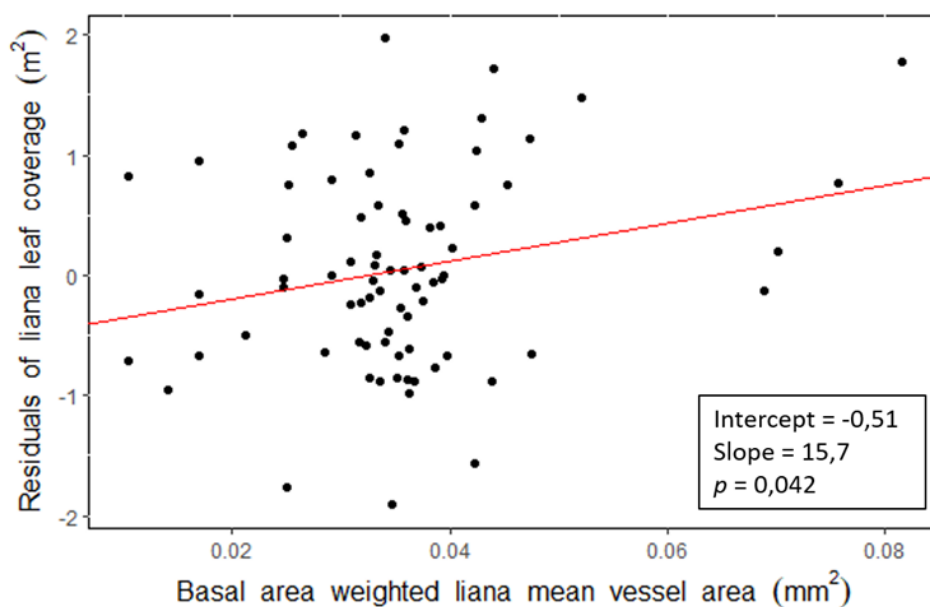
To improve the link between species- and community-level patterns, I propose (i) further studies on the role and importance of intraspecific variability in liana species traits along environmental variables, but also along different ontogenic stages (intraindividual variability). Since the classical traits used to describe tree species performance may not be the most relevant for lianas (Liu et al. 2021), I would recommend focusing on traits more related to liana life history, i.e., stem traits and especially traits related to juvenile stage or flexibility (the heterogeneous character of liana stems). Because of the difficulties mentioned above in finding large numbers of individuals to sample and measure, I would recommend focusing initially on a few focal species selected based on tradeoffs between abundance and representation of the functional diversity observed at the community level. Simplifying the liana community to a few dominant species does not mean that important trait variation is completely ignored, but can facilitate measurements in the field (Schnitzer et al. 2023). Simulations can also be used to quantify and test the effects of intraspecific trait variability on patterns of community assembly (Albert et al. 2011). In our case, we would need to create a combination of stochastic and deterministic simulation to account for trait variability and to account for both variability between individuals of a given species due to unclear mechanisms and within individuals due to the time of anchorage of the individual on a host and transition from the self-supporting to the climbing phase (see discussion section 6.1.; Albert et al. 2011). While simulations suggest that stochastic variability in traits has little effect when community-weighted means are used to examine community assembly (Figure 18), the effects of ontogeny may be more problematic if neglected (Albert et al. 2011).



**Figure 18.** Individuals trait values distributions for three simulation runs considering intraspecific trait variability stochastically (normal distribution) in back dotted curves and without in grey dotted curves. The full black curves represent species mean trait values distribution and highlight the small effect of intraspecific variability on community average. At the species level dissimilarities between species

seemed more affected by intraspecific trait variability (ITV). The illustration is taken from Albert et al. (2011) and modified. Trait values distribution within species (grey curves), density represents their relative abundance in the assemblage.

In addition, I would suggest (ii) the development of field methods and simplifications between traits. In particular, the development of new field methods for accessing different variables of interest for lianas, such as ontogenic developmental stage (through anatomy) or accessibility to light (through drone or terrestrial laser scanning), seems promising (van der Heijden et al. 2022). Determining their relationships to other functional traits of lianas, rather than just diameter as in currently available allometric methods, would also improve the use of proxies and scaling (Figure 19). Further studies to develop and better understand these relationships would help to better understand how functional traits and patterns vary with scale. Last but not least, to ensure complementarity of different approaches, whether with functional ecology or with ground or drone data, (iii) botanical identification of liana species remains an important challenge, especially when one wants to upscale individual-based approaches to the community level (Muller-Landau and Wright 2023). I believe that botanical knowledge of liana species deserves more attention, as it is an indispensable prerequisite for any study that seeks to elucidate the mechanisms underlying distribution patterns of lianas at different scales.



**Figure 19.** Additional preliminary analyses linking liana leaf coverage over tree crowns (from chapter 1) and macro-anatomical traits (from chapter 3) revealed that mean wood vessel area was the only trait significantly positively related to the spread of liana leaves over tree crowns. The figure illustrates the relationship between the basal area weighted liana wood mean vessel area and the residuals of

the selected linear model predicting liana leaf coverage from total liana basal area. It suggests that larger vessels tend to allow lianas to deliver more water to leaves more quickly (Hacke and Sperry 2001) and thus lead to potentially greater liana leaf development in the canopy. This trend highlights that traits related to stem water-use strategies, such as vessel diameter, might serve as promising avenues to calibrate relationships estimating liana leaf distribution in forest canopies.

## 6.4 Perspectives

### 6.4.1 Development of tools for the botanical identification of lianas

In all ecological studies based on plant species, the first and fundamental requirement is the ability to identify plant species. In central Africa, and particularly in North Congo, there is a critical lack of botanists, especially for recognizing liana taxa, despite strong traditional knowledge on plants. Furthermore, most regional floras are either botanical descriptions without pictures or based mainly on the reproductive parts of the plants that are sparsely available in the field. The difficulty of plant identification from the field and the accessibility of local identification books can sometimes be a major setback in studies. For example, in Barro Colorado Island (BCI, Panama), one of the largest tropical forest research stations, the publication of Croat's Flora (Croat 1978), with precise descriptions of all plants and an identification key based on sterile plant parts, was a major turning point for the scientific study of plants (Muller-Landau and Wright 2023). To make the flora more accessible and available to everyone, BCI's researchers published two field guides in 2008 and 2011 with photographs and more accessible descriptions of a total of 210 and 493 tree species respectively (R. Pérez 2008; Condit, Pérez, and Daguerre 2010), which again significantly boosted research for ecologists working with trees. They, however, considered lianas only in 2015 with the publication of a guide with descriptions and photographs of 124 liana species in BCI (Pérez et al. 2015). Accordingly, BCI has also been one of the pioneering areas for research on liana community ecology for more than 40 years, since the publication of Croat's flora (Schnitzer and Carson 2023). Therefore, ease of identification of liana species for ecologists is an important prerequisite for the study of liana ecology in the years to come.

I believe that producing field guides with field photos to identify liana species with simple descriptions accessible to everyone is an effort worth spending time on and necessary for further studies, at least in areas where permanent plots have been established. For the Sangha Trinational Landscape, which includes the northern Congo, a field identification guide for tree species exists (Harris, Wortley, and Wise 2008; Wortley et al. 2014). However, to my knowledge, there has never been an identification guide for liana species. My thesis took place in a permanent forest dynamics

experimental site where the first liana inventory was conducted in 2017. In 2022, we conducted a second inventory and trained field technicians to identify liana species using the field identification booklet I created, which includes 100 liana species with photos (see general introduction, section 2.4.3.). In order to boost studies in this area, I believe it is necessary to publish an open-access field identification guide to ensure permanent access to botanical knowledge over time. I am currently in collaboration with David Harris, a botanist from the Royal Botanic Garden in Edinburgh and expert of the flora of central Africa, to check liana species identifications and validate botanical descriptions, as I am not a botanist by training. When a first version will be set, I plan to contact a few other botanists or liana experts from tropical Africa to offer them the possibility to contribute.

As illustrated in my thesis, the use of molecular barcoding data can be of major help for identifying lianas. The main current limitation of this approach is the poor availability of reference data in large open access data repositories such as genbank (<https://www.ncbi.nlm.nih.gov/genbank/>). By generating 235 new RbCl and matK markers, my thesis contributed to fill this gap but this effort must be pursued by integrating more species and potentially other specific markers such as the ITS (Cheng et al. 2016).

In addition, the development of recent tools such as image-based plant identification systems are a promising way to facilitate plant identification in the field. Tools such as PI@ntNet, originally developed for plant identification in Western Europe, now cover all continents and provide flora for every region of the world. A region's flora data can also be downloaded in advance and the application's offline mode used to identify plants in study areas where there is no or poor network connectivity. Such tools, which can identify plant species by leaves that are overall difficult to access from the ground, may also be a promising avenue when combined with drone images, as it is now possible to capture drone images at very high resolution where species leaves can be clearly seen. For liana species, while efforts still need to be made to validate the identifications and create training datasets for artificial intelligence, the accessibility of these user-friendly applications could benefit not only ecological studies but also other fields such as ethnobotany.

#### 6.4.2 Assessing knowledge on the resistance and resilience of lianas to disturbance to improve liana predictions under climate change

Improving our knowledge about the ability of liana stems to endure, survive and heal from disturbances is an important notion to better understand their responses with the increase of natural and anthropogenic disturbances under a rapidly changing climate (Seidl et al. 2017). Associating liana functional characteristics to resistance and resilience measures on the field was part of the initial goals

of my thesis. However, because of the limited time frame and the difficulty of identifying disturbance (between a real disturbance and the result of an adaptation of the liana stem to its environment), I did not pursue this study, but nevertheless collected a dozen samples impacted by disturbances for future analyses. However difficult it may be, especially given the variety of different field situations and the general complexity of lianas, given the importance of lianas in tropical forests (see Introduction, Section 1.1.), I believe it is nevertheless important to attempt to better understand and thus predict liana damage and recovery rates, as is the case with trees (Curran et al. 2008).

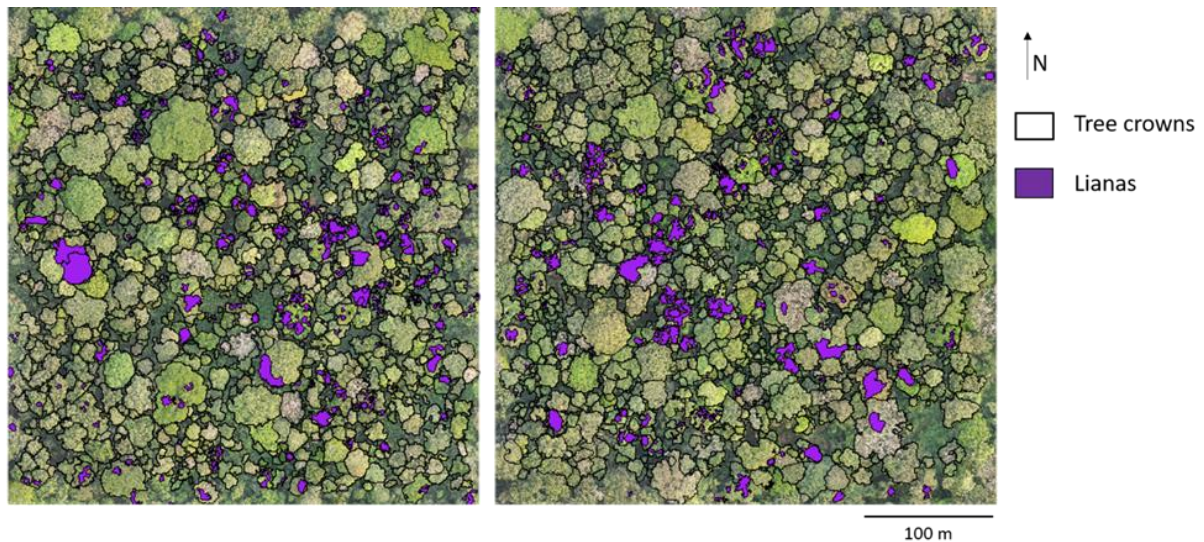
Thus, I propose to focus on clearly identified disturbed areas, such as canopy gaps due to a treefall, or along skidding trails of logging activities, or in areas impacted after a storm. In the experimental site of northern Congo (Loundoungou), such situations can be found either in the western block because it has been subjected to logging activities (see perspectives, section 6.4.4.) or in the eastern bloc through natural tree falls and storm impacts. Drone acquisitions have been done every year since 2018 (except in 2021 due to COVID restrictions) and allow to well identify and characterize perturbation events in the study area. Liana resistance and resilience to injury could be measured on a predefined area around the center of the disturbance. To assess the resistance of liana stems, we could categorize all lianas by the impact of the disturbance on them from: (0) no impact, (1) minor impact (partial rupture of the stem cylinder, up to 50% of the diameter) and (2) major impact (total rupture or more than 50% of the stem cylinder). To assess a more quantitative measure of the resistance and the mechanisms underlying that resistance, I measured and collected on a dozen samples the diameter and a cross-section of the stem before, in the middle, and after the part of the stem affected by the disturbance. This would have allowed us to associate different tissue developments, anatomical configurations or traits (such as heterogeneity or cambial variants or wood density) and their potential mechanical properties (see discussion point 6.2.), to a major or minor resistance degree by diameter. Mirroring the approach for resistance, for resilience we could measure for each liana the re-sprouting and stem healing rates (% of re-sprouts, healed and dead stems), and note the way they healed (for example division into multiple strands before re-uniting as one). Cross-sections of the liana stem can then also help associate different resilience degrees to different anatomical traits, cambial variants, and mechanical properties. Even if I expect to encounter many different situations and difficulties in following a standardized protocol in the field, I believe it is important to tackle the subject to shed more light into the critical question of how lianas survive in different environments?

### 6.4.3 The role of liana functional composition on liana-tree interactions and effect on forest dynamics

To my knowledge, no study already investigated the influence of lianas on tree stand dynamics in central Africa. In the Neotropical sites, results differed. Most of the studies found a significant negative impact of lianas on tree growth in liana-infested forests at the tree individual scale (Becknell et al. 2021; Ingwell et al. 2010; Van der Heijden and Phillips 2009; Venegas-González et al. 2020). However, Tymen et al. (2016) found higher tree growth rates in a liana-infested forest than in a high canopy forest in French Guiana at the stand scale, because the gap dynamics was higher in the liana-infested forest and fast-growth species thus recruited more. Hence, while the effect of lianas on tree individuals is negative, e.g. through a direct competition for light, liana infestation may also lead to faster dynamics at the stand scale by promoting gap dynamics. Hence the effect of lianas on forest dynamics appears scale dependent and is probably more complex than previously thought.

In my thesis I have revealed that the functional composition of lianas might lead to significantly different liana leaf coverage over tree crowns, directly impacting the relationship between lianas and trees for light competition. Considering the functional composition and diversity of ecological strategies of lianas in liana-tree interactions and their relative effect on tree individual growth and tree stand dynamics might then help better understand and estimate the role of lianas in forest dynamics and predict their impact on the carbon cycle of tropical forests. Up to now, no prediction model has ever considered lianas as a heterogeneous plant group and used different plant functional types to model liana interactions and impact on trees and forest dynamics (Meunier et al. 2021; Porcia e Brugnara et al. 2019).

During my thesis I initiated through multiple field missions a study aiming at investigating the impact of liana communities on individual trees and stand level dynamics in my study area. At the tree individual level, I associated the ground tree inventory identification to its crown identified by drone images (see general introduction and field missions, section 2.3.), to be able to link individual tree annual demographic data since 2017 to different crown variables derived from LiDAR and drone data (such as liana leaf coverage or crown illumination). At the stand level, I began delineating all tree crowns semi-manually and all liana leaves manually (see details in chapter 1), to assess liana leaves distribution over the experimental site. For the moment only 18-ha (out of 36) has been entirely delineated (Figure 20), and there is still a considerable amount of data processing before the analyses. The final objective of this study is to better understand the effects of lianas on tree growth and stand dynamics, taking into account light exposure of crowns and functional identity of lianas.



**Figure 20.** Map of liana leaves over the forest canopy of 18-ha of the experimental site in northern Congo (Loundoungou). A total of 1627 individual tree crowns were delineated over the 18-ha of the experimental site, with 269 of them infested by lianas. In total, liana loads seemed present on 17% of all individual canopy tree crowns, representing approximately 10% of the total canopy photosynthetic surface over the 18-ha of tropical forest.

#### 6.4.4 Liana dynamics and functional shifts over 5 years (2017-2022), in stable and disturbed environments

In Neotropical forests, an increasing number of studies have pointed out a rise in liana density under the combined effects of climate change and anthropogenic disturbances (Laurance et al. 2014; Phillips et al. 2002; Schnitzer and Bongers 2011). However, the lack of data acquired on other tropical forests, in particular African forests, makes very uncertain the pantropical nature of this increase and the real impact of lianas in natural dynamics and tree stand recovery in the long term (Bongers et al. 2020; Bongers and Ewango 2015; Caballé and Martin 2001; Ewango 2010; Thomas et al. 2014). Monitoring lianas is crucial to better understand liana proliferation over long periods of time, the mechanisms underlying their proliferation and their impact on forest dynamics, but also for future forest forecasts and forest management.

The western block of the experimental site in northern Congo has been logged at the end of 2018, with a low logging intensity of 0.3 trees/ha. In May 2022 we launched the second inventory of lianas in the same plots as the first 2017 inventory. This second inventory was conducted with a higher effort for the botanical identifications of lianas, to clearly distinguish different “qualities” of vernacular names, corresponding to different botanical species. Same as the 2017 inventory, all woody lianas and

rattans  $\geq 1$  cm in diameter were marked with paint and their diameter measured according to international protocols (Gerwing et al. 2006; Schnitzer, Rutishauser, and Aguilar 2008). For each liana root, the distance and identity to the closest tree, the identity of the host tree and, if applicable, the identity of the second host tree were noted, making it possible to link an important proportion of lianas to their initial measure in 2017 and thus to estimate growth and mortality rates for at least a subset of liana individuals.

Using the knowledge about the ecological strategies of liana species determined in my thesis in chapter 3 and the functional composition of the liana community in chapter 2, I plan to assess through the new inventory of 2022 the temporal patterns of liana abundance and functional composition, to help provide a more mechanistic understanding of both their natural and post-disturbance dynamics in a central African context. This study aims at investigating the following questions: How does the functional composition of lianas vary over time and are there any differences in growth rates according to liana ecological strategies? This study could also test how functional traits potentially related to resilience to disturbances and early-life strategies vary over time in disturbed and control plots?

#### 6.4.5 Inspirations for smart, soft robotics technology

Lianas and, in general, climbing plants have sparked the interest of biologists since the 19th century with Darwin's work "The movements and habits of climbing plants" (1875). Due to their diversity of complex levels of development providing them the ability to attach and climb on different types of supports, but also to adapt and heal from environmental hazards, they have also recently sparked the interest of engineers and scientists working on soft robotics technology (Soffiatti and Rowe 2020; Mazzolai, Beccai, and Mattoli 2014). In this recently developed branch of technology, they have succeeded in using climbing plants as a consistent source of inspiration in terms of growth strategies, specialized tissues and organs, and their plasticity in terms of structural and functional properties to create soft robots capable of growing by adapting to their environment and intelligent robots capable of controlling their growth direction (Bastola, Soffiatti, et al. 2021; Soffiatti and Rowe 2020; Del Dottore et al. 2018). Recently developed smart soft robots are even capable of adapting their shape through a soft hydrogel elastomer system with 3D printers, mimicking the shape shifts of a climbing cactus during its development from young to adult stages (Bastola, Rodriguez, et al. 2021). In practice, these intelligent soft robots have great potential to explore unstructured environments where humans have difficulty or no access to find hard-to-reach objects by quickly adapting their movements and shape to the local environment (Del Dottore et al. 2018). They can be used in many



fields, from monitoring disasters such as earthquakes to archaeological or space exploration (Walker 2015).

My thesis work could, on the one hand, contribute to the development of this new technology by providing an idea of how different functional associations respond in forest environments and, in particular, to local environmental variations. The great diversity of anatomical stem strategies found in lianas and the presence of a wide range of anatomical combinations that balance efficiency, safety, and survival offer great adaptive potential for technological applications. In addition, ecological studies of communities help predict how plant-inspired robots might respond in real-world environments. The fact that wood water- use and resilience to disturbance strategies of lianas seem not sensitive to local variations in forest structure provides a great freedom in the development and design of robotic structures. On the other hand, smart soft robots can also help in the field of liana ecology by accessing the canopy layer of the forest, often considered the most important but also the most difficult to access. This access could open new horizons for scientific research, as we could closely follow the development of lianas, measure their length without error-prone allometric equations, and even collect leaves or stems of lianas in sunlight conditions in the canopy to measure functional traits and deepen our understanding of liana ecology.

## 7 References

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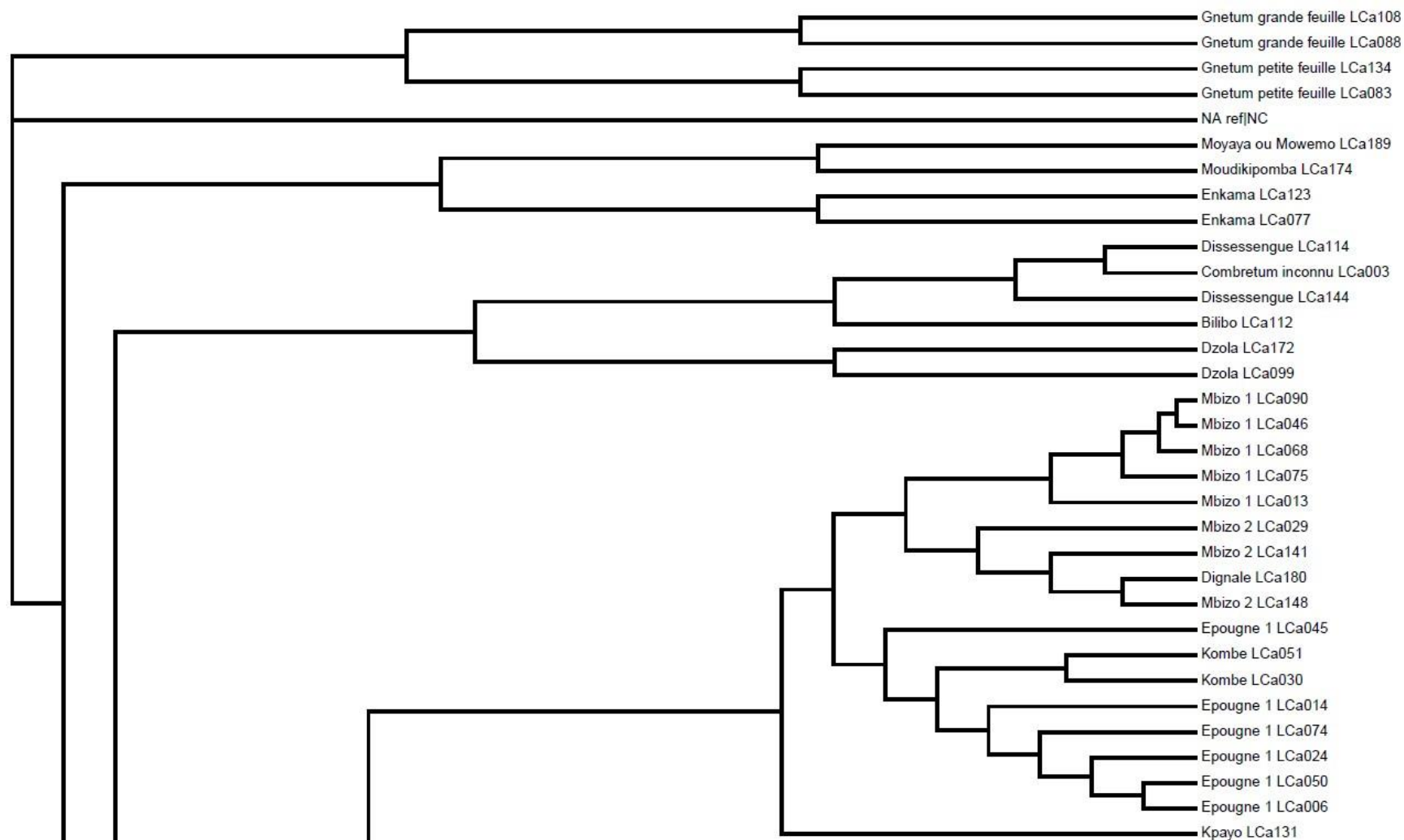
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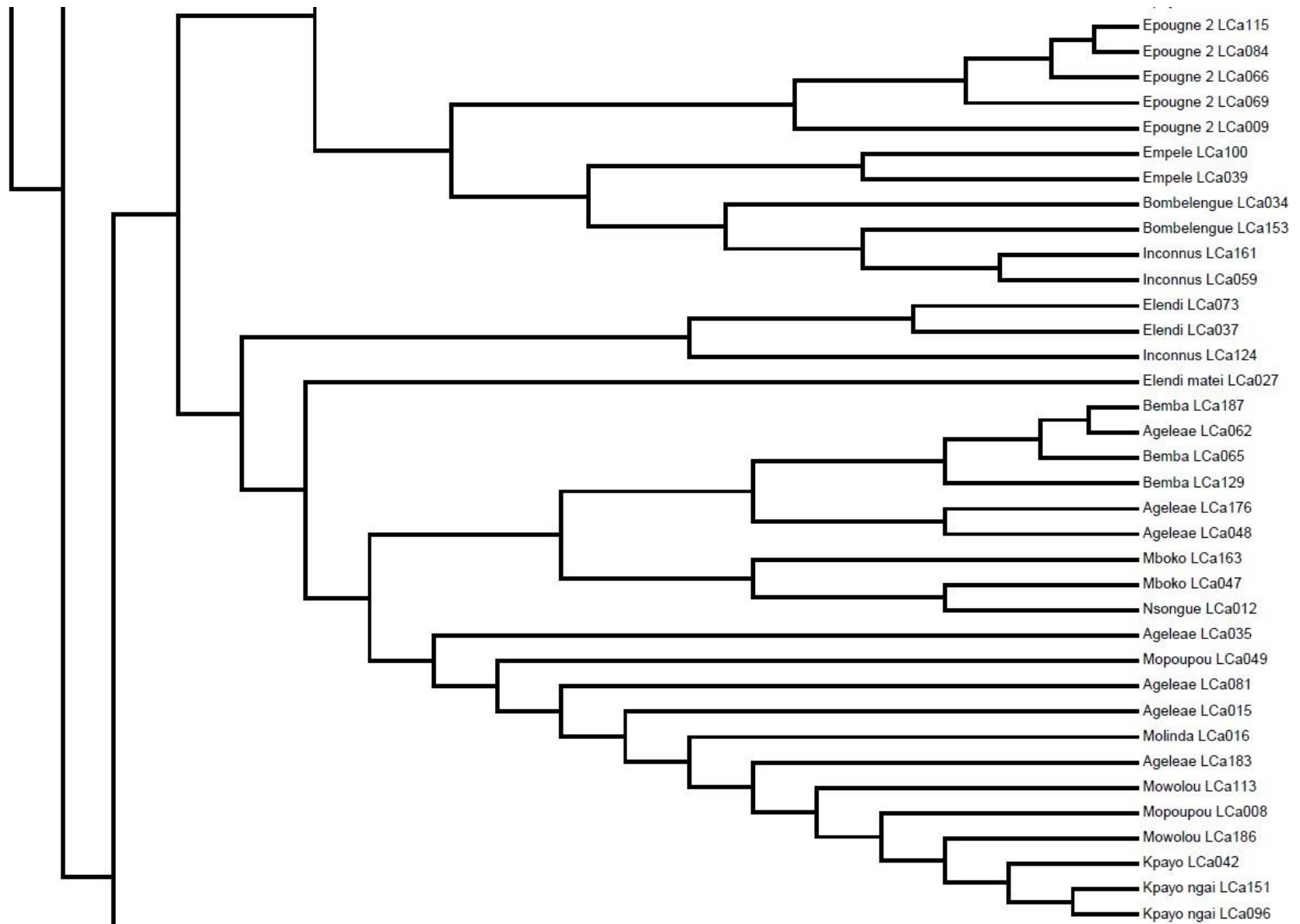


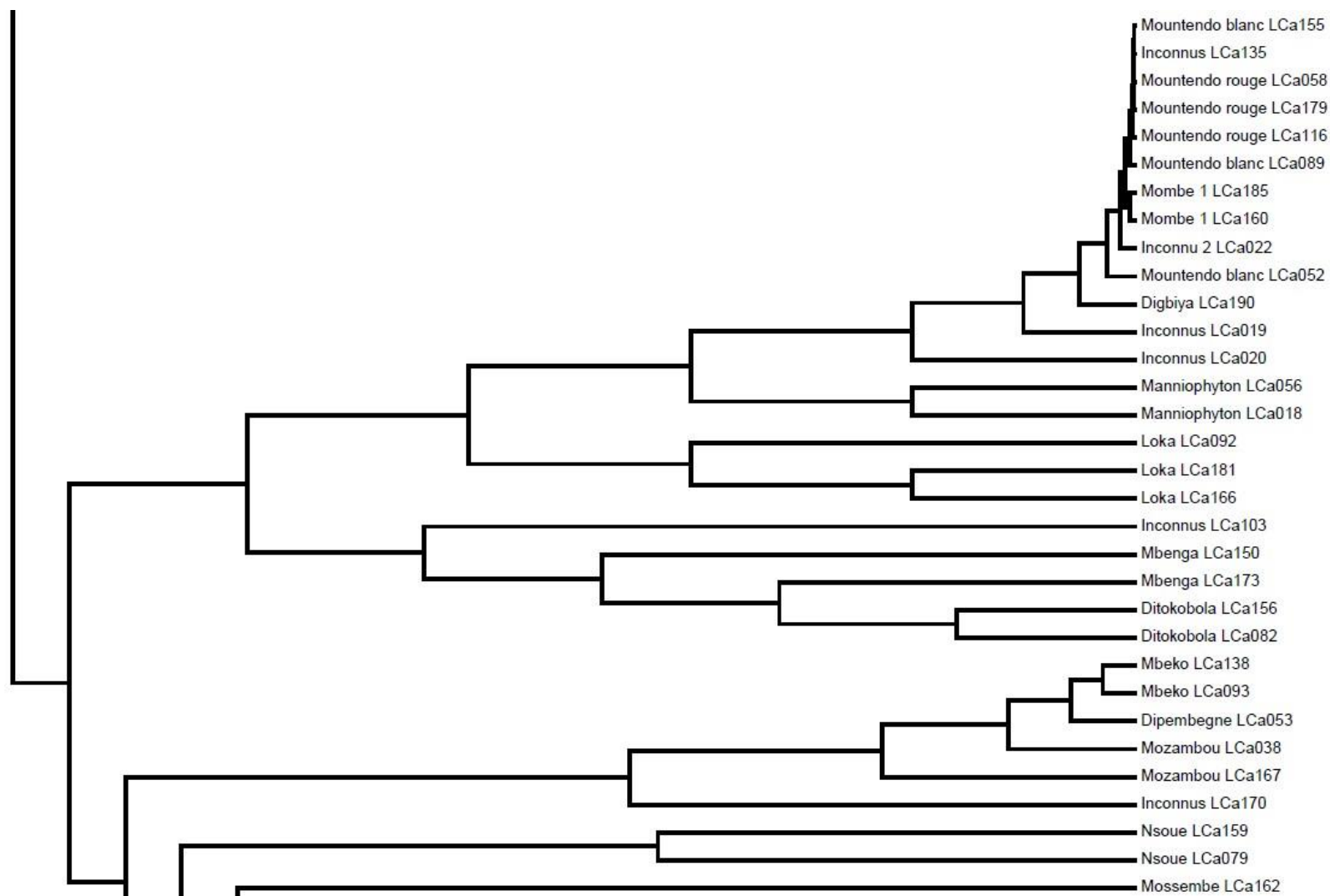
## 8 Supplementary materials

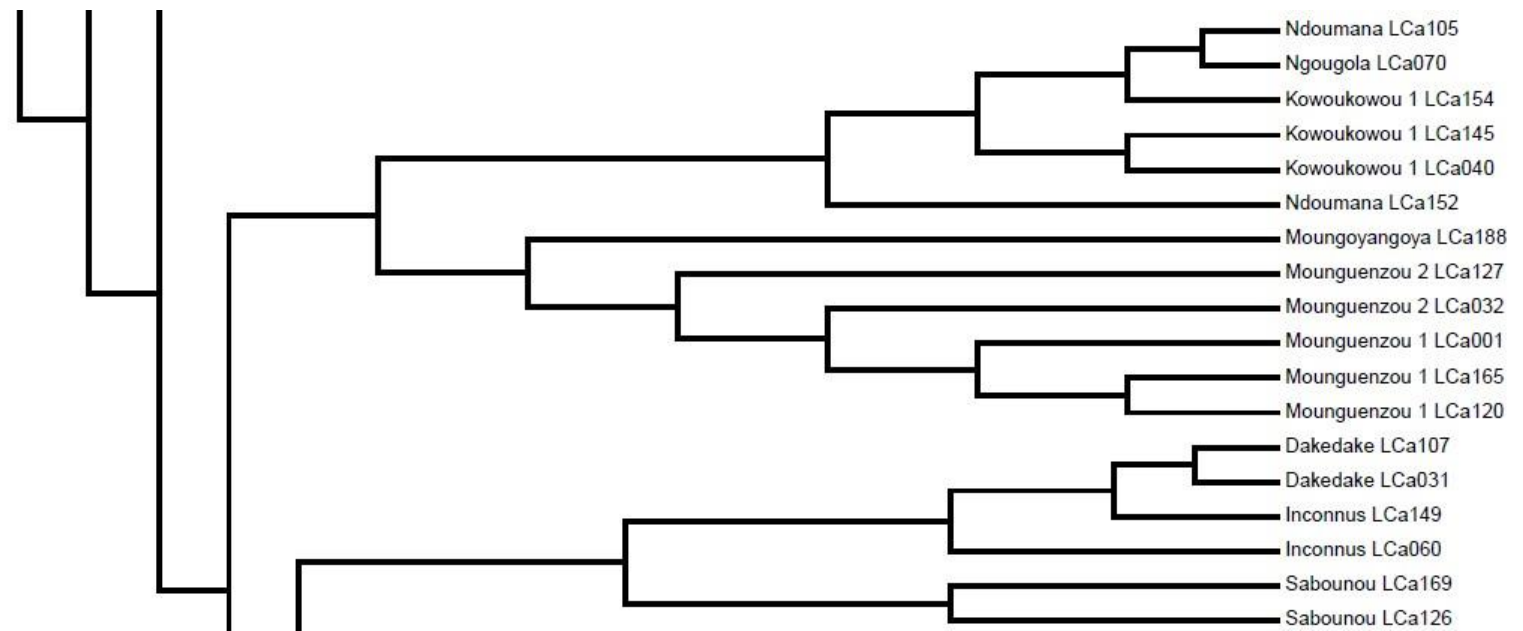
### 8.1 Supplementary of the general introduction

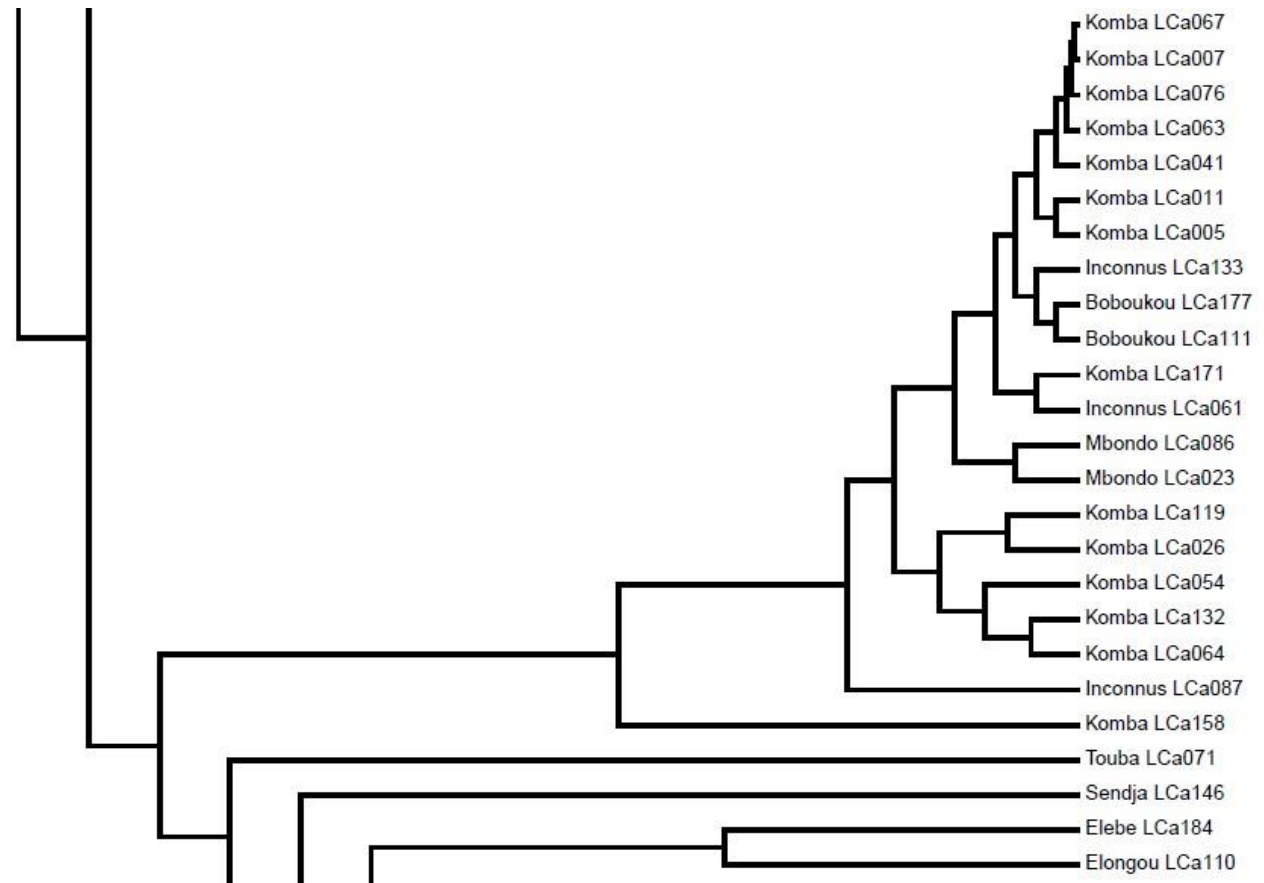


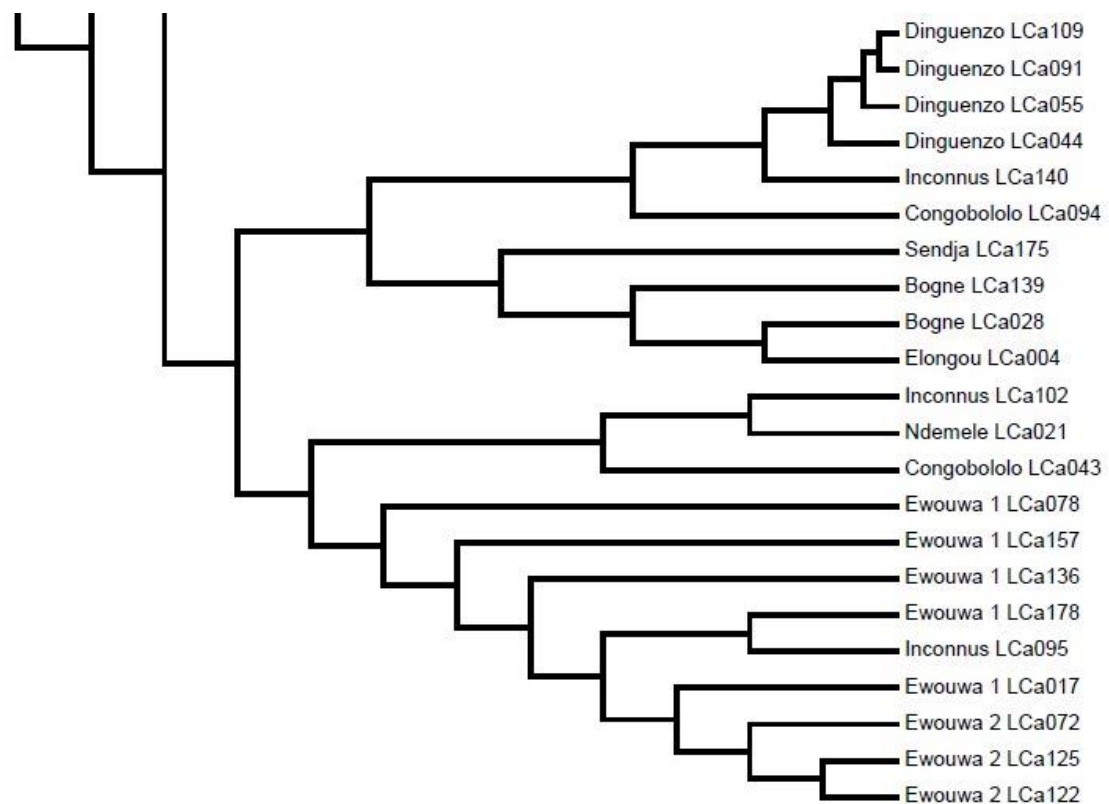






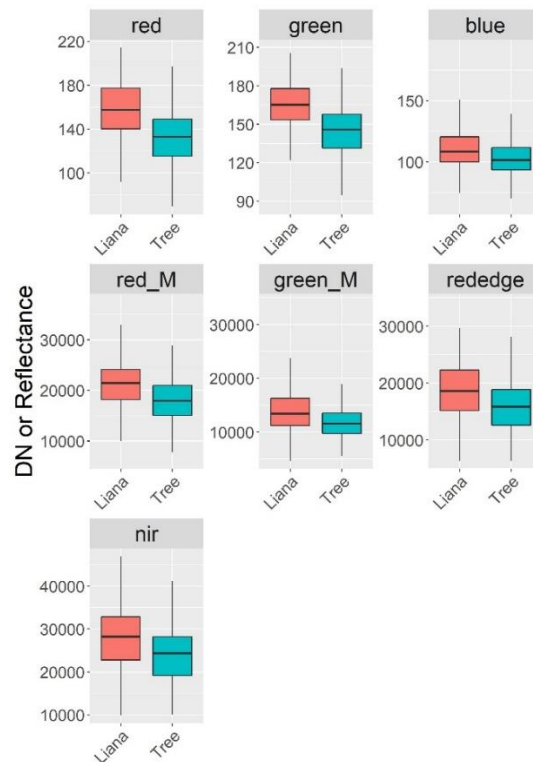






**Supplementary Figure S1.** Maximum likelihood phylogenetic tree with liana vernacular names to check taxonomic coherence.

## 8.2 Supplementary of chapter 1



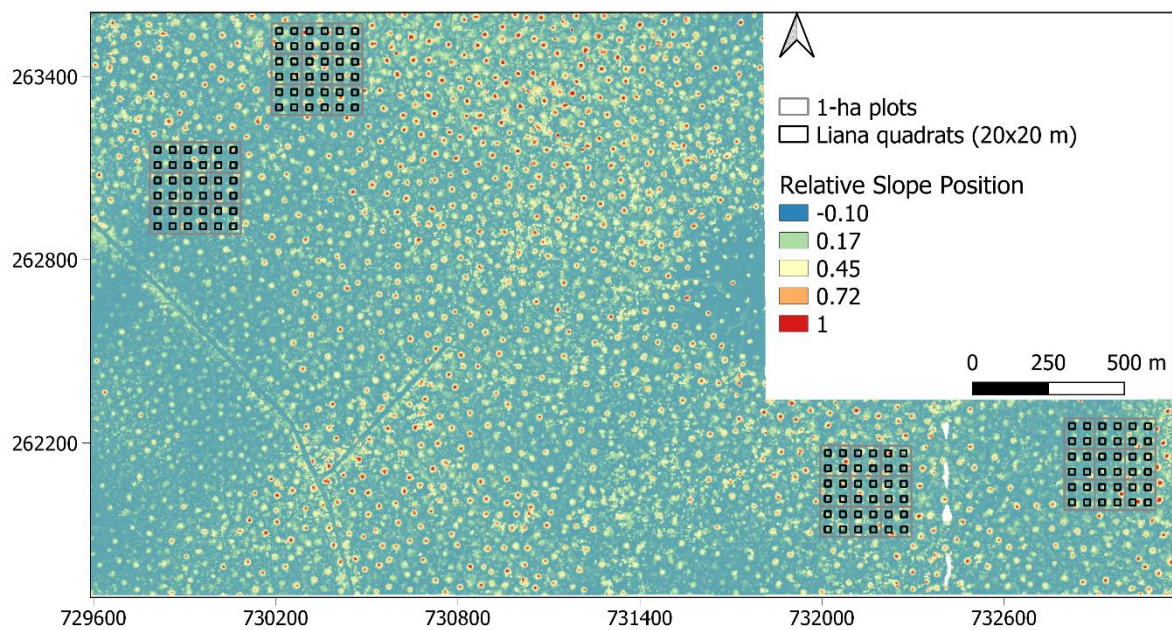
**Supplementary Figure S1.** Distribution of the mean DN and reflectance values per tree crown or liana patch for each RGB (red, green, blue) and multispectral (red\_M, green\_M, rededge, nir) bands. Liana patches and tree crowns are represented in red and green boxplots respectively.

## 8.3 Supplementary of chapter 2

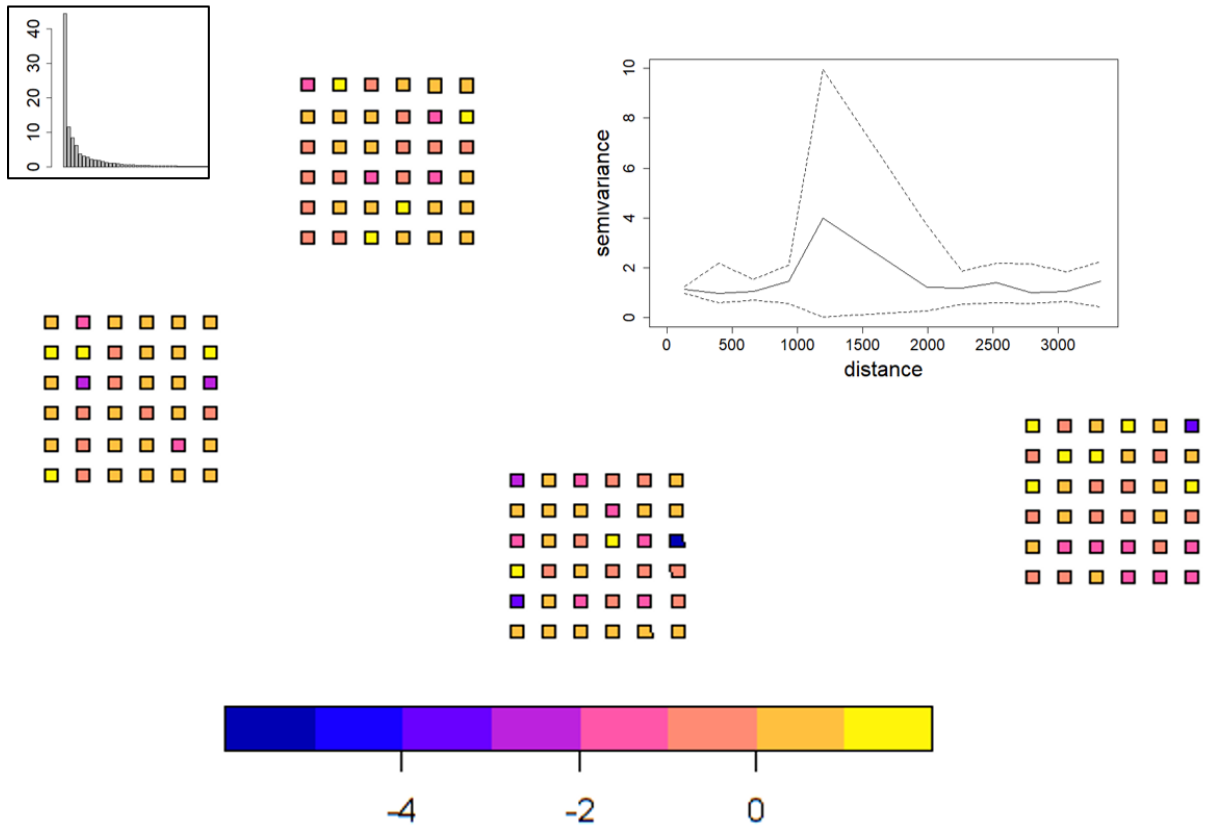
**Box – Genetic analyses.** DNA was successfully extracted from 192 dried liana leaf tissue samples, with at least one extraction per vernacular name, and then, focusing on samples for which taxonomic uncertainty was the highest or on genera known to contain several lianescent species. We sequenced two plastid genes, *rbcl* and *matK*, as these two loci have been identified as the best candidates for barcoding terrestrial land plants (CBOL Plant Working Group1, 2009). All DNA extractions were achieved using a Qiagen kit (QIAamp, 2010) and the Polymerase Chain Reaction (PCR) was performed following the protocol from Dunning and Savolainen (2010) for *matK* and *rbcl*. All isolates were sequenced in both directions (Forward and Reverse) using the Sanger method (Gonzalez et al., 2009). Consensus sequences from forward and reverse reads were built using the Geneious software (Geneious, 2018). Then, all sequences were aligned in the MEGA software (Kumar et al., 2018). Basic Local Alignment Search Tool (BLAST), an algorithm used to compare DNA sequences and identify similar sequences above a certain threshold was run through GenBank (Benson et al., 2008). We identified each specimen using first the BLAST results to restrict the identification to a given taxonomic group and then using taxa identification keys based on vegetative or fertile (when available) characters in the herbarium samples and



**Supplementary Figure S2.** Termite mounds within the permanent plots in the study site.

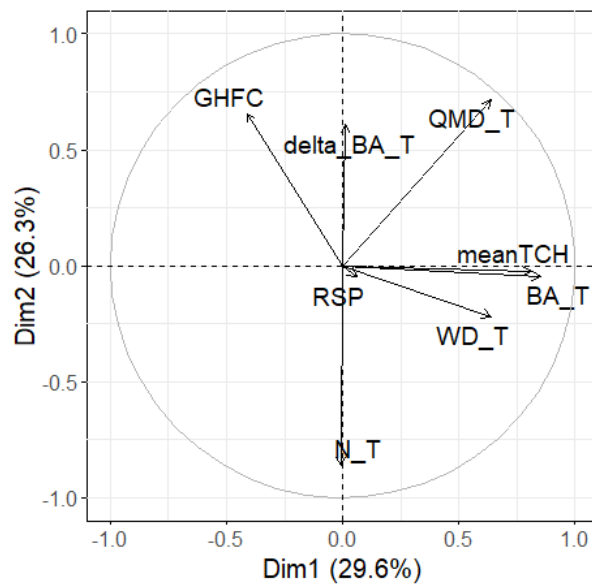


**Supplementary Figure S3.** Relative slope position index derived from lidar-based elevation model over the study area and capturing well the termite mounds (high values in red).



**Supplementary Figure S4.** Spatial distribution of NSCA axis 2 scores of liana floristic composition on the 144 quadrats with eigenvalues (top left corner). The insert graph gives the variogram of NSCA axis 2 scores (See appendix 5 for the axis 2). The dotted lines on the variogram represent the confidence intervals at 95% and the solid lines the variogram.

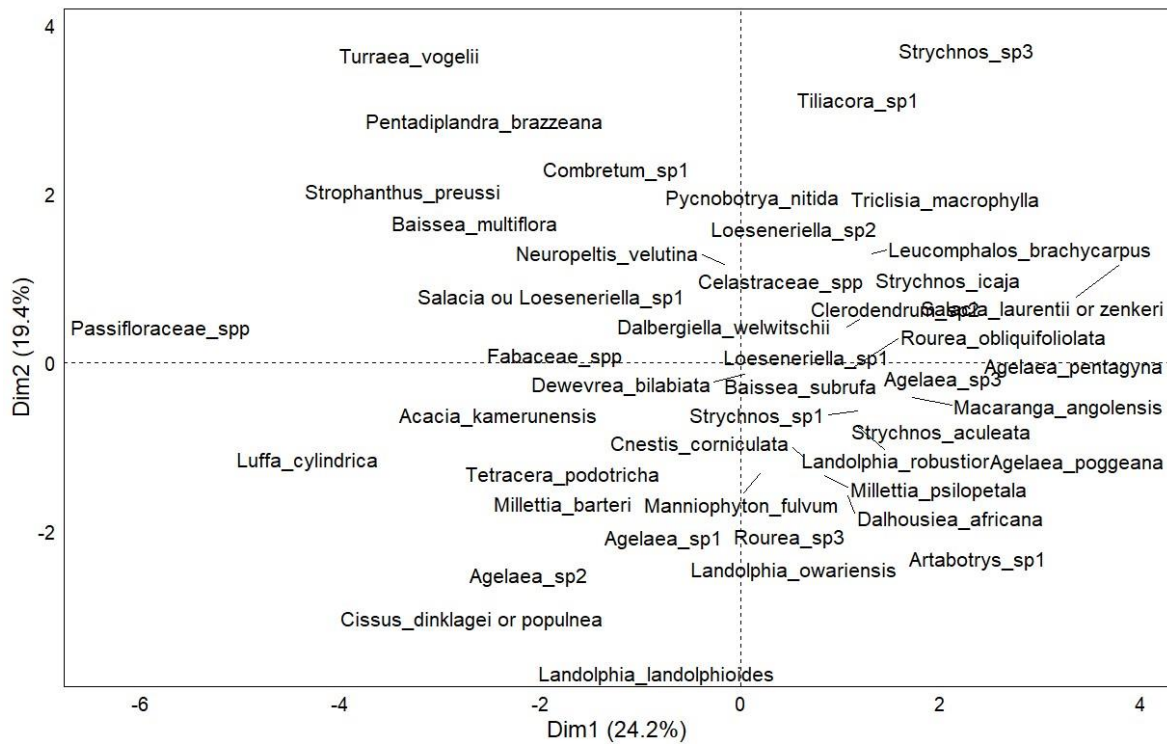
### 8.4 Supplementary of chapter 3



**Supplementary Figure S1.** Plan 1-2 of a PCA on environmental variables. GHFC: giant herbs foliar cover; delta\_BA\_T: tree basal area increment; QMD\_T: tree quadratic mean diameter; meanTCH:



mean canopy height; BA\_T: tree basal area; WD\_T: mean tree wood density; N\_T: tree stem density; RSP: relative slope position (termite mounds).



**Supplementary Figure S2.** Plan 1-2 of a Principal Coordinate Analysis performed on leaf and stem functional traits of 46 liana species with species distribution.



**Supplementary Figure S3.** Stem of *Loeseneriella sp.1* splitting into several separate strands and reforming as a single stem with scattered wood.

## 9 Résumé en français

### STRATEGIES ECOLOGIQUES DES LIANES D'AFRIQUE CENTRALE : DE LA DIVERSITE MACRO-ANATOMIQUE AUX STRUCTURES DES COMMUNAUTES

#### 9.1 Introduction générale

Les lianes sont un des constituants de plus en plus reconnus pour leur importance dans la diversité et la dynamique des forêts tropicales. Dans les forêts néotropicales, les lianes peuvent représenter 35% de la diversité des plantes ligneuses et 25% de la densité des plantes (Schnitzer et al. 2012 ; Schnitzer 2015), envahir plus de la moitié des couronnes des arbres de canopée (Ingwell et al. 2010), et modifier de manière significative le cycle du carbone des forêts tropicales (Porcia e Brugnara et al. 2019). Les lianes sont des plantes qui germent au sol, et après une phase juvénile autoportante de croissance exploratoire et d'attachement, perdent leur capacité à se soutenir et ont besoin de supports physiques externes tels que les arbres pour atteindre la canopée de la forêt (Caballé 1998 ; Darwin 1875 ; Putz 1984 ; Putz et Chai 1987). Ce changement physiologique de mode de vie vers une forme lianescente et grimpante est lié au développement d'une diversité d'organisations vasculaires complexes (Chery et al. 2020 ; Angyalossy, Pace, et Lima 2015 ; Hegarty 1991), qui confèrent aux tiges des lianes une flexibilité suffisante pour grimper et s'adapter à différents types de supports, mais aussi une robustesse pour survivre et guérir des aléas environnementaux (Rowe et Speck 2015 ; Fisher et Ewers 1991 ; Putz et Holbrook 1991 ; Dobbins et Fisher 1986 ; Putz 1984).

Les lianes réduisent la diversité, la croissance et le stockage du carbone des arbres, tout en limitant fortement la résilience des forêts tropicales (Laurance et al. 2014; Schnitzer & Carson, 2010 ; Tymen et al., 2016 ; van der Heijden et al., 2015). Investissant moins de biomasse dans le diamètre pour atteindre la canopée que les arbres, les lianes ont tendance à former une monocouche de feuilles au-dessus de la canopée, réduisant la disponibilité en lumière et entrant directement en compétition avec les arbres pour les ressources aériennes (Avalos, Mulkey et Kitajima 1999 ; Visser et al. 2018). Les lianes peuvent occuper 30 % de la surface foliaire de la forêt, tout en représentant moins de 5 % de la biomasse de tiges ligneuses (Geertje M. van der Heijden et al. 2013). De plus, elles sont en concurrence directe avec les arbres pour les ressources souterraines, car elles sont mieux capables d'explorer et de capturer les ressources du sol (Collins, Wright et Wurzbürger 2016 ; Smith-Martin et al. 2019 ; De Deurwaerder et al. 2018). En raison de la compétition et du stress mécanique des lianes sur les arbres, elles ont surtout été étudiées au niveau de la communauté pour leur impact négatif sur la démographie des arbres et la dynamique forestière, et principalement en tant que groupe homogène héliophile

(Laurance et al., 2014 ; Schnitzer & Carson, 2010 ; G. M. F. van der Heijden et al., 2015). Pour mieux comprendre le rôle des lianes, quantifier, et prédire leur impact sur les écosystèmes forestiers tropicaux, nous devons être en mesure d'estimer avec précision leur distribution spatio-temporelle.

Nonobstant, ayant évolué dans plus de 130 familles d'angiospermes (Gentry 1991), avec un mode de vie unique, les lianes possèdent l'un des systèmes vasculaires les plus complexes du règne végétal (Darwin 1875). Mais jusqu'à récemment, elles ont reçu relativement peu d'attention dans les études écologiques (Schnitzer et Bongers 2002 ; Marshall et al. 2020). La grande diversité des formes de croissance, les incertitudes taxonomiques, le manque de botanistes et les difficultés d'identification sur le terrain ont conduit à exclure les lianes de la plupart des études contemporaines portant sur l'écologie des communautés (Schnitzer et Bongers 2002). Globalement, notre compréhension de l'écologie des lianes et de leur rôle dans l'écosystème a pris beaucoup de retard par rapport à celle des arbres, et c'est encore plus vrai en Afrique centrale où la littérature est d'autant plus rare.

Peut-être en raison des difficultés mentionnées ci-dessus, de la plupart des études en écologie les ont considérées comme un "groupe fonctionnel unique" afin de comprendre leur distribution et leur dynamique dans l'espace et dans le temps. Cependant, les quelques études qui ont considéré les lianes comme un groupe véritablement hétérogène, ont étudié les tendances des traits fonctionnels tels qu'ils sont utilisés pour les arbres et dans les analyses explorant les spectres économiques du bois et des feuilles (comme la surface spécifique foliaire (SFS), l'épaisseur des feuilles, la densité du bois...). Jusqu'à présent, les études récentes ont suggéré que (i) les lianes sont aussi diverses sur le plan fonctionnel que les arbres (Medina-Vega et al. 2021 ; Meunier et al. 2020 ; Sun et al. 2022), (ii) leurs schémas de traits fonctionnels peuvent varier le long des gradients environnementaux (Rocha et al. 2022), et (iii) les traits fonctionnels classiquement prescrits ne révèlent pas les changements dans les histoires de vie des lianes et les connexions avec l'environnement aussi fortement qu'ils le font pour les arbres (Liu et al. 2021).

Une compréhension plus approfondie de l'écologie des lianes, en particulier les liens entre les traits, l'anatomie et la structure des communautés de lianes, est nécessaire pour mieux prédire leur distribution spatio-temporelle, leur dynamique et leurs effets sur les fonctions forestières. L'objectif de ma thèse est d'élargir nos connaissances sur les stratégies écologiques des lianes, de la diversité macro-anatomique aux structures des communautés, en utilisant à la fois des données de terrain au sol et par drone, et des mesures de traits fonctionnels en laboratoire. Mes études ont été menées dans un site expérimental de recherche sur la dynamique forestière au nord de la République du Congo, une région peu étudiée pour les lianes. A travers le prisme de l'écologie fonctionnelle, j'étudie (i) le lien entre les mesures de lianes au sol couramment utilisées et les mesures par drone de la couverture

foliaire des lianes sur les couronnes des arbres ; (ii) l'influence de la topographie locale, de la structure forestière et de la composition du peuplement d'arbres sur la structure de la communauté de lianes et sa composition floristique et fonctionnelle ; et (iii) les stratégies associées à la diversité macro-anatomique des lianes, leurs liens avec le spectre économique des feuilles, et leurs distributions à travers une phylogénie et le long des gradients environnementaux. Plus précisément, j'aborderai les questions suivantes :

- Les mesures au sol des lianes couramment utilisées permettent-elles de prédire les mesures par drone de la couverture foliaire des lianes au-dessus des couronnes d'arbres ? Dans quelle mesure cette relation est-elle influencée par la composition fonctionnelle des lianes ?
- Comment les communautés de lianes sont-elles réparties le long des gradients environnementaux ? Dans quelle mesure la structure forestière et la composition floristique du peuplement d'arbre, ainsi que la topographie, influencent-elles la structure, la composition floristique et fonctionnelle des communautés de lianes ?
- Quelles sont les différentes stratégies écologiques des lianes au sein d'une communauté ? Quelle est la diversité anatomique des espèces de lianes, et les variantes cambiales ainsi que les traits fonctionnels dérivés sont-ils associés à des stratégies différentes ? Comment ses stratégies sont intégrées et quelles sont leurs contributions aux spectres économiques classiques ?

J'explorerai ces questions à travers trois chapitres distincts sous la forme d'articles scientifiques. Ces articles sont actuellement soit acceptés dans une revue scientifique, soit en cours de préparation. Pour ces derniers, ils continueront probablement à évoluer jusqu'à leur publication. Chaque chapitre présente plusieurs approches complémentaires visant à caractériser les stratégies écologiques et fonctionnelles des lianes, de l'observation des individus à celle des communautés. Un dernier chapitre propose une discussion transversale et conclut ma thèse par des perspectives.

## 9.2 Chapitre 1 - Le lien entre les mesures de liane par drone et au sol dans une forêt congolaise

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Publié dans *Frontiers in Forests and Global Change*, [doi: 10.3389/ffgc.2022.803194](https://doi.org/10.3389/ffgc.2022.803194)

Avec l'émergence de la télédétection par drone, des données à très haute résolution peuvent être obtenues sur la distribution des lianes au-dessus de la canopée. Dans ce premier chapitre, j'ai évalué la relation entre les mesures courantes des lianes au sol et la couverture foliaire des lianes au-dessus des couronnes d'arbres déterminée par drone. J'ai testé si cette relation était influencée par la composition fonctionnelle des lianes et j'ai comparé la signature spectrale des patches de feuilles de lianes et des feuilles d'arbres à travers les images drone. En utilisant des plateformes de drones, nous avons acquis des images RVB et multispectrales à très haute résolution et des données LiDAR sur deux parcelles permanentes de 9 ha situées dans le nord de la République du Congo. La couverture foliaire des lianes et les couronnes d'arbres individuelles ont été délimitées à partir de ces données. Au cours d'une mission de terrain concomitante, nous nous sommes concentrés sur 275 arbres infestés ou non par des lianes, pour lesquels nous avons mesuré toutes les lianes  $\geq 1$  cm de diamètre grimpant sur eux ( $n=615$ ) et estimé leur indice d'occupation du houppier (COI). Nous avons également mesuré ou enregistré la densité du bois et les mécanismes d'attaches de la plupart des taxons de lianes.

Contrairement à des résultats récents, nous avons trouvé des relations significatives entre la plupart des mesures dérivées du sol et la couverture foliaire des lianes au-dessus de la couronne des arbres. L'infestation des couronnes d'arbres par les lianes est expliquée principalement par la quantité de lianes grimpant sur eux, et est influencée négativement par la hauteur des arbres. La couverture foliaire des lianes sur les couronnes d'arbres individuelles était le mieux prédite par la surface terrière des lianes et négativement influencée par la densité du bois des lianes, avec un rapport surface foliaire-diamètre plus élevé pour les lianes à bois plus léger. Les scores de COI concordaient avec les estimations des drones, mais les deux tiers différaient de ceux obtenus à partir des mesures des drones. Enfin, les patches de feuilles de lianes avaient une réflectance lumineuse et une variation des réponses spectrales plus élevées que celle des arbres dans tous les spectres étudiés. Toutefois, le chevauchement important entre les réponses spectrales des lianes et des arbres remet en question la possibilité d'une détection automatique des feuilles de lianes dans les canopées. Dans l'ensemble, nous montrons que l'utilisation conjointe des données de terrain et de drone permet d'approfondir notre compréhension des mécanismes d'infestation des lianes et de leur diversité fonctionnelle et spectrale. Nous nous attendons à ce que les données des drones transforment bientôt le domaine de l'écologie des lianes.

### 9.3 Chapitre 2 – La structure forestière locale et la spécificité de l'hôte influencent toutes deux la composition de la communauté de lianes dans une forêt humide d'Afrique centrale

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Alors que les lianes sont une composante importante de la diversité et de la dynamique des forêts tropicales, nous connaissons encore mal les déterminants de la structure et de la composition des communautés de lianes, dont les variations spatiales peuvent fournir des explications importantes sur le fonctionnement des forêts tropicales. En combinant des données LiDAR et des données de terrain, nous avons étudié l'influence de la topographie locale, de la structure forestière et de la composition floristique des arbres sur la structure et la composition floristique et fonctionnelle de la communauté de lianes dans une forêt humide d'Afrique centrale. Nous avons inventorié toutes les lianes ayant un diamètre de tige  $\geq 1$  cm dans 144 quadrats de 20×20 m situés dans quatre parcelles permanentes de 9 ha, où tous les arbres et les herbacées géantes ont été inventoriés dans le nord de la République du Congo. Pour caractériser les stratégies fonctionnelles des lianes, nous avons mesuré un ensemble de traits foliaires et de bois liés à l'utilisation des ressources chez des représentants sélectionnés des principaux taxons de lianes.

La structure forestière locale influence principalement la structure des communautés de lianes, avec des abondances et des surfaces terrières totales plus élevées dans les forêts à canopée relativement ouverte où les lianes semblent entrer en compétition avec les herbacées géantes. La composition floristique des lianes présente une faible structure spatiale au niveau du site d'étude, mais est faiblement influencée localement par la structure forestière et la topographie. Seule la structure forestière a eu un effet faible mais significatif sur la composition fonctionnelle des lianes. Les forêts hautes et denses sont caractérisées par des lianes avec des stratégies plus conservatrices - une plus grande densité de tissus (bois) de la tige et une concentration foliaire de PO<sub>4</sub> et des valeurs de SFS plus faibles. Enfin, nous constatons une spécificité de support, avec un comportement d'attraction ou de répulsion significative entre certaines espèces de lianes et d'arbres les plus communes.

La structure de la communauté de lianes est fortement déterminée par la structure forestière locale dans les forêts d'Afrique centrale. D'autre part, malgré un large éventail de stratégies écologiques, la composition floristique et fonctionnelle des lianes n'est que faiblement déterminée par la structure forestière locale. Cependant, nous montrons que la variation floristique inexpliquée peut

être en partie due à une spécificité importante entre les espèces d'arbres et de lianes. Une recherche plus approfondie des traits des lianes ciblant des histoires de vie spécifiques permettra de mieux comprendre comment les communautés de lianes varient en fonction des conditions locales et interagissent avec les communautés d'arbres.

#### 9.4 Chapitre 3 - Traits fonctionnels et macro-anatomie des lianes de la République du Congo : lien entre les variantes cambiales et les stratégies d'histoire de vie

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Les lianes sont des formes de croissance emblématiques des forêts tropicales. Cependant, leur diversité originelle et unique de structures anatomiques et de fonctions associées est rarement prise en compte dans les études à l'échelle de la communauté. Ici, nous avons examiné comment les traits fonctionnels spécifiques aux modes de vie des lianes, tels que les variantes cambiales et le bois juvénile, sont liés aux stratégies écologiques des lianes et varient selon les espèces et la structure forestière locale. Nous avons collecté 164 tiges de lianes adultes d'un diamètre compris entre 2 et 6,4 cm près de parcelles permanentes de suivi des lianes dans le nord du Congo. Nous avons trié fonctionnellement toutes les tiges selon différentes variantes cambiales, allant d'une compartimentalisation simple à une compartimentalisation complexe, et nous avons dérivé des traits fonctionnels associés au premier stade de la croissance, à la résilience face aux perturbations et aux stratégies hydrauliques. Nous avons utilisé des analyses multivariées et bivariées à l'échelle des espèces et de la communauté pour révéler les stratégies écologiques principales des lianes et leur évolution le long de la phylogénie et des gradients de la structure forestière locale.

Les variantes cambiales étaient généralement spécifiques aux taxons, mais possédaient une plasticité entre les types de variantes en fonction de l'ontogenèse, de l'environnement et de l'histoire de vie de chaque individu de liane. Les variantes cambiales se répartissent entre des formes simples présentant une certaine rigidité juvénile et à trouver des hôtes, et des formes plus complexes présentant une certaine flexibilité à l'âge adulte et une résilience aux perturbations. Nous avons trouvé des preuves d'un compromis entre l'efficacité hydraulique et la sécurité hydraulique qui ne diffère que légèrement entre les variantes cambiales. La densité du bois reflète une sécurité hydraulique mais pas entièrement la capacité de survie. Deux axes principaux de stratégies écologiques ont été identifiés : un axe basé sur les feuilles lié à l'acquisition de nutriments et un axe basé sur le bois lié à l'utilisation de l'eau et à la résilience. Contrairement à d'autres études, les espèces de lianes présentent des

stratégies couplées à un certain niveau entre les feuilles et le bois. Le long de la phylogénie, les stratégies des feuilles et du bois des espèces de lianes ont montré une évolution significative chez les espèces apparentées. Cependant, à l'échelle de la communauté, seules les stratégies d'acquisition et de conservation des feuilles ont été influencées par la structure forestière locale, les espèces les plus conservatrices étant présentes dans les forêts hautes, à canopée dense, avec des arbres de grande taille et à bois dur. La diversité des stratégies relatives au bois des lianes semble exister indépendamment des changements de la structure forestière locale. Dans l'ensemble, les lianes présentent diverses stratégies visant à équilibrer l'efficacité, la sécurité et la survie, ce qui peut leur permettre de prospérer dans divers environnements. La coordination entre les caractéristiques des feuilles et du bois révèle la complexité de la diversité fonctionnelle des lianes et leur adaptation à différentes niches écologiques.

## 9.5 Discussion générale et perspectives

Un des défis importants de ma thèse était d'explorer et approfondir nos connaissances sur l'écologie des lianes dans le nord de la République du Congo à différentes échelles. A l'échelle de l'individu ou de l'espèce, j'ai étudié différents traits des feuilles et du bois pour mieux comprendre le fonctionnement des lianes. À l'échelle du peuplement, j'ai utilisé des technologies de drone de dernière génération pour comprendre comment les lianes se répartissent sur les couronnes d'arbres et comment cela est relié aux mesures classiques au sol de terrain. Enfin, j'ai combiné des mesures de traits fonctionnels avec des données de terrain à l'échelle de la communauté pour comprendre les déterminants écologiques des assemblages de lianes. Ci-dessous, je résume les principaux résultats associés à ces approches et les discute dans le contexte de la littérature actuelle.

À l'échelle de l'espèce, mon travail a permis de mieux comprendre le potentiel des lianes à concilier efficacité, sécurité et résilience par le biais de différents compromis entre traits. Les lianes semblent avoir de multiples stratégies écologiques liées à l'acquisition de nutriments, à l'utilisation de l'eau, à la résilience mécanique en début de vie et à la flexibilité au cours de leur développement. Néanmoins, à l'échelle de la communauté, les gradients environnementaux n'ont qu'une faible influence sur l'assemblage et les fonctions des lianes, ce qui suggère que la diversification des stratégies écologiques, en particulier les stratégies des lianes liées au bois, s'est produite indépendamment de la structure forestière, par exemple. Une hypothèse pour le faible effet de l'environnement sur la composition des lianes dans notre zone d'étude pourrait être due à l'homogénéité de l'environnement abiotique et à la possibilité que les variations locales de la structure forestière rendent difficile l'observation de filtres environnementaux sur les stratégies des lianes, en raison de l'effet de masse (Shmida and Wilson, 1985 ; Réjou-Méchain and Hardy, 2011 ; Zeleny et al., 2010). Une autre hypothèse est l'influence



potentielle des variations intraspécifiques des traits, qui peuvent différer le long de gradients environnementaux, entre et au sein des espèces, ce qui pourrait atténuer le lien entre l'environnement et la composition fonctionnelle des plantes (Viollet et al., 2012 ; Kichenin et al., 2013 ; Jung et al., 2010 ; Albert et al., 2011). D'autres études menées dans des environnements plus hétérogènes et prenant en compte la variabilité intraspécifique des traits des espèces le long de gradients environnementaux plus importants sont nécessaires pour mieux mettre en évidence les mécanismes responsables de la répartition spatiale des espèces de lianes.

Les traits fonctionnels existants pour les arbres sont souvent utilisés pour étudier les lianes, mais les lianes ont des caractéristiques physiologiques différentes en raison de leur port grimpant (Liu et al., 2021). Dans ma thèse, j'ai proposé de nouveaux traits, davantage liés à la physiologie des lianes, tels que l'indice d'hétérogénéité, le rapport phloème/xylème ou le bois juvénile. Mais il est nécessaire de poursuivre des études pour valider leurs relations avec les performances des lianes (Ménard et al., 2009). Les propriétés mécaniques et hydrauliques associées aux caractéristiques des lianes doivent faire l'objet de plus amples analyses, en particulier à l'échelle de la communauté (Dobbins and Fisher, 1986 ; Fisher and Ewers, 1989 ; Fisher and Ewers, 1991).

Pour approfondir notre compréhension de l'écologie et de la distribution spatio-temporelle des lianes, mon travail a montré l'importance de combler le fossé entre les études à l'échelle de l'espèce et à l'échelle de la communauté, mais de nombreuses limites demeurent. Les principales limites étaient l'insuffisance de données sur les traits des différentes espèces de lianes et les difficultés d'échantillonnage sur le terrain, à cause du caractère destructif des méthodes et qui prenaient beaucoup de temps. Un échantillonnage plus important ou la combinaison des analyses avec des simulations est nécessaire pour mieux comprendre la variabilité intraspécifique et intra-individuelle des caractéristiques des lianes (Albert et al., 2011). En se concentrant sur des espèces focales sélectionnées sur la base de compromis entre l'abondance et la représentation de la diversité fonctionnelle observée à l'échelle de la communauté, il serait possible de simplifier la communauté de lianes à quelques espèces dominantes et de faciliter les mesures sur le terrain (Schnitzer et al., in press). Le développement de nouvelles méthodes de terrain et la simplification des relations entre les traits pourraient aussi aider à faciliter l'étude des lianes. De plus, l'identification botanique précise des espèces de lianes est cruciale pour comprendre les patrons de distribution à différentes échelles (Muller-Landau and Wright, in press). Dans l'ensemble, ma thèse met en évidence la complexité de l'écologie des lianes, la nécessité de poursuivre les recherches et les défis liés à l'étude de ces plantes grimpantes.



*The end :)*