THÈSE PRÉSENTÉE
POUR OBTENIR LE GRADE DE

DOCTEUR DE L'UNIVERSITÉ DE BORDEAUX

ÉCOLE DOCTORALE SCIENCES ET ENVIRONNEMENTS
ÉCOLOGIE ÉVOLUTIVE, FONCTIONNELLE ET DES COMMUNAUTÉS

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GÉNOMIQUE ÉCOLOGIQUE DE L'EXPLOITATION DE NICHE ET DE LA PERFORMANCE INDIVIDUELLE CHEZ LES ARBRES FORESTIERS TROPICAUX

Sous la direction de Myriam HEUERTZ
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Soutenue le 10 Décembre 2020

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Génomique écologique de l'exploitation de niche et de la performance individuelle chez les arbres forestiers tropicaux

Résumé : Les forêts tropicales abritent la plus grande diversité d'espèces au monde, un fait qui reste en partie inexpliqué et dont l'origine est sujette à débat. Même à l'échelle de l'hectare, les forêts tropicales abritent des genres riches en espèces, avec des espèces d'arbres étroitement apparentées qui coexistent en sympatrie. En raison de contraintes phylogénétiques, on s'attend à ce que les espèces étroitement apparentées possèdent des niches et des stratégies fonctionnelles similaires, ce qui questionne les mécanismes de leur coexistence locale. Les espèces étroitement apparentées peuvent former un complexe d'espèces, composé d'espèces morphologiquement similaires ou qui partagent une importante proportion de leur variabilité génétique en raison d'une ascendance commune récente ou d'hybridation, et qui peut résulter d'une radiation écologique adaptative des espèces selon des gradients environnementaux. Malgré le rôle clé des complexes d'espèces dans l'écologie, la diversification et l'évolution des forêts néotropicales, les forces éco-évolutives qui créent et maintiennent la diversité au sein des complexes d'espèces néotropicales restent peu connues. Nous avons exploré la variabilité génétique intraspécifique comme un continuum au sein de populations structurées d'espèces étroitement apparentées, et mesuré son rôle sur la performance individuelle des arbres à travers la croissance dans le temps, tout en tenant compte des effets d'un environnement finement caractérisé au niveau abiotique et biotique. En combinant des inventaires forestiers, des données topographiques, des traits fonctionnels foliaires et des données de capture de gènes dans la station de recherche de Paracou, en Guyane Française, nous avons utilisé la génomique des populations, les analyses d'associations environnementales et génomiques, et la modélisation Bayésienne sur les complexes d'espèces *Symphonia* et *Eschweilera* clade *Parvifolia*. Nous avons montré que les complexes d'espèces d'arbres couvrent l'ensemble des gradients locaux de topographie et de compétition présents dans le site d'étude alors que la plupart des espèces qui les composent présentent une différenciation de niche marquée le long de ces mêmes gradients. Plus précisément, dans les complexes d'espèces étudiés, la diminution de la disponibilité en eau, par exemple depuis les bas-fonds jusqu'aux plateaux, a entraîné une modification des traits fonctionnels foliaires, depuis des stratégies d'acquisition à des stratégies conservatrices, tant entre les espèces qu'au sein de celles-ci. Les espèces de *Symphonia* sont génétiquement adaptées à la distribution de l'eau et des nutriments, elles coexistent donc localement en exploitant un large gradient d'habitats locaux. Inversement, les espèces d'*Eschweilera* sont différentiellement adaptées à la chimie du sol et évitent les habitats les plus humides et hydromorphes. Enfin, les génotypes individuels des espèces de *Symphonia* sont différentiellement adaptés pour se régénérer et croître en réponse à la fine dynamique spatio-temporelle des trouées forestières, avec des stratégies adaptatives de croissance divergentes le long des niches de succession. Par conséquent, la topographie et la dynamique des trouées forestières entraînent des adaptations spatio-temporelles à fine échelle des individus au sein et entre les espèces des complexes d'espèces *Symphonia* et *Eschweilera* clade *Parvifolia*. Je suggère que les adaptations à la topographie et à la dynamique des trouées forestières favorisent la coexistence des individus au sein et entre les espèces des complexes d'espèces, et peut-être plus généralement entre les espèces d'arbres de forêts matures. Dans l'ensemble, je soutiens le rôle primordial des individus au sein des espèces dans la diversité des forêts tropicales, et suggère que nous devrions élaborer une théorie de l'écologie des communautés en commençant par les individus, car les interactions avec les environnements se produisent après tout au niveau de l'individu.

Mots clés : Coexistence des espèces ; Complexe d'espèces ; Distribution des espèces ; Forêts tropicales ; Indice d'encombrement du voisinage ; Indice d'humiditétopographique ; Niche écologique ; Paracou ; Syngameon ; Variabilité intraspécifique

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Ecological genomics of niche exploitation and individual performance in tropical forest trees

Abstract: Tropical forests shelter the highest species diversity worldwide, a fact that remains partly unexplained and the origin of which is subject to debate. Even at the hectare-scale, tropical forests shelter species-rich genera with closely-related tree species coexisting in sympatry. Due to phylogenetic constraints, closely related species are expected to have similar niches and functional strategies, which raises questions on the mechanisms of their local coexistence. Closely related species may form a species complex, defined as morphologically similar species that share large amounts of genetic variation due to recent common ancestry and hybridization, and that can result from ecological adaptive radiation of species segregating along environmental gradients. Despite the key role of species complexes in Neotropical forest ecology, diversification, and evolution, little is known of the eco-evolutionary forces creating and maintaining diversity within Neotropical species complexes. We explored the intraspecific genomic variability as a continuum within structured populations of closely related species, and measured its role on individual tree performance through growth over time, while accounting for effects of a finely-characterized environment at the abiotic and biotic level. Combining tree inventories, LiDAR-derived topographic data, leaf functional traits, and gene capture data in the research station of Paracou, French Guiana, we used population genomics, environmental association analyses, genome-wide association studies and Bayesian modelling on the tree species complexes *Symphonia* and *Eschweilera* clade *Parvifolia*. We showed that the species complexes of Neotropical trees cover all local gradients of topography and competition and are therefore widespread in the study site whereas most of the species within them exhibit pervasive niche differentiation along these same gradients. Specifically, in the species complexes *Symphonia* and *Eschweilera* clade *Parvifolia*, the decrease in water availability due to higher topographic position, e.g., from bottomlands to plateaus, has led to a change in leaf functional traits from acquisitive strategies to conservative strategies, both among and within species. *Symphonia* species are genetically adapted to the distribution of water and nutrients, hence they coexist locally through exploiting a broad gradient of local habitats. Conversely, *Eschweilera* species are differentially adapted to soil chemistry and avoid the wettest, hydromorphic habitats. Last but not least, individual tree genotypes of *Symphonia* species are differentially adapted to regenerate and thrive in response to the fine spatio-temporal dynamics of forest gaps with divergent adaptive growth strategies along successional niches. Consequently, topography and the dynamics of forest gaps drive fine-scale spatio-temporal adaptations of individuals within and among distinct but genetically connected species within the species complexes *Symphonia* and *Eschweilera* clade *Parvifolia*. Fine-scale topography drives genetic divergence and niche differentiation with genetic adaptations among species, while forest gap dynamics maintains genetic diversity with divergent adaptive strategies within species. I suggest that adaptations of tree species and individuals to topography and dynamics of forest gaps promote coexistence within and among species within species complexes, and perhaps among mature forest tree species outside species complexes. Overall, I defend the primordial role of individuals within species in tropical forest diversity, suggesting that we should develop a theory of community ecology starting with individuals, because interactions with environments happen after all at the individual level.

Keywords: Ecological niche; Intraspecific variability; Neighbourhood crowding index; Paracou; Species coexistence; Species complex; Species distribution; Syngameon; Topographic wetness index; Tropical forests

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Unité de recherche: Univ. Bordeaux, INRAE, BIOGECO, 69 route d'Arcachon, 33610 Cestas France

REMERCIEMENTS

À l'heure où je boucle ces trois années de thèse, je ne peux que me sentir reconnaissant et chanceux de toutes les personnes qui m'ont accompagné et dont j'ai croisé la route aussi bien lors de ma thèse que lors du long du chemin qui m'y a amené. Malgré l'ensemble de la rédaction que j'ai dû réaliser pour arriver jusque là, il me semble difficile de remercier exhaustivement les personnes qui ont compté pour moi, et je m'excuse grandement auprès de celles que j'aurais le malheur d'oublier. Bien que j'aime à discuter de la biodiversité des arbres tropicaux, le parcours qui m'a amené jusqu'ici a aussi été l'occasion de me confronter à une richesse humaine extraordinaire aux quatres coins du monde !

L'écriture de cette thèse a été un long travail, mais je n'imagine pas le travail que cela représente de l'évaluer. Je remercie donc les rapporteurs, **Xavier Vekemans** et **Tamara Münkemüller**, ainsi que les examinateurs, **Olivier Hardy**, **Céline Teplitsky**, **Caroline Scotti-Saintagne** et **Marta Benito-Garzón** pour leur intérêt et l'honneur qu'ils me font de participer à mon jury de thèse.

Je ne pourrais commencer sans citer l'incomparable mais aussi diverse équipe d'encadrants géniaux qui m'a supervisé et accompagné pendant trois ans. La richesse de cette thèse commence en effet avec vous qui venez des quatres coins de l'Europe et du monde. Vous qui vivez chacun sur votre continent où vous m'avez toujours accueilli au delà de mes espérances. Vous qui par votre diversité fonctionnelle, autant académique qu'humaine, créez, à mon humble avis, la richesse et la force de cet encadrement. Merci à **Myriam Heuertz** pour ton dynamisme et ta force pour toujours avancer, que tu as su me prêter dans la réalisation de mon doctorat. Mais aussi merci pour ce cadre humain que tu as pu donner à mes trois années: merci pour l'accueil à Bordeaux lors de mon retour de Guyane, merci pour l'incroyable opportunité que tu m'as donné avec l'Équateur qui fut involontairement un magnifique cadeau d'anniversaire, et j'espère pouvoir courir un jour le marathon de Bordeaux avec toi. Merci à **Bruno Hérault** d'avoir accepté de partager ces réflexions incessantes qui m'ont permis d'aller au delà d'où je pouvais espérer atterrir. Je pense que ta manière de réfléchir et de toujours remettre en question ce qui peut être trop facilement admis est primordiale, et j'espère qu'elle restera avec moi au cours de mes futurs travaux. Merci pour ton humanité qui valorise une existence hors du travail, merci pour le vélo, les repas, les rigolades et discussions chez toi, chez moi, au bureau ou sur le terrain. Merci enfin à **Niklas Tysklind** d'avoir depuis la première minute et encore aujourd'hui beaucoup plus cru en moi que moi-même ! À l'heure où nous essayons de pousser le chapitre 4 vers une revue prestigieuse, je ne peux m'empêcher de me rappeler que dès le début tu m'a dit le premier, alors que cela me paraissait totalement inatteignable, que j'arriverais à ce stade. Enfin en plus du fait que tu es toujours aussi agréablement positif et à te réjouir de nos travaux, je suis pour ma part admiratif de ta capacité à rester humble et garder une vie personnelle épanouie, et tu es réellement un modèle pour moi sur ce point. Vous variez peut être du point de vue de l'administration, mais vous êtes à mes yeux tous les trois aussi importants. Je n'ai eu cesse de me rendre compte de la chance que j'ai eu de vous avoir tous les trois au cours de ces années. Au delà de l'opportunité que vous m'avez donné de m'épanouir au sein de cette thèse, je vous remercie pour l'encadrement académique mais surtout pour votre humanité. Je n'ai qu'une demande à vous faire, s'il vous plaît ne changez pas sur votre ambivalence académique et humaine !

Bien que ma thèse ait démarré le 1er septembre, ma passion pour les forêts tropicales a eu lieu dès mon année de césure et s'est poursuivie au cours de mon master 2. Je tiens donc à remercier toute la génialissime équipe du laboratoire d'écologie végétale appliquée de l'Institut Agronomique néo-Calédonien : **Philippe Birnbaum**, **Robin Pouteau**, **Dimitri Justeau**, **Santiago Trueba Sanchez**, **Florian de Boissieu**, **Élodie Blanchard**, **Laure Barrabé**, **Vanessa Hequet**, **Céline Chambrey**, **Hervé Vandrot** et bien entendu **Tanguy Jaffré** . À vous qui m'avez transmis cette passion pour la biodiversité des forêts tropicales tout en me berçant déjà de comptes sur la folie du bassin Amazonien. De la même manière je suis reconnaissant à tout ce qu'ont pu me procurer botaniquement, scientifiquement et humainement les différentes personnes que j'ai pu croiser à l'Institut Français de Pondichéry en Inde : **Maxime Réjou Méchain**, **François Munoz**, **Valérie Raevel**, **Narayanan Ayyappan**, **Natesan Balachandran**, et **Natesan Barathan,** mais aussi **Jules Morel**, **Anaïs Valance**, **Sonia Dinh**, **Grégoire Bobo**, **Charles Trivandrum**, **Maéva Sinou** et **Élodie da Silva**. Sans vous et les judicieux conseils de **Bruno Ferry**, je ne serais sans doute jamais allé rencontrer l'Amazonie lors de mon master 2 en Guyane.

Je ne compte plus mes passages en Guyane, et il est par conséquent compliqué de remercier chronologiquement toutes les personnes qui sont responsables de mon envie incessante de retourner dans le bassin Amazonien. J'ai une première pensée pour mes camarades de master 2 avec qui j'ai partagé la découverte de ce territoire magique : **Timothée Audinot**, **Amandine Confais**, **Solène D'Angelo**, **Oksana Grente**, **Pauline Guillaumeau**, **Mathieu Jegu**, **Morgan Knoster**, **Laurie Lefebvre**, et **Hugo Reizine**. Je remercie grandement l'équipe d'encadrants du master qui ont su patiemment nous transmettre leur passion et leur savoir des forêts tropicales tout en créant des conditions d'étude adorables que j'ai rarement pu rencontrer en France : **Eric Marcon**, **Stéphane Traissac**, **Timothy Chubb**, **Sabrina Coste**, **Jean-Christophe Roggy**, **Patrick Heuret**, et **Pascal Petronelli**. Je remercie les stagiaires, doctorants, et amis qui ont accompagné mon stage de master 2 : **Sébastien Levionnois**, **Camille Dezécache**, **Camille Piponiot**, **Ariane Mirabel**, **Élodie Boriau**, **Louise Authier**, **Jean Legay**. Je dois un éternel remerciement à **Saint-Omer Cazal** avec qui j'ai vécu tous ces mois de terrain à Paracou et sans qui toute cette thèse ne serait pas ce qu'elle est. J'en profite pour remercier la très joviale équipe de génétique, **Valérie Troispoux**, **Éliane Louisanna**, et **Adrien Lalagüe**, avec qui j'ai adoré me réunir autour d'un café après un petit nettoyage de laboratoire. Je remercie toutes les personnes qui m'ont accompagné sur le terrain : **Josselin Cazal**, **Ilke Gelaldi**, et **Fabien Lehuede.** Mais aussi ma génialissime équipe de module FTH : **Adeline Adam**, **Agathe Benfredj Zaleski**, **Numa Faucherre**, et **David Zipper**. Je pense ne jamais oublier nos trajets vers la parcelle 16 accompagné des chants sur "Margot". Il m'est difficile de remercier tous les stagiaires, masters, doctorants, et amis croisés sur le campus ou dans Kourou, mille excuses par avance aux oubliés. Merci à, **Adrien**, **Alexandre**, **Dimitri**, **Alex**, **Emma**, **Eva**, **Guillaume**, **Irene**, **Laurent**, **Maelle**,

Margot, **Maxim**, **Paloma**, **Tom**, **Warren**, **Xavier** d'avoir rendu ces moments si vivants. Et pour la fin, je tiens à remercier les stagiaires que j'ai pu encadrer : **Émilie Ducouret**, **Nino Page**, et **Anne Barranger**, ainsi que **Géraldine Derroire** avec qui j'ai eu la chance de réaliser cet encadrement. Vous êtes aussi géniaux que divers, et vous m'avez sans aucun doute appris autant que ce que j'ai pu vous transmettre.

Bien que la Guyane ait sans doute été le lieu le plus marquant de ma thèse, mes passages à Bordeaux, en Équateur et en Côte d'Ivoire ont aussi été marqués par des personnes remarquables. Je remercie entre autre **Katharina Budde**, **Santiago González Martinez**, **Arthur Demené**, **Juliette Archambeau**, **Elena Valdés-Correcher**, le personnel de la Plateforme Génome Transcriptome de Bordeaux, les membres de l'équipe E4E et plus généralement mes collègues de BIOGECO de leur accueil chaleureux au sein de l'unité. Merci à **Gonzalo Francisco Rivas Torres** et **Pieter van 't Hof** de m'avoir fait aimer l'Équateur en si peu de temps, et de m'avoir emmené dans la station de recherche de Tiputini, sans doute la plus incroyable qu'il m'ait été donné de connaître. Enfin mon passage en Côte d'Ivoire s'est aussi bien déroulé malgré la crise sanitaire qui m'a contraint à y rester plus longtemps que prévu grâce à l'incroyable qualité de l'accueil et la sympathie des personnes rencontrées à Yamoussoukro. On m'avait vanté la qualité de l'accueil en Afrique de l'ouest, mais la réalité dépasse une fois de plus les attentes ! Je remercie de tout mon coeur la **famille Hérault**, **Amani Bienvenu Hippolyte Konan**, **Irie Casimir Zo-Bi, Aimé**, **Marie**, **Ibe**, **Kassi**, **Edi**, **Antoine de Troij**, **Noémie Glapa**, et **Vincyane Badouard** avec qui j'ai passé ces six mois et à cause de qui je n'avais plus envie de quitter le pays à l'heure où la frontière à réouverte !

J'aimerais terminer ces remerciements par ma famille d'adoption et ma vraie famille. En effet mes colocataires qui m'ont innocemment accueilli à Bordeaux au début de ma thèse, sont désormais pour moi une vraie famille d'adoption dans cette ville qui m'était jusqu'alors inconnue. Merci à **Pauline Daniel**, **Mathilde Faisant**, **Thomas Devaux**, **Lola Vivant**, **Kévin Huonic**, **Tom Allibert**, **Rémy Boudet**, **Antoine Buquen**, et les nombreux sous-loc qui ont partagé mon toit au cours de ces trois années, je ne peux imaginer une vie à Bordeaux sans vous ! Je souhaite profondément remercier mes parents qui m'ont transmis cet amour du vivant qui m'a poussé à devenir qui je suis aujourd'hui : **Bernard Schmitt** et **Thérèse Piel**. J'aurais toujours un éternel respect pour ce que vous avez accompli, qui restera à mes yeux toujours plus important et concret que n'importe lequel de mes travaux. Merci aussi à mes frères et soeur qui composent la diversité de cette famille **Aurore**, **Emmanuel**, et **Mikaël**. Mille mercis plus généralement à toutes les personnes qui ont gravité autour de moi pendant ces trois années de thèse aux quatres coins du monde.

Pour finir, je souhaite dédier cette thèse à mon neveu **William** et ma nièce **Océane** en espérant qu'ils aient l'opportunité de voir une nature aussi belle que celle que ces magnifiques années ont pu m'apporter !

CONTENTS

List of Tables

List of Figures

LIST OF MANUSCRIPTS

Chapter 1: **Sylvain Schmitt, Niklas Tysklind, Géraldine Derroire & Myriam Heuertz.** Topography shapes the local coexistence of tree species within species complexes of Neotropical forests. Submitted to *Oecologia*.

Chapter 2. **Sylvain Schmitt, Bruno Hérault, Émilie Ducouret, Anne Baranger, Niklas Tysklind, Myriam Heuertz, Éric Marcon, Saint Omer Cazal, Géraldine Derroire. 2020.** Topography consistently drives intra- and inter-specific leaf trait variation within tree species complexes in a Neotropical forest. *Oikos* **129**:1521-1530. doi 10.1111/oik.07488

Chapter 3. **Sylvain Schmitt, Niklas Tysklind, Bruno Hérault, Myriam Heuertz.** Topography drives microgeographic adaptations of closely-related species in two tropical tree species complexes. Submitted to *New Phytologist*.

Chapter 4. **Sylvain Schmitt, Niklas Tysklind, Myriam Heuertz, Bruno Hérault.** Forest gap dynamics: an underexplored factor that drives divergent adaptive growth strategies within tropical tree species. In preparation for *Proceedings of the National Academy of Sciences*.

Résumé substantiel

Introduction

La biodiversité dans les espèces étroitement liées des forêts tropicales du bassin de l'Amazone

Les forêts tropicales abritent la plus grande diversité d'espèces au monde, un fait qui reste en partie inexpliqué et dont l'origine est sujette à débat. Même à l'échelle de l'hectare, les forêts tropicales abritent des genres riches en espèces, avec des espèces d'arbres étroitement apparentées qui coexistent en sympatrie. En raison de contraintes phylogénétiques, on s'attend à ce que les espèces étroitement apparentées possèdent des niches et des stratégies fonctionnelles similaires, ce qui questionne les mécanismes de leur coexistence locale. Les espèces étroitement apparentées peuvent former un complexe d'espèces, composé d'espèces morphologiquement similaires ou qui partagent une importante proportion de leur variabilité génétique en raison d'une ascendance commune récente ou d'hybridation, et qui peut résulter d'une radiation écologique adaptative des espèces selon des gradients environnementaux. Malgré le rôle clé des complexes d'espèces dans l'écologie, la diversification et l'évolution des forêts néotropicales, les forces éco-évolutives qui créent et maintiennent la diversité au sein des complexes d'espèces néotropicales restent peu connues.

Les individus présentent eux mêmes des variations de performance, de phénotypes et de gènes au sein des espèces. La variation phénotypique, représentant *in fine* la variabilité intraspécifique, est façonnée par (i) le patrimoine génétique, au travers des génotypes, (ii) l'environnement (abiotique et biotique) avec une hétérogénéité spatiale et temporelle, et (iii) des facteurs stochastiques aléatoires. La variabilité intraspécifique est un sujet central en écologie et pourtant relativement inexplorée. Par conséquent, les complexes d'espèces et la variabilité intraspécifique pourraient être les clés pour démêler les forces éco-évolutives qui entraînent la coexistence locale d'espèces étroitement liées.

Coexistence locale des espèces : considérations écologiques et évolutives

La coexistence locale d'espèces proches, similaires sur le plan écologique et phénotypique, est régie par des processus écologiques et évolutifs, qui dépendent de l'histoire de la spéciation et de la différenciation des niches. Une fois en contact, les écologistes considèrent avant tout la compétition pour les ressources et la différenciation de niche qui en résulte, alors que les biologistes évolutionnistes s'intéressent davantage au niveau d'isolement reproductif. Pour une coexistence stable, la théorie des niches évoque que les espèces maximisent les différences de niches écologiques, tandis que la “théorie des similarités émergentes” réconcilie la théorie des niches et la théorie neutre en suggérant la coexistence de groupes distincts d’espèces qui sont fonctionnellement similaires au sein d’un groupe. Les espèces fonctionnellement similaires doivent avoir une fitness similaire comme condition supplémentaire pour une coexistence stable, et les espèces récemment divergentes doivent avoir développé un isolement reproductif suffisant pour éviter la désagrégation des différences et leur homogénéisation génétique lors d’un contact secondaire.

Contexte de l’étude : le site d’étude à long terme de Paracou dans une forêt côtière du Bouclier guyanais

Toute l’étude de doctorat a été menée dans la station de terrain de Paracou (latitude 5°18’N et longitude 52°53’W), riche en biodiversité et en sciences, située dans la région côtière de la Guyane française. La topographie est caractérisée par des microconditions hétérogènes dues à de nombreuses petites collines ne dépassant généralement pas 45 m d’altitude. Une vieille forêt tropicale d’une richesse exceptionnelle pousse dans ce paysage à dominance de Fabaceae, Chrysobalanaceae, Lecythidaceae et Sapotaceae. Une expérimentation d’exploitation forestière a été lancée en 1984 avec douze parcelles de 9 hectares, puis trois parcelles de 6,25 hectares et une parcelle de 25 hectares non perturbée. Le diamètre des arbres à hauteur de poitrine a été recensé tous les 1 à 2 ans depuis 1984. Les arbres ont été cartographiés au mètre près et identifiés botaniquement, souvent au niveau de l’espèce. Le temps et le climat sont enregistrés en permanence grâce à une tour à flux. La pédologie et l’hydrologie ont été finement caractérisées pour plusieurs parcelles. Enfin, des campagnes LiDAR aéroportées ont été menées pendant plusieurs années à Paracou, ce qui a permis de caractériser avec précision la topographie et la structure des forêts. Cette accumulation de données environnementales de haute qualité dans un écosystème aussi riche sur le plan biologique a conduit à de nombreuses découvertes liées à la dynamique éco-évolutive de la biodiversité néotropicale. Par conséquent, la caractérisation fine de la diversité des forêts tropicales, des variations spatio-temporelles abiotiques et biotiques et de leurs relations éco-évolutives fait de Paracou un endroit parfait pour étudier la dynamique éco-évolutive d’espèces d’arbres tropicaux étroitement liées.

Modèles d’étude : *Symphonia globulifera* et *Eschweilera* clade *Parvifolia*, deux complexes d’arbres localement abondants

Symphonia globulifera L. f. est une espèce d’arbre hypervariable pantropicale appartenant à la famille des Clusiacées. *S. globulifera* est répandu de la Guinée Bissau à la Tanzanie dans les paléotropiques africains et du Mexique au Brésil dans les néotropiques américains. *S. globulifera* présente une différenciation écotypique avec la topographie, avec deux morphotypes actuellement reconnus en Guyane française : *S. globulifera sensu stricto* qui pousse dans les bas-fonds inondés de façon saisonnière et *S. sp1* qui pousse sur les pentes et plateaux plus secs.

Eschweilera est un genre hyper abondant appartenant à la famille des Lécythidacées. Les genres *Lecythis* et *Eschweilera* sont paraphylétiques et se composent de huit clades, dont le clade *Eschweilera Parvifolia.* Les espèces abondantes d'*Eschweilera* clade *Parvifolia* à Paracou sont *E. coriacea* (DC.) S.A.Mori, *E. sagotiana* Miers, et *E. decolorans* Sandwith. Comme les morphotypes de *Symphonia*, *E. sagotiana* et *E. coriacea* présentent une différenciation de niche en fonction de la topographie.

Objectifs et plan général

Nous avons exploré la variabilité génétique intraspécifique comme un continuum au sein de populations structurées d'espèces étroitement apparentées, et mesuré son rôle sur la performance individuelle des arbres à travers la croissance dans le temps, tout en tenant compte des effets d'un environnement finement caractérisé au niveau abiotique et biotique. En combinant des inventaires forestiers, des données topographiques, des traits fonctionnels foliaires et des données de capture de gènes dans la station de recherche de Paracou, en Guyane française, nous avons utilisé la génomique des populations, les analyses d'associations environnementales et génomiques, et la modélisation bayésienne sur les complexes d'espèces *Symphonia* et *Eschweilera* clade *Parvifolia* pour répondre à la question générale suivante :

Les génotypes et phénotypes individuels sont-ils adaptés aux environnements abiotiques et biotiques microgéographiques au sein et entre les espèces des complexes d'espèces ?

Nous avons émis l'hypothèse que la variabilité génétique et phénotypique individuelle au sein des espèces et entre elles promeut la coexistence locale au sein des complexes d'espèces par le biais d'adaptations microgéographiques et d'un cloisonnement des niches à travers la topographie et la dynamique des trouées forestières.

Chapitre 1 : La topographie façonne la coexistence locale des espèces d'arbres au sein des complexes d'espèces des forêts néotropicales

Dans cette étude, nous avons exploré la distribution à petite échelle de cinq complexes d'espèces et de 22 espèces au sein des complexes d'espèces. En combinant des inventaires forestiers, une détermination botanique de haute qualité et des données topographiques dérivées du LiDAR sur 120 ha de parcelles permanentes, nous avons utilisé un cadre de modélisation bayésien pour tester le rôle de la topographie à échelle fine et du voisinage des arbres sur la présence de complexes d'espèces et la distribution relative des espèces au sein des complexes.

Les complexes d'espèces d'arbres néotropicaux étaient largement répartis le long de la topographie à l'échelle locale. Les espèces au sein des complexes d'espèces ont montré une différenciation de niche marquée le long des gradients de position topographique, d'accumulation d'eau et de compétition. En outre, les préférences en matière d'habitat étaient coordonnées entre les espèces au sein de plusieurs complexes d'espèces : les espèces plus tolérantes à la compétition pour les ressources poussent sur des plateaux et des pentes plus secs et moins fertiles. S'ils sont soutenus par un isolement reproductif partiel des espèces et une introgression adaptative au niveau des complexes, nos résultats suggèrent que la spécialisation des habitats des espèces au sein des complexes d'espèces et la large distribution écologique des complexes d'espèces pourraient expliquer le succès de ces complexes d'espèces néotropicales à l'échelle régionale.

Chapitre 2 : La topographie entraîne systématiquement une variation intra- et interspécifique des traits foliaires au sein des complexes d'espèces d'arbres dans une forêt néotropicale

Nous avons examiné la variation des traits fonctionnels des feuilles en fonction de la topographie dans une forêt tropicale hyperdiversifiée du Bouclier guyanais. Nous avons collecté les traits fonctionnels des feuilles de 766 arbres appartenant à cinq espèces dans deux complexes d'espèces sur des parcelles permanentes englobant une diversité de positions topographiques. Nous avons testé le rôle de la topographie sur la variation des traits fonctionnels des feuilles à l'aide d'un modèle bayésien hiérarchique, en contrôlant l'effet du diamètre de chaque arbre.

Nous montrons que, à l'image de ce qui a été observé précédemment parmi les espèces et les communautés, les traits foliaires individuels varient d'une stratégie d'acquisition à une stratégie de conservation au sein des espèces. De plus, la diminution de l'humidité des bas-fonds aux plateaux a été associée à un changement des traits foliaires d'une stratégie d'acquisition à une stratégie conservatrice, à la fois au sein des espèces apparentées et entre elles. Nos résultats suggèrent que la variabilité des traits intraspécifiques élargit les niches des espèces et converge aux marges des espèces où les niches se chevauchent, impliquant potentiellement des processus locaux neutres. La variabilité des caractères intraspécifiques favorise l'adaptation locale et la divergence des espèces étroitement apparentées au sein des complexes d'espèces. Elle est potentiellement maintenue grâce au partage interspécifique de la variation génétique par hybridation.

Chapitre 3 : La topographie est le moteur des adaptations microgéographiques des espèces proches dans deux complexes d'espèces d'arbres tropicaux

En combinant les données topographiques dérivées du LiDAR, les inventaires forestiers et les polymorphismes nucléotidiques simples (SNP) provenant d'expériences de capture de gènes, nous avons exploré la structure génétique des populations à l'échelle du génome, la covariation des variables environnementales et l'association génotype-environnement pour évaluer les adaptations microgéographiques à la topographie au sein des complexes d'espèces *Symphonia* et *Eschweilera*, avec trois espèces par complexe et respectivement 385 et 257 individus génotypés.

Au sein des complexes d'espèces, les espèces d'arbres étroitement apparentées ont des optima réalisés différents pour les niches topographiques définies par l'indice d'humidité topographique ou l'altitude relative, et les espèces présentaient des signatures génétiques d'adaptations. Les espèces de *Symphonia* sont différemment adaptées à la distribution de l'eau et des nutriments, tandis que les espèces d'*Eschweilera* évitent les sols hydromorphes et sont différemment adaptées à la chimie du sol.

Nos résultats suggèrent que la topographie représente un puissant moteur de la biodiversité des forêts tropicales, en favorisant des adaptations différentielles et en stabilisant la coexistence locale d'espèces d'arbres étroitement liées au sein de complexes d'espèces d'arbres.

Chapitre 4 : La dynamique des trouées forestières : un facteur sous-exploré qui entraîne des stratégies de croissance adaptative divergentes au sein des espèces d'arbres tropicaux

La dynamique des trouées naturelles dues aux chutes d'arbres est l'un des principaux moteurs du fonctionnement des écosystèmes dans les forêts tropicales. Les arbres réagissent à la dynamique des trouées forestières par une grande variété de stratégies écologiques, mais ces stratégies ont longtemps été étudiées entre les espèces, négligeant la variabilité génétique au sein des espèces. Nous fournissons ici des preuves génétiques de diverses stratégies de croissance adaptative des individus au sein d'espèces d'arbres de forêts matures qui leur permettent de croître dans une diversité d'environnements de lumière et de compétition qui varient avec le temps depuis la dernière chute d'arbre. Nous montrons que la fine dynamique spatio-temporelle des trouées forestières est un facteur précédemment négligé qui, avec d'autres, contribue à maintenir au sein des espèces d'arbres tropicaux la diversité génétique, la matière première de l'évolution.

Discussion

Malgré le rôle clé des complexes d'espèces dans l'écologie, la diversification et l'évolution des forêts néotropicales, on sait peu de choses sur les forces éco-évolutives qui créent et maintiennent la diversité au sein des complexes d'espèces néotropicales. Ici, nous avons montré que la topographie et la dynamique des trouées forestières entraînent des adaptations spatio-temporelles à échelle fine des individus au sein et entre des espèces distinctes mais génétiquement liées au sein des complexes d'espèces *Symphonia* et *Eschweilera* clade *Parvifolia.* Je suggère que les adaptations à la topographie et à la dynamique des trouées forestières favorisent la coexistence des individus au sein et entre les espèces des complexes d'espèces, et peut-être plus généralement entre les espèces d'arbres de forêts matures. Dans l'ensemble, je soutiens le rôle primordial des individus au sein des espèces dans la diversité des forêts tropicales, et suggère que nous devrions élaborer une théorie de l'écologie des communautés en commençant par les individus, car les interactions avec les environnements se produisent après tout au niveau de l'individu.

INTRODUCTION

Biodiversity in tropical forests from the Amazon Basin

Tropical forests' outstanding biodiversity

The maintenance of biodiversity is a long-standing issue for both ecology (Hutchinson 1941) and evolution (Darwin 1909). Biodiversity is characterized by nested levels, from genes, through individuals and species, to ecosystems. Ecosystems hold the biological community of interacting organisms. Earth presents a large number of terrestrial and marine ecosystems. Among them, the outstanding biodiversity of tropical rainforests has always fascinated biologists (Connell 1978). Tropical forests shelter the highest species diversity worldwide (Gaston 2000), a fact that remains partly unexplained and the origin of which is subject to debate (Wright 2002).

Threats that affect tropical forests

Tropical forest disturbances are increasing under the influence of human activities (Davidson et al. 2012, Lewis et al. 2015). Human activities induce direct disturbances on tropical forests, such as forest logging and fires (Pearson et al. 2017), or indirect disturbances, such as global change affecting regional climates (Lewis et al. 2004). For instance, climate change is predicted to increase the frequency of drought events (Davidson et al. 2012) and of convective storms (Negrón-Juárez et al. 2018), among other things. Increasing disturbance threatens many species around the world and is leading to a global and tropical biodiversity crisis (Cardinale et al. 2012). However, biodiversity itself helps tropical forests to cope with disturbances by increasing their resilience (Schmitt et al. 2019). Consequently, there is an increased and urgent need to understand and predict biodiversity dynamics in response to global change.

Regional and local species richness in the Amazon Basin

Among tropical forests, the Amazon Basin is the world's most diverse terrestrial ecosystem. Neotropical rainforests harbour around one hundred thousand species of seed plants accounting for ca. 37% of all seed plants worldwide (Gentry 1982, Eiserhardt et al. 2017, Antonelli and Sanmartín 2011). Lowland Amazonia alone is estimated to shelter around sixteen thousand tree species (Steege et al. 2013). Even at the hectare-scale, tropical forests shelter up to several hundred tree species (Gentry 1988). Among tree species, a few defined as oligarchies are abundant from local to regional scale (Pitman et al. 2001). Similarly at the regional scale, 1.4% of the estimated total of Amazonian tree species represent more than half of the total number of observed stems above ten centimeter diameter at breast height and are thus called hyperdominant (Steege et al. 2013).

The paradoxical coexistence of closely-related tree species in sympatry

The five thousand species of trees described in Amazonia belong to only height hundred ten genera (Steege et al. 2013), including thus many species rich genera. Even at the hectare-scale, tropical forests shelter species-rich genera with closely-related species coexisting in sympatry (Caron et al. 2019). Closely-related species are expected to share similar niche and functional strategies due to phylogenetic constraints (Wiens et al. 2010). Niche and functional similarities are commonly expected to lead to increased competition between closely-related species and ultimately to local competitive exclusion of one species by the other (but see competitive combining, Aarssen 1983). Despite the local abundance and regional success of closely-related species growing in sympatry (Gentry 1988, Steege et al. 2013, Pinheiro et al. 2018), little is known of eco-evolutionary forces driving the local coexistence of closely-related species.

Biodiversity in closely-related species

Species concepts and their limits

Carl von Linné, considered as the father of modern taxonomy, characterised species as follows:

> All species reckon the origin of their stock in the first instance from the veritable hand of the Almighty Creator: for the Author of Nature, when He created species, imposed on his Creations an eternal law of reproduction and multiplication within the limits of their proper kinds. He did indeed in many instances allow them the power of sporting in their outward appearance, but never that of passing from one species to another. Hence to-day there are two kinds of difference between plants: one a true difference, the diversity produced by the all-wise hand of the Almighty, but the other, variation in the outside shell, the work of Nature in a sportive mood. (Linnaeus 1938)

Obviously, Carl von Linné's contributions were tremendous for modern taxonomy, and new definitions of species appeared after the introduction of the theory of evolution (Darwin 1909). Species have been defined as groups of organisms which reproduce among themselves and are isolated from other such groups, protecting the integrity of their genotypes (Mayr 1996). This reflects the biological species concept based on reproductive isolation. But species concepts and definitions have been largely debated (Mayden 1997), especially concerning plants. Many species concepts have been defined, such as phylogenetic, biological, ecological, morphological, or genetic species (De Queiroz 2007). However, tree species in species-rich genera have a higher level of genetic polymorphism (Caron et al. 2019) and exchange genes across species boundaries more often among congeners (Whitney et al. 2010) than species in species-poor genera. Despite the usefulness of the species concept in ecology and evolution, these observations push it to its limits and force us to go beyond the pre-Darwinian view of species that is too persistent in ecology.

Beyond species: species complexes and syngameons

Interspecific hybrids occur in 16% of plant genera (Whitney et al. 2010). Hybrids are often anecdotic as they may be sterile, less fertile, or less fit than their parents, although some survive and reproduce allowing the transfer of adaptations across species boundaries (Runemark et al. 2019). Species that are morphologically similar and/or share large amounts of genetic variation due to recent common ancestry and/or hybridization are defined as species complexes (Pernès and Lourd 1984). Species complexes can result from ecological adaptive radiation characterised by species segregation along environmental gradients (Seehausen 2004). More specifically, closely-related species living in sympatry connected by limited, but recurrent, interspecific gene flow are called syngameon (Suarez-Gonzalez et al. 2018). Syngameons are evolving at two contrasting levels, they maximize each species' adaptation to its ecological niche, and they evolve at the syngameon level benefiting all the constituent species. As a whole, they might decrease the overall risk of syngameon extinction, while allowing ecological adaptation of their species (Cannon and Lerdau 2015). Consequently, syngameons are not necessarily a transitional stage before complete speciation but may be a successful evolutionary state *per se* (Cannon and Petit 2019). In addition, Neotropical forests potentially contain a high frequency of species complexes and/or syngameons whose evolutionary role in forest diversity is underestimated (Caron et al. 2019). Despite the key role and potential abundance of species complexes and syngameons in Neotropical ecology, diversification, and evolution (Pinheiro et al. 2018), little is known of the ecological drivers creating and maintaining diversity within Neotropical species complexes (Baraloto et al. 2012a, Levi et al. 2019a, Steege et al. 2013, Cannon and Petit 2019).

The neglected intraspecific variability

Individuals display variation in performance, phenotypes, and genes within species. Intraspecific variability is ultimately represented by phenotypic variation among communities and ecosystems. Phenotypic variation will be shaped by (i) genetic heritage, through genotypes, (ii) the environment (both abiotic and biotic) with spatial and temporal heterogeneity, and (iii) random stochastic factors (Whitlock et al. 2007). Intraspecific variability is a central topic in ecology and yet relatively unexplored (Hallgrímsson and Hall 2005). For instance, tree variability regarding crown size and light interception is often relegated to an error term and ignored when interpreting ecological processes (Vieilledent et al. 2010). Nevertheless, authors advocate for a better understanding of the role of intraspecific variability in ecology (Chave 2004, Clark 2010, Albert et al. 2010b, 2011, Violle et al. 2012).

Recent work has shown that intraspecific trait variation is relatively large. Vieilledent et al. (2010) found individual variability to account for a large amount of the variation in tree allometric relations. Several authors particularly assessed intraspecific variation of phenotypic traits. Hulshof and Swenson (2010b) partitioned variation of leaf traits in Costa Rican dry forest, and found that intraspecific trait variability accounted for 36 to 83% of total variance; while Messier et al. (2010a) found only 12 to 30% of variation associated to intraspecific trait variability in lowland tropical forests. At the community level, the meta-analysis of Siefert et al. (2015b) found on average an overall intraspecific trait variation of 25% within communities and 32% among communities. Finally, Le Bagousse-Pinguet et al. (2014) estimated the intraspecific level to represent between 13.5 and 33.6% of total functional diversity in limestone grasslands. This results further question the percentage of individual variation with a functional role compared to putative stochastic noise.

Beyond the assessment of intraspecific trait variation, some studies investigated the role of intraspecific variability in community assembly. Messier et al. (2010a) found a lack of variance at the plot level that they interpreted as a trait-based environmental filtering and an important role of intraspecific trait variability in plant community assembly. The role of intraspecific trait variability was highlighted in community assembly shift due to environmental gradients in space or time. Siefert and Ritchie (2016) found intraspecific trait variability to drive shifts of mean height, leaf area, and specific leaf area (*i.e.* area divided by dry weight) following grassland fertilization. Jung et al. (2010a) found community mean specific leaf area and height significantly varying along a flooding gradient, where intraspecific trait variability accounted for 44 and 32%, respectively of the trait-gradient relationships. Moreover, patterns of niche differentiation were revealed only when intraspecific trait variability was taken into account (Jung et al. 2010a). Similarly, Paine et al. (2011) found intraspecific trait data to be more sensitive and a better indicator of both niche differentiation and environmental filtering than interspecific trait data. Finally, complementary studies used simulations to investigate possible long term impact of intraspecific variability on communities. Barabás and D'Andrea (2016) models highlighted a higher resilience and stability of community assembly for heritable traits. Vellend (2006) models highlighted the role of intraspecific genetic variability through genetic diversity on both community species diversity and composition. Consequently, species complexes and intraspecific variability might be keys to unravel the eco-evolutionary forces driving the local coexistence of closely-related species.

Local coexistence of species: ecological considerations

Niche and neutral theory

At the species level, different ecological theories have been developed to explain the coexistence of species and thus the persistence of biodiversity. Niche theory explains species local coexistence based on ecological niche differences limiting competitive exclusion (Weiher and Keddy 1995, Lortie et al. 2004a). The heterogeneity of resources distribution in space and time defines fine-scale habitat where species can coexist. For instance, the topography spatially drives water and nutrient distribution in tropical forest (John et al. 2007). Therefore, topography has a pervasive effect in differentiating habitat preference among species (Gunatilleke et al. 2006, Kraft et al. 2008, Allié et al. 2015). In particular, soil nutrients, also influenced by topography through hydromorphy, directly influence the spatial distribution of forest tree species (Jucker et al. 2018, John et al. 2007). Additionally, forest gap dynamics is a strong driver of above- and below-ground competition for resources in space and time (Hubbell et al. 1999, Breugel et al. 2012). Access to light has been recognized as a driver of closely-related species coexistence through habitat differentiation (Yamasaki et al. 2013). Conversely, neutral theory explains the local coexistence of functionally equivalent species through stochastic life, death, reproduction, and dispersal dynamics (Hubbell 2001). The emerging similarity theory reconciles niche and neutral theories by suggesting coexistence of distinct groups of species that are functionally similar within groups (Scheffer and Van Nes 2006, Hérault 2007). Functionally similar species must have similar fitness as an additional condition for stable coexistence (Chesson 2000a, Tobias et al. 2014, Turcotte and Levine 2016). In addition, fitness averaging among species can generate patterns congruent with the two theories, and is thus underlining the role of intraspecific variability in ecology (Chave 2004). But, numerous other theories exist to explain species coexistence (Wright 2002), in particular competition and forest succession among tropical tree species.

Neighbours and competition

Theories have also explored biotic interactions to explain the coexistence of species. The Janzen-Connell hypothesis explains species coexistence and the maintenance of tropical diversity with the interactions of two effects: (i) dispersal from parents, with more likely dispersal at short than long distance, and (ii) distance and density-dependent survival of offspring due to competition, pathogens, and herbivores, with more likely survival at long than short distance from parents (Clark and Clark 1984, Hyatt et al. 2003). Consequently, the inverted probability distribution with distance between the two effects results in a higher recruitment probability at intermediate distances according to the hypothesis. Other authors suggested theories focused on density-dependence. A model of symmetric density-dependent survival reproduced similar distributions of species abundances than abundance distributions found with neutral dispersal limitation models, advocating for the existence of one mechanism or the combination of density-dependent survival and neutral dispersal limitations in natural populations (Volkov et al. 2005). Moreover, asymmetric density-dependence of survival with different levels of competition with conspecific and heterospecific predicted well the rarity and abundance of species in tropical tree communities (Comita et al. 2010).

Treefall and succession

Beyond density-dependence, theories have explored the peculiar and paramount role of treefalls and succession in natural tropical forests. Aboveground competition for light due to forest gap dynamics is often greater than the effect of belowground competition for water and nutrient dynamics, even in early successional stages (Breugel et al. 2012). The intermediate disturbance hypothesis explains diversity with disturbance, positing a maximal diversity at intermediate regime of disturbances (Molino and Sabatier 2001). The intermediate disturbance hypothesis advocates thus for a primordial role of forest gap dynamics in natural tropical forests (Canham et al. 1990). After a treefall, pioneer species grow first in light-gaps, whereas late-successional species grow later under closed-canopy (Craven et al. 2015), defining successional niches among species (Herault et al. 2010). Abiotic factors also play a role in the distribution of treefalls and forest gap dynamics (Ferry et al. 2010a, Goulamoussène et al. 2017). Consequently, forest gap dynamics stress the importance to consider temporal as well as spatial dynamics to understand species coexistence (Soininen 2010).

Intraspecific variability

Despite the role of intraspecific variability in the forest community (Siefert et al. 2015a, Messier et al. 2010b), previous ecological theories often ignore individual diversity within species' local populations (Chave 2004). However, several authors suggested the hypothesis or have shown evidence that intraspecific genetic or phenotypic variability promotes species coexistence (Lichstein et al. 2007). Following observations of community trait shifts due to intraspecific variability, Jung et al. (2010a) concluded that intraspecific trait variability promotes species coexistence, by facilitating species to pass through environmental filtering. Studying limestone grassland functional diversity, Le Bagousse-Pinguet et al. (2014) were able to relate increasing interspecific trait overlap through increased intraspecific variability to a greater species coexistence. Clark (2010) suggested that intraspecific variability allows species to differ in their distribution of responses to the environment and thus to pass environmental filtering, which would have occurred on species' mean phenotype. Clark (2010) found this hypothesis to be consistent with theories that predict a coexistence of more species with competition being stronger within than between species. Similarly, Chesson (2000b) suggested that intraspecific variability promotes species coexistence through stabilizing mechanisms "if negative intraspecific interactions tend to be greater than interspecific interactions". Some authors suggested that the intraspecific level should hold evidence of mechanisms promoting species coexistence and thus biodiversity. Laughlin and Laughlin (2013) suggested testing the limiting similarity hypothesis in the trait space incorporating intraspecific variability. And, Laughlin et al. (2012) suggested that intraspecific variability could answer paradoxes in theories of species coexistence.

Intraspecific variability might play a different role depending on the studied organism. Specifically, long-lived species, such as tropical trees, have high ontogenetic variation and phenotypic plasticity that might be a result from a high intraspecific variability to face environmental hazards before they reach sexual maturity (Sultan 1987, Borges 2009). Callaway et al. (2012) suggested that intraspecific variability, through phenotypic plasticity in response to neighbours, might promote community diversity and species coexistence, letting species adjust the composition of their populations. Aarssen (1983) suggested the "competitive combining ability" hypothesis which hypothesizes species coexistence to be based on the ability of each species to respond to spatial and variable selection imposed by neighbouring species. Following his hypothesis, the species' ability to respond to selection promotes biodiversity through species coexistence and stabilizes species composition among communities (Vellend 2006).

Demography and fundamental trade-offs

Ultimately, the introduced theories try to predict species demography to explain species coexistence. Tree demography rests on individual performance in recruitment, growth, survival, and reproduction (Violle et al. 2007, Baraloto et al. 2005, Poorter and Bongers 2006, Román-Dañobeytia et al. 2012). The ability of trees to grow, survive, and reproduce can be measured by growth rates (Baraloto et al. 2005, Herault et al. 2010, Osazuwa-Peters et al. 2017), mortality rates (Aubry-Kientz et al. 2015a, Osazuwa-Peters et al. 2017)), and monitoring of cohorts and allele frequencies (Unger et al. 2016), respectively. Fundamental trade-off exists between performance components. For instance, tropical trees have been shown to present a trade-off between growth and survival (Wright et al. 2010, Buchman et al. 1983). In particular, a trade-off was identified between survival in shade and growth in gaps (Baraloto et al. 2005, Herault et al. 2010). Globally, some authors suggested the existence of a fast-slow continuum decoupled with a reproductive strategy to represent all plant demographic strategies (Salguero-Gómez 2017).

Functional traits: from fundamental trade-offs to ecological niches

To bridge the gap between ecological niches and demography, functional traits reflect fundamental trade-offs determining the species' ecological niches along environmental gradients (Wright and Westoby 2002) and shape the structure (Paine et al. 2011) and dynamics (Hérault and Piponiot 2018) of species in conjunction with their environment (Kraft et al. 2008).

Functional traits have been specifically defined as traits which impact fitness indirectly through their effect on performance (Violle et al. 2007). Functional traits can be numerous and classified into traits related to biochemistry, physiology, anatomy, morphology, and phenology.

Several studies have related tree performance to functional traits. Hérault et al. (2011) related tree growth to stem economics (sensu Chave et al. 2009) and adult stature. Aubry-Kientz et al. (2013) related tree mortality to wood density, maximum height, laminar toughness, and stem and branch orientation, highlighting the trade-off between fast- and slow-growing species (Reich 2014a). Philipson et al. (2014) found that wood density was shaping the growth-mortality trade-off. On the opposite, Poorter and Bongers (2006) found that leaf traits underlie the growth-mortality trade-off, with short-lived physiologically active leaves resulting in higher growth capacity but lower survival chance. Finally, less is known about functional drivers of reproduction performance with tropical trees, but Niklas and Enquist (2003) were able to estimate the annual reproductive biomass thanks to the two-thirds power of the aboveground biomass of standing trees.

In addition, functional strategies related to fundamental demographic trade-offs have been identified among tropical tree species, better bridging demographic and trait-based approaches (Salguero-Gómez et al. 2018). Functional traits covary among species (Díaz et al. 2016) and communities (Bruelheide et al. 2018) along distinct economics spectra of leaf (Osnas et al. 2013, Wright et al. 2004, but see Lloyd et al. 2013) and wood (Chave et al. 2009). The leaf economics spectrum opposes acquisitive ecological strategies, with high photosynthetic carbon assimilation, to conservative ones with high investment in leaf defence and durability (Wright et al. 2004). The wood economics spectrum opposes fast growing to slow growing species (Chave et al. 2009). Nevertheless, some authors advocate for a unique plant economics spectrum (Reich 2014a).

Adaptive evolution: from individual genomes to tree species

Bridging ecology and evolution: ecological genomics

Traditionally, theories and studies in community ecology focused on species, ignoring genotypic and phenotypic variation within species (Mcgill et al. (2006); but see the literature in the intraspecific variability paragraph). Consequently, ecological theories and related studies often ignore evolutionary forces driving the past and future of biodiversity. Conversely, geneticists are often focused on the function of genes outside of their natural environment. But “nothing in biology makes sense except in the light of evolution” (Dobzhansky 1973). The assumption that evolution and ecology play at very different spatial- and time-scales might have been an impediment to understand the role of eco-evolutionary processes in species coexistence (Pelletier et al. 2009). However, eco-evolutionary processes have been documented for a while

(Tutt 1896) and can play an important role in the dynamics of both species and communities (Bailey et al. 2009). To bridge the gap between ecology and evolution, ecological genomics specifically explores the genetic mechanisms that underlie the responses of organisms to their natural environments (Savolainen et al. 2013, Holliday et al. 2017).

The genomic basis of adaptation

Genetic variability is the genetic differences we find within and among genomes of individuals within and among populations. Thus genetic variability is ultimately formed of polymorphisms. A locus can contain one or several polymorphisms resulting in several alleles of the given locus. Genetic variability always arises from new mutations inside the genome of an individual (e.g. Plomion et al. 2018). If mutations directly promote individual fitness through its phenotype in its local environment, they may become a source of adaptation. They can, thus, also contribute beneficial alleles to the pool of standing genetic variation into the population, allowing eventually for further adaptation of other individuals from the population (Barret and Schluter 2008). Finally, both new mutations and standing genetic variation can be transferred and be beneficial in other populations through adaptive introgression (Tigano and Friesen 2016). The establishment of beneficial new mutations and fixation of standing genetic variation will depend on genetic drift, and the strength of selection over gene flow, where gene flow can be disruptive but bear adaptive introgressions (Tigano and Friesen 2016).

A first step in understanding the link between phenotypic and genetic variation is to estimate the genetic component of phenotypic variation. Genotypic and population components of phenotypic variation can be assessed through the use of a mixed model, known as the animal model (Wilson et al. 2010). Next, a simple way to detect the genomic basis of adaptation is to map variants with an adaptive phenotype, using genome wide association studies (GWAS; Korte and Farlow 2013). The major issue is to correctly deal with population structure in natural populations to avoid false positive discovery, using for instance mixed models (Zhou and Stephens 2012). But phenotypes are not always available, and we can try to detect genomic adaptations based on the genetic signatures left by selection. Different models of selection have been developed and imply varying methodology to detect signatures of selection (Flood and Hancock 2017). The hard sweep model describes the fast selection of a new variant which rapidly increases to high frequency, ‘sweeping’ previous variation in the region due to hitchhiking of neutral variation (Smith and Haigh 1974). Consequently, the simplicity of this model allows the detection of the signature of selection thanks to the sweep based on linkage disequilibrium (Sabeti et al. 2002), allele frequency change (Fay and Wu 2000), and population differentiation (Gaggiotti and Foll 2010). Nevertheless, more complex scenarii can exist in nature. Soft sweep models predict multiple haplotypes with adaptive variants (Messer and Petrov 2013), jeopardizing traditional hard sweep detection. Indeed, many phenotypes investigated by evolutionists are expected to be polygenic, e.g. human height (Zeng et al. 2018). Finally, adaptive introgression represents the transfer between divergent lineages of adaptive variants thanks to hybridization. Adaptive introgression might be important among plants with hybrids occurring in 16% of genera (Whitney et al. 2010). All genetic adaptations originate within an individual's genome but spread among individuals and ultimately species.

Individual microgeographic adaptations

Individual adaptation in trees has traditionally been studied among populations thanks to common gardens representing provenances sampled on wide ecological and spatial gradients (e.g. Dewoody et al. 2015). Individual adaptations among populations is called local adaptation, based on the fact that local populations tend to have a higher mean fitness in their native environment than in other environments (Savolainen et al. 2013, Lascoux et al. 2016). But fine spatio-temporal scale environmental variations can happen locally and lead to individual adaptations too. Evidence exists for eco-evolutionary processes at microgeographic scale, e.g. within the dispersal neighbourhood of the organism (Richardson et al. 2014), and under gene-flow (Tigano and Friesen 2016, Savolainen et al. 2007). Microgeographic adaptation participates in the local drivers of intraspecific variability with phenotypic plasticity (Benito Garzón et al. 2019). Topography and abiotic habitat have been evidenced to promote intraspecies divergences and microgeographic adaptations in Neotropical tree species (Brousseau et al. 2013, 2015). Other studies revealed microgeographic change in genetic structure and diversity of Neotropical trees without identifying adaptations (Jones and Hubbell 2006, Audigeos et al. 2013), including effect of topography (Torroba-Balmori et al. 2017), logging (Degen et al. 2006, Leclerc et al. 2015) and forest gaps (Scotti et al. 2015). Few studies further identified traits underlying genetic adaptations to local factors, like serotiny adaptations to fire in Meditarranean pine (Budde et al. 2014). Beyond the microgeographic adaptations of individuals within populations, local adaptation translates into adaptations of individuals between populations. But a strong disruptive selection between locally adapted populations to different habitats may be deleterious, revealing a potential transition from local adaptation to ecological speciation (Lascoux et al. 2016).

Species adaptive radiations

Savolainen et al. (2006) were able to evidence an event of sympatric ecological speciation with species sympatry, sister relationships, reproductive isolation, and highly unlikely earlier allopatric phase. But the latter might be hard to evidence in continental species. Closely-related species growing in sympatry in differentiated ecological niches form an adaptive radiation, such as Darwin's finches in the Galapagos (Grant and Grant 2019, Seehausen 2004). Consequently, evolutionary history behind adaptive radiations falls within a continuum from sympatric ecological speciation to secondary contacts of species ecologically specialised in allopatry or parapatry (Rundell and Price 2009). Few studies evidenced adaptive radiation driven by topography or other abiotic habitats for tropical trees (Pillon et al. 2014, Paun et al. 2016).

Species complexes can result from adaptive radiations and species segregation along environmental gradients. Species complexes may combine and reshuffle genetic features among species in hybrid swarms (Seehausen 2004), exploring the whole niche breadth and multiplying the number of potential ecological niches, reducing competition among closely-related species, and helping species gain reproductive isolation (Runemark et al. 2019). Indeed, hybrid or derived species require some degree of reproductive isolation from their progenitors to avoid becoming an evolutionary melting pot. Nevertheless, simulations suggest that low hybridization success among closely-related species promotes coexistence of species in the community by allowing the survival of rare species through hybridisation (Cannon and Lerdau 2015). Species-specific adaptations may be maintained or even maximised under gene flow, especially with selective pressures varying in space and or time (Tigano and Friesen 2016). For instance, the European white oaks form one of the best known syngameons (Cannon and Petit 2019). European white oaks' species lack private haplotypes indicating extensive hybridisation (Petit et al. 2002), but show unique ecological niches with regard to drought, cold, and tolerance to alkaline-soils (Leroy et al. 2019, Cannon and Petit 2019). The coexistence of the different species is partly due to the genes allowing their survival in different ecological niches (Leroy et al. 2019).

Eco-evolutionary peculiarities of trees

Forest trees are a major group of organisms due to their combined ecological, economic, and societal importance (Holliday et al. 2017). Trees have eco-evolutionary peculiarities (Petit and Hampe 2006), such as their great size, long life time, numerous seeds, large effective population sizes and overlapping generations (Heuertz et al. 2006, Brown et al. 2004). Tree seedlings undergo strong selection in early life stages (Kremer et al. 2012). Tree species often have outcrossing mating systems, maintain high levels of gene flow (Hamrick et al. 1992, Nybom 2004, Petit et al. 2004), and have low speciation rates (Petit and Hampe 2006). As a result, forest trees present a large degree of adaptation (Savolainen et al. 2013), and high levels of genetic variability. Woody species have been shown to harbour more genetic diversity within populations but less among populations than non woody species (Hamrick et al. 1992). Consequently, tropical trees are well suited to explore eco-evolutionary dynamics in closely-related species and their impact on Neotropical biodiversity.

Study context: the long-term study site of Paracou in a coastal forest of the Guiana Shield

The Guiana Shield

The Guiana Shield is covered by a Precambrian geologic formation (more than 1.9 Gyr old) of over 2 million square kilometers, in northern South America, from the Amazon river in the Brazilian state of Amapa in the South-East to the Orinoco river in Venezuela in the West (Hammond 2005). Soils developed from volcanic, plutonic, and metamorphic materials of the Paleoproterozoic (Delor et al. 2003), and are now heavily eroded, thick, and chemically poor (Ferry et al. 2003). Specifically in French Guiana, the elevation is relatively low (Bellevue mountains culminate at 851m) and topography is characterised by numerous small hills carving out seasonally-flooded bottomlands (Epron et al. 2006). Precise geomorphological characterisation and maps of French Guiana can be found in Guitet et al. (2013).

Guiana Shield geology and pedology compared with lowland western Amazon results in a major gradient in soil fertility directly affecting tree composition and function across Amazonia (Steege et al. 2006). Soil properties, including organic carbon, phosphorous, arbuscular mycorrhizal fungi, clay, and toxic elements, drive forest dynamics, through tree growth and mortality, in the phosphorus-depleted Guiana Shield (Soong et al. 2020). Poorer soils with slower nutrient cycling have lower tree growth but longer longevity compared to richer clay soils, which are better able to retain phosphorus and organic matter (Soong et al. 2020).

Ninety percent of the Guiana Shield is covered by tropical forests, whereas less than 2 million people inhabit the area, mainly on the coasts, which results in the highest level of forest cover per capita worldwide (Hammond 2005). Contrary to previous expectations, the Guiana Shield has been inhabited for a long time, with pre-Columbian occupations still influencing current forest structure and composition (Odonne et al. 2019). Although well conserved, the forests of the Guiana Shield are subject to numerous anthropogenic pressures including selective logging, gold mining, and land use change (Dezécache et al. 2017a). Selective logging affects 2 Mha of Amazonian forest per year but forests recover faster in the Guiana Shield than in western Amazonia (Piponiot et al. 2016). Gold mining primarily affects the forests of the Guiana Shield in South America with an exponential increase since the early 2000's (Dezécache et al. 2017b).

The long-term study site of Paracou

The whole PhD study was conducted in the biologically- and scientifically-rich Paracou field station (latitude 5°18'N and longitude 52°53'W), in the coastal region of French Guiana. The site is characterized by an average annual rainfall of 3041 mm and a mean air temperature of 25.71 °C, with a marked seasonal variation (Aguilos et al. 2018). Topography is characterised by lowlands with heterogeneous micro-conditions due to numerous small hills generally not exceeding 45 m a.s.l. An old tropical forest with an exceptional richness (i.e. over 200 woody species per hectare) grows in this landscape with a dominance of Fabaceae, Chrysobalanaceae, Lecythidaceae, and Sapotaceae (Gourlet-Fleury et al. 2004).

A logging-experiment was initially launched with twelve 9-ha plots in 1984, further filled with three 6.25-ha, and one 25-ha undisturbed plots. Nine of the original plots were logged in 1986 with a range of disturbance intensities resulting in diverse biotic environments (details in Hérault and Piponiot 2018). Tree diameters at breast height (DBH) have been censused every 1-2 years since 1984. Trees have been mapped to the nearest meter and botanically identified, often to the species level. Weather and climate is continuously recorded thanks to an eddy flux tower (Bonal et al. 2008). Pedology and hydrology have been finely characterised for several plots (Ferry et al. 2010a). Finally, airborne LiDAR campaigns were conducted for several years at Paracou, which allowed the accurate characterization of forest topography and structure (Vincent et al. 2012).

This accumulation of high-quality environmental data in such a biologically-rich ecosystem led to numerous discoveries related to eco-evolutionary dynamics in Neotropical biodiversity. Among others, climate has a strong impact on forest dynamics, with, for instance, a drought resistance in species with high wood density and small stature favored by climate (Aubry-Kientz et al. 2015b). Topography effects on nutrient distribution and water availability drive forest dynamics (Ferry et al. 2010a) and result in pervasive habitat differentiation among species (Allié et al. 2015). Water availability (Wagner et al. 2011, 2012) and forest gaps (Herault et al. 2010) particularly drive tree growth. And a relation exists between tree growth and survival (Aubry-Kientz et al. 2013, 2015a). In addition to demography, co-variation of functional traits, their composition, and their relations to environment and demography have been explored (Baraloto et al. 2010a, Hérault et al. 2011). Finally, fine-scale genetic structures resulting from the identified ecological dynamics have also been documented. Gene dispersal inferences suggested limited gene and seed dispersal (gene dispersal from 150m to 1200m), possibly increasing local tree density (Degen et al. 2004, Hardy et al. 2005). Abiotic and biotic factors have been evidenced to structure genetic variation and diversity (Audigeos et al. 2013, Scotti et al. 2016), including topography (Brousseau et al. 2013), logging (Leclerc et al. 2015), and forest gaps (Scotti et al. 2015). But only few studies evidenced genetic adaptations (Brousseau et al. 2015). Therefore, the fine characterization of tropical forest diversity, fine abiotic and biotic spatio-temporal variations, and their eco-evolutionary relationships makes Paracou a perfect place to study eco-evolutionary dynamics in closely-related species of tropical trees.

Study models: *Symphonia globulifera* and *Eschweilera* clade Parvifolia two species complexes of locally abundant trees

Symphonia

Symphonia globulifera L. f. is a hypervariable pantropical tree species belonging to the Clusiaceae family. The *Symphonia* genus also includes a radiation of ca. 20 endemic sister-species in Madagascar (Perrier de la Bâthie 1951). *S. globulifera* is widespread from Guinea Bissau to Tanzania in the African Paleotropics and from Mexico to Brazil in the American Neotropics (Budde et al. 2013). *Symphonia* is an ancient genus with pollen identified in the Niger delta dated to 45Ma, that colonized the Americas from Africa ca. 18-16 Ma (Dick et al. 2004). *S. globulifera* is mainly outcrossing, even if selfing occurs, and disperses mostly over short distances (Degen et al. 2004, Hardy et al. 2005, Carneiro et al. 2009). *S. globulifera* is pollinated by hummingbirds, perching birds, and lepidoptera in the Neotropics and sunbirds in Africa (Torroba-Balmori et al. 2017). *S. globulifera* is dispersed by bats and tapirs in the Neotropics and small mammals in Africa (Torroba-Balmori et al. 2017). *S. globulifera* used many refugia during the Quaternary glaciations (Dick and Heuertz 2008, Budde et al. 2013). *S. globulifera* shows fine-scale genetic structure with topography throughout its distribution (Torroba-Balmori et al. 2017). Moreover, *S. globulifera* has possible ecotypic differentiation with topography and wetness, with two currently recognized morphotypes in French Guiana: *S. globulifera sensu lato* growing in seasonally-flooded bottomlands and *S. sp1* growing in drier slopes and plateaus (Allié et al. 2015). In addition, the two morphotypes of French Guiana have different seasonal water stress tolerance (Baraloto et al. 2007), functional traits (Baraloto et al. 2010a, Fortunel et al. 2012) and growth potential (Hérault et al. 2011). Reciprocal transplantation experiments of Symphonia seedlings have shown that survival and growth performance of each morphotype is better in their home environment than in the opposite environment, showcasing how the two morphotypes are differently adapted to their respective environments (Tysklind et al., 2020). The two local morphotypes of *S. globulifera* might thus form a species complex in French Guiana (Baraloto et al. 2012a, Gonzalez et al. 2009). Genetic resources have been developed for *S. globulifera* with a published low-coverage genome sequenced in an individual from Africa (Cameroon; Olsson et al. 2017), an unpublished draft genome from an American individual (I. Scotti pers. com.), and an annotated transcriptome from an American individual, as well (N. Tysklind pers. com.).

Eschweilera

Eschweilera is a hyberabundant genus belonging to the Lecythidaceae family. *Lecythis* and *Eschweilera* genera are paraphyletic and consist of eight clades, including the *Eschweilera* clade

Parvifolia (Mori et al. 2016, Huang et al. 2015). Abundant species of the *Eschweilera* clade *Parvifolia* in Paracou are *E. coriacea* (DC.) S.A.Mori, *E. sagotiana* Miers, and *E. decolorans* Sandwith (besides numerous others such as *E. wachenheimii* (Benoist) Sandwith and *E. squamata* S.A.Mori). *Eschweilera coriacea* is hyperdominant in all six Amazonian regions (Pitman et al. 2001, Steege et al. 2013) and showed high genetic heterogeneity compared to other sympatric closely-related species (Heuertz et al. 2020). Similarly to *Symphonia* morphotypes, *E. sagotiana* and *E. coriacea* exhibit niche differentiation with topography (Allié et al. 2015), different water stress tolerance (Baraloto et al. 2007), functional traits (Baraloto et al. 2010a, Fortunel et al. 2012) and growth potential (Hérault et al. 2011). *Eschweilera* clade *Parvifolia* is a species complex with low phylogenetic resolution and high plastid DNA sharing (Baraloto et al. 2012a, Heuertz et al. 2020, Gonzalez et al. 2009, Huang et al. 2015). *Eschweilera* species share more haplotypes among species than neutral expectations (Caron et al. 2019), suggesting the interspecific gene flow characteristic of syngameons. *Eschweilera* clade *Parvifolia* species are diploid but some include a strong signature of a past genome duplication (Heuertz et al. 2020). Genetic resources for *Eschweilera* calde *Parvifolia* include a Lecythidaceae bait set (Vargas et al. 2019) developed *in silico* and tested on previous genome skimming (Thomson et al. 2018).

Aims and general plan

The main objective of the PhD thesis was to explore the genotype-environment interactions in shaping individual phenotypic diversity within and among closely-related species belonging to species complexes of Neotropical trees. The study site for the thesis was the lowland rainforest in the research station of Paracou, French Guiana, where detailed inventory and tree growth data, as well as environmental characterization are available. I specifically wished to consider the intraspecific genomic variability as a continuum within structured populations of closely related species, and measure its role on individual tree performance through growth over time, while accounting for effects of a finely-characterized environment at the abiotic and biotic level. Combining tree inventories, LiDAR-derived topographic data, leaf functional traits sampling, gene capture experiments, population genomics, environmental association analyses, genome wide association studies and Bayesian modelling for species distribution, functional traits variation, and growth on *Symphonia* and *Eschweilera* species complexes, I addressed the following general question:

General: Are individual genotypes and phenotypes adapted to microgeographic abiotic and biotic environments within and among species of species complexes?

I hypothesised individual genetic and phenotypic variability within and among species to promote local coexistence within species complexes through microgeographic adaptations and niche partitioning across topography and forest gap dynamics (Fig. 1). This general hypothesis will be explored all along the thesis with subsequent questions, hypotheses and corresponding chapters.

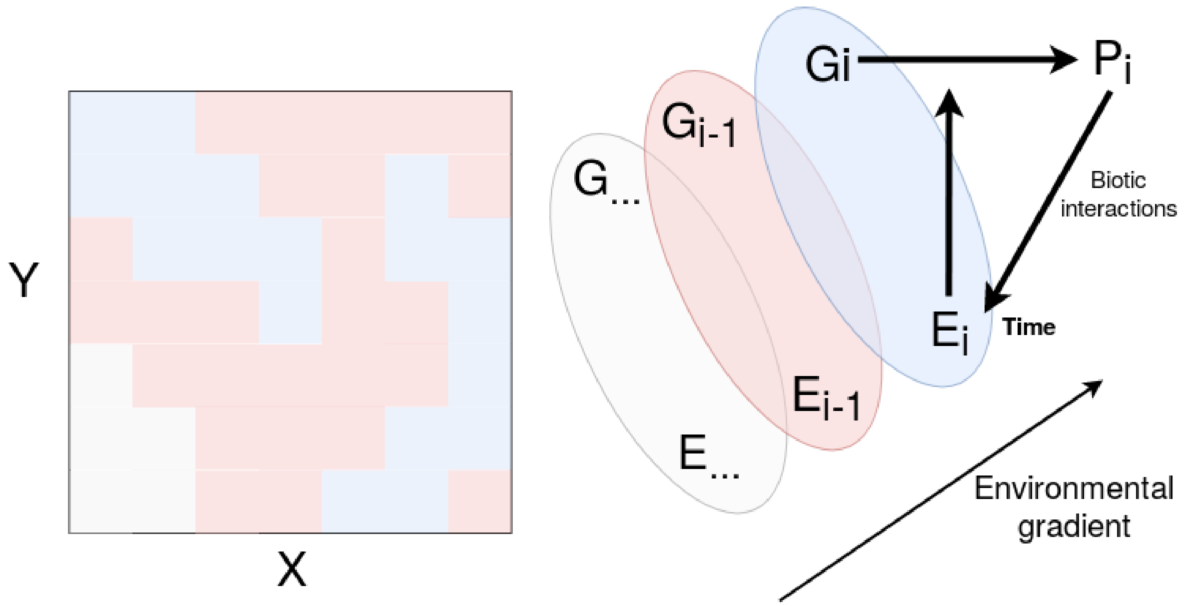

Figure 1: Microgeographic adaptations among sympatric species within a species complex. Different genetic species G grow in sympatry in specific habitats E along an environmental gradient. The interaction of local environment E_i and genotype G_i result in phenotype P_i . Phenotype P_i feeds back to its local environment through biotic interactions. Temporal variation of the environment influences the phenotype of the established genotype.

To explore genotype-environment interactions, I needed first to characterise abiotic and biotic factors structuring ecological niches within and among species complexes (E_i in Fig. 1). I addressed the following question:

***Chapter 1*. How are species distributed within and among species complexes along biotic and abiotic gradients in Paracou?**

I hypothesised species complexes to be widely spread across biotic and abiotic environments; whereas biotic and abiotic environments favour niche differentiation among species within species complexes.

To continue in the ecological theater, I needed to explore the role of abiotic and biotic environment on functional traits within and among closely-related species (E_i to P_i in Fig. 1). I addressed the following question:

***Chapter 2*. How does the abiotic environment influence individual leaf trait values among and within closely-related species within species complexes?**

I hypothesised the abiotic environment to shape trait variation both among and within species in interaction with tree diameter and access to light within species complexes.

Once ecological niches defined and their relations with phenotypes explored, I could dive into individual and species adaptive genomics ($E_i \times G_i$ to P_i in Fig. 1). I addressed individual and species adaptation to topography with the following question:

***Chapter 3*. Are tree species and individuals adapted to the fine-scale abiotic gradient?**

I hypothesised species to be delimited along topography with fixed neutral and adaptive variants among and within species of species complexes.

Similarly, I addressed individual and species adaptation to forest gap dynamics with the following question:

***Chapter 4*. Are tree species and individuals adapted to a trade-off between growth and light access in response to forest gap dynamics?**

I hypothesised individual genotypes to be adapted to a trade-off between growth and light access in response to forest gap dynamics.

Finally, once I explored the biotic and abiotic niches of individuals and species within species complexes, the resulting phenotypes and the underlying genomic adaptations, I was able to study the role of genotype-environment interactions in the coexistence of individuals and species within species complexes. I addressed the following question:

Discussion*. *How do tree species' and individual's adaptations to microgeographic topography and forest gap dynamics drive coexistence within and among species of the* Symphonia *species complex ?

I hypothesised genotypic adaptations within species of *Symphonia* to decrease the risk of a stochastic local extinction due to wide successional niches which respond to fine spatio-temporal dynamics of forest gaps; and adaptations among species to stabilize local coexistence with differentiated species' topographic niches within the *Symphonia* species complex.

Chapter 1: Topography shapes the local coexistence of tree species within species complexes of Neotropical forests

Submitted the 7th of April 2020 and under review in Oecologia

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Abstract

Lowland Amazonia includes around five thousands described tree species belonging to more than height hundred genera, resulting in many species-rich genera. Numerous species-rich tree genera share a large amount of genetic variation either because of recent common ancestry and/or recurrent hybridization, forming species complexes. Despite the key role that species complexes play in understanding Neotropical diversification, and the need for exploiting a diversity of niches for species complexes to thrive, little is known about local coexistence of Neotropical species complexes in sympatry.

By taking advantage of a study site in a hyperdiverse tropical forest of the Guiana Shield, we explored the fine-scale distribution of five species complexes and 22 species within species complexes across wetness and neighbor crowding gradients representing abiotic and biotic environments respectively. Combining full forest inventories, high-quality botanical determination, and LiDAR-derived topographic data over 120ha of permanent plots, we used a Bayesian modelling framework to test the role of fine-scale topography and tree neighbourhood on the presence of species complexes and the relative distribution of species within complexes.

Species complexes of Neotropical trees were widely spread across topography at the local-scale. Species within species complexes showed pervasive niche differentiation along topographic position, water accumulation, and competition gradients. Moreover, habitat preferences along topography and competition were coordinated among species within several species complexes: species more tolerant to competition for resources grow in drier and less fertile plateaux and slopes as opposed to wet and fertile bottom-lands, where species less tolerant to competition for resources are more abundant. If supported by at least partial reproductive isolation of species and adaptive introgression at the complex level, our results suggest that both habitat specialisation of species within species complexes and the broad ecological distribution of species complexes might explain the success of these Neotropical species complexes at the regional scale.

Keywords

species distribution; syngameon; habitat specialisation; Paracou

Introduction

Tropical forests shelter the highest level of biodiversity worldwide (Gaston 2000), as already showcased by Connell (1978). Lowland Amazonia includes around 5,000 described tree species belonging to 810 genera (Steege et al. 2013), resulting in many species-rich genera. To understand the processes leading to such diversity, it is pivotal to understand what ecological mechanisms lead to the relative success of these species-rich genera. Among them, many have been shown to have a higher level of genetic polymorphism than species-poor genera, oftentimes sharing haplotypes among species, which is likely related to introgression among congeneric species (Caron et al. 2019). Indeed, interspecific hybrids occur in 16% of genera, and more often so in species-rich genera (Whitney et al. 2010). Hybrids are often sterile or less fertile than their parents, although some survive and reproduce allowing the transfer of adaptive variance across species boundaries (Runemark et al. 2019). Species that are morphologically similar, or have blurry morphological differences, and/or share large amounts of genetic variation due to recent common ancestry and/or hybridization are defined as species complexes (Pernès and Lourd 1984). Species complexes can result from adaptive radiation and segregation among species in the use of environmental variable gradients, through a combination and reshuffling of genetic features among species in hybrid swarms (Seehausen 2004), which may multiply the number of potential ecological niches, in turn reducing competition among the species and helping the species gain reproductive isolation (Runemark et al. 2019). The establishment of a hybrid or derived species requires some degree of reproductive isolation from its progenitors to avoid becoming an evolutionary melting pot. Nevertheless, simulations suggest that low hybridization success among congeneric species promotes coexistence of species in the community by allowing the survival or rare species through hybridisation (Cannon and Lerdau 2015). Furthermore, the way we perceive the role of genetic connectivity among populations and species is quickly changing, where species-specific adaptations may be maintained or even maximised despite high levels of gene flow, especially if selective pressures are spatially and/or temporally variable (Tigano and Friesen 2016). When closely related but distinct species that live in sympatry are connected by limited, but recurrent, interspecific gene flow, they are called a syngameon (Suarez-Gonzalez et al. 2018). Syngameons are particular in that they evolve responding to two contrasting evolutionary pressures, those acting at the species level maximizing species-level adaptations to a niche that reduces competition among species, and those acting at the syngameon level which benefit all constituent species. Syngameons as a whole might thus have a selective advantage, decreasing the overall risk of genus extinction, maximising population size, all the while allowing adaptation of their distinct species to specific niches and reducing competition among species (Cannon and Lerdau 2015). Consequently, and in juxtaposition to other types of species complexes, syngameons are not necessarily a transitional or incipient phase of a process towards complete speciation but may be a highly successful evolutionary status *per se* (Cannon and Lerdau 2015). In one of the best known syngameons, the European white oak, the constituent species lack private cpDNA haplotypes indicating extensive hybridisation (Petit et al. 2002), but each of its constituent species has unique ecological preferences, including drought and cold tolerance, and adaptation to alkaline soils (Leroy et al. 2019, Cannon and Petit 2019). The maintenance of the different species is orchestrated, in part, by the genes allowing survival in their ecological niche preferences (Leroy et al. 2019).

Similarly, Neotropical tree species show pervasive species-habitat associations (Fine et al. 2004, Esteves and Vicentini 2013). Specifically, congeneric species pairs may have contrasting preferences for topography and soil type (Allié et al. 2015, Lan et al. 2016, Itoh et al. 2003), and sometimes may grow in the same abiotic habitat but segregate according to light access (Yamasaki et al. 2013). Habitat specialization may thus support congeneric species coexistence in sympatry. Among Neotropical congeneric tree species, many share genetic variation (Caron et al. 2019), which leads us to hypothesize that they may operate as syngameons.

Despite the key role of species complexes and syngameons in Neotropical ecology, diversification, and evolution (Pinheiro et al. 2018), little is known of the ecological drivers creating and maintaining diversity within Neotropical species complexes (Baraloto et al. 2012a, Levi et al. 2019a, Steege et al. 2013, Cannon and Petit 2019). Particularly, the generality of niche specialisation to environmental variables among species within species complexes, as a potential driver of speciation and maintenance of species complexes, has not been addressed.

Here, we assessed the relative importance of the abiotic environment and biotic interactions in shaping species distribution within and among species complexes. We took advantage of the Paracou study site with more than 75,000 censused and geolocalized individual trees in a highly diverse tropical forest site located within the Guiana Shield in Amazonia. The Paracou site encompasses a diversity of micro-habitats through topographic variation ranging from seasonally flooded bottomlands to drier plateaus (Gourlet-Fleury et al. 2004) and displays variation in canopy gap size distribution (Goulamoussène et al. 2017) and forest turn-over (Ferry et al. 2010a). Combining tree inventories and LiDAR-derived topographic data, we used Bayesian modelling to address the following questions: (1) Are species complexes widely spread across biotic and abiotic environments, i.e. as generalists, or do they occupy specific niches, i.e. as specialists? (2) Do species within complexes also behave as generalists or does the biotic and abiotic environment favor niche differentiation within species complexes ?

Material and Methods

Study site

The study was conducted in the northernmost part of the Guiana Plateau region, at the Paracou field station. The site is characterized by an average of 3,102 mm annual rainfall and mean air temperature of 25.7°C (Aguilos et al. 2018). Old tropical forest with an exceptional richness (e.g. over 750 woody species) develops in this area across a succession of small hills rising to 10–40 m *a.s.l.* (Gourlet-Fleury et al. 2004). We used seven undisturbed permanent inventory plots from Paracou (i.e. six plots of 6.25 ha and one of 25 ha) which have been censused (i.e. diameter at breast height > 10 cm) every 1-2 years since 1984.

Species complexes

From the Paracou database, we identified five species complexes based on evidence for low (phylo-)genetic resolution or plastid DNA sharing in the clade (Baraloto et al. 2012a, Gonzalez et al. 2009, Caron et al. 2019): *Eschweilera clade Parvifolia* (Lecythidaceae; Chave et al. unpublished; Heuertz et al. 2020); *Licania* (Chrysobalanaceae; Bardon et al. 2016); *Iryanthera* (Myristicaceae); *Symphonia* (Clusiaceae; Torroba-Balmori et al. (2017)]; and *Talisia* (Sapindaceae). We removed species with less than ten individuals in Paracou in 2015, which resulted in five species complexes each including two to nine species (Tab. 1). The species in the five species complexes are dispersed by animals and/or birds (*Eschweilera* see Mori et al. (1993); *Iryanthera* see Howe (1983); *Licania* see Hammond and Brown (1995), *Symphonia* see Forget et al. (2007); *Talisia* see Julliot (1996) and Larpin and Larpin (1993)). In addition, *Eschweilera*, *Licania*, and *Talisia* share haplotypes between species pairs (Caron et al. 2019) and *Symphonia* shows introgression between species pairs (S. Schmitt in prep.), suggesting interspecific gene flow characteristic of syngameons.

Table 1: Identified species complexes with species including more than 10 individuals in Paracou.

Complex	Genus	Species	N
Iryanthera	Iryanthera	sagotiana	381
Iryanthera	Iryanthera	hostmannii	335
Licania	Licania	alba	1117
Licania	Licania	membranacea	442
Licania	Licania	canescens	164
Licania	Licania	micrantha	139
Licania	Licania	ovalifolia	95
Licania	Licania	sprucei	76
Licania	Licania	laxiflora	37
Licania	Licania	parvifructa	12
Licania	Licania	densiflora	6
Parvifolia	Eschweilera	sagotiana	1208
Parvifolia	Eschweilera	coriacea	500
Parvifolia	Eschweilera	decolorans	84
Parvifolia	Eschweilera	wachenheimii	19
Parvifolia	Eschweilera	grandiflora	14
Parvifolia	Eschweilera	pedicellata	14
Symphonia	Symphonia	sp.1	382
Symphonia	Symphonia	globulifera	71
Talisia	Talisia	hexaphylla	60

Complex	Genus	Species	N
Talisia	Talisia	praealta	37
Talisia	Talisia	simaboides	31

Environmental variables

Two near-uncorrelated (Pearson's $r = 0.12$, see supplementary material Fig. 28) environmental descriptors were chosen to depict the distribution of species complexes and that of species within complexes. Topographic wetness index (TWI) identifies water accumulation areas and is thus critical for species distribution at local scale in tropical ecosystems (Ferry et al. 2010a, Allié et al. 2015). TWI was derived from a 1-m resolution digital elevation model built based on data from a LiDAR campaign done in 2015 using SAGA-GIS (Conrad et al. 2015).

A neighbourhood crowding index (NCI; Uriarte et al. 2004b) was calculated from field censuses and used as a descriptor of the biotic interactions among trees. Although we recognize their potential non-negligible role in explaining species distributions, other biotic effects, such as variance in herbivory pressure and pathogen species richness, were not directly included into our analyses. The neighbourhood crowding index NCI_i for each tree individual i was calculated with the following formula:

$$NCI_i = \sum_{j|\delta_{i,j}<20m}^{J_i} DBH_j^2 e^{-\frac{1}{4}\delta_{i,j}} \tag{1}$$

where DBH_j is the diameter of neighbouring tree j and i, j its distance to individual tree i. NCI_i is computed for neighbours at a distance i, j of up to 20m because NCI showed negligible effect beyond 20m in preliminary analysis. The size effect of neighbours was taken as their squared DBH, and hence proportional to their basal area. The distance effect of neighbours was set to -1/4, corresponding to neighbours beyond 20m having less than 1% effect compared to the effect of neighbours at 0m.

Analyses

Distribution of complexes The distribution of each species complex was inferred separately. We considered the occurrences of all individuals from species belonging to the species complex as presences, and all occurrences of trees belonging to other species as pseudo-absences. The presence of each species complex Presencespecies complexk was inferred with a logistic regression within a Bernoulli distribution (which corresponds to the best model form among several forms tested, see supplementary material Tab. 6 and Fig. 29):

$$Presence_{species\ complex_k} \sim Bernoulli[logit^{-1}(\alpha_k + \beta_k * X + \gamma_k * X^2)] \qquad (2)$$

were X is the matrix of environmental descriptors (TWI and NCI), α is the intercept, β is a vector representing the slope of environmental descriptors and γ is a vector representing the quadratic form of effects of environmental descriptors for every species complex k.

Distribution of species Joint distributions of species were inferred within each species complex. We used a softmax regression within a conjugated Dirichlet Process and Multinomial distribution:

$$Presence_{species_i|species\ complex_k} \sim Dirichlet\ Multinomial(softmax(\alpha_i + \beta_i * X + \gamma_i * X^2)) \quad (3)$$

were $Presence_{species_i|species\ complex_k}$ represents the species i for every individual as a simplex of 0s and 1s (i.e. 0 for all other species from the species complex and 1 for the considered species), X is the matrix of environmental descriptors (i.e. TWI and NCI), α is the vector of species intercepts, β is a matrix representing the slope of environmental descriptors and γ is a matrix representing the quadratic form of effects of environmental descriptor for every species iof the species complex k.

Environmental descriptors were all reduced in order to ease model inference and compare the strength of the effects among environmental descriptors. A Bayesian method was used to infer parameters of all models using stan language (Carpenter et al. 2017, see supplementary material Species complex code and Species code) and rstan package (Stan Development Team 2018) in the R environment (R Core Team 2020).

Results

The topographic wetness index (TWI) and the neighbourhood crowding index (NCI) had globally null or weak effects on the abundance of species complexes, at the exception of an effect of TWI on *Eschweilera clade Parvifolia*, *Licania*, and *Iryanthera* (Fig. 2). Wet habitats ($TWI > 4$) resulted in increased abundance of the species complexe Iryanthera but a decreased abundance of the species complexes *Licania* and *Eschweilera clade Parvifolia* (Fig. 1B). Despite TWI did not change species complex ranking in abundance.

Conversely, the TWI strongly influenced the species distribution within complexes with a shift in species dominance, while the effect of the NCI was substantial but did not shift species dominance within species complex. TWI and NCI effects are illustrated by a gradient of response from positive and parameters (*i.e.* increasing curve) to negative and parameters (*i.e.* decreasing curve) within each complex, besides a few positive-negative associations of parameters indicating a bell curve with a local extremum (Fig. 3). For instance, *I.*

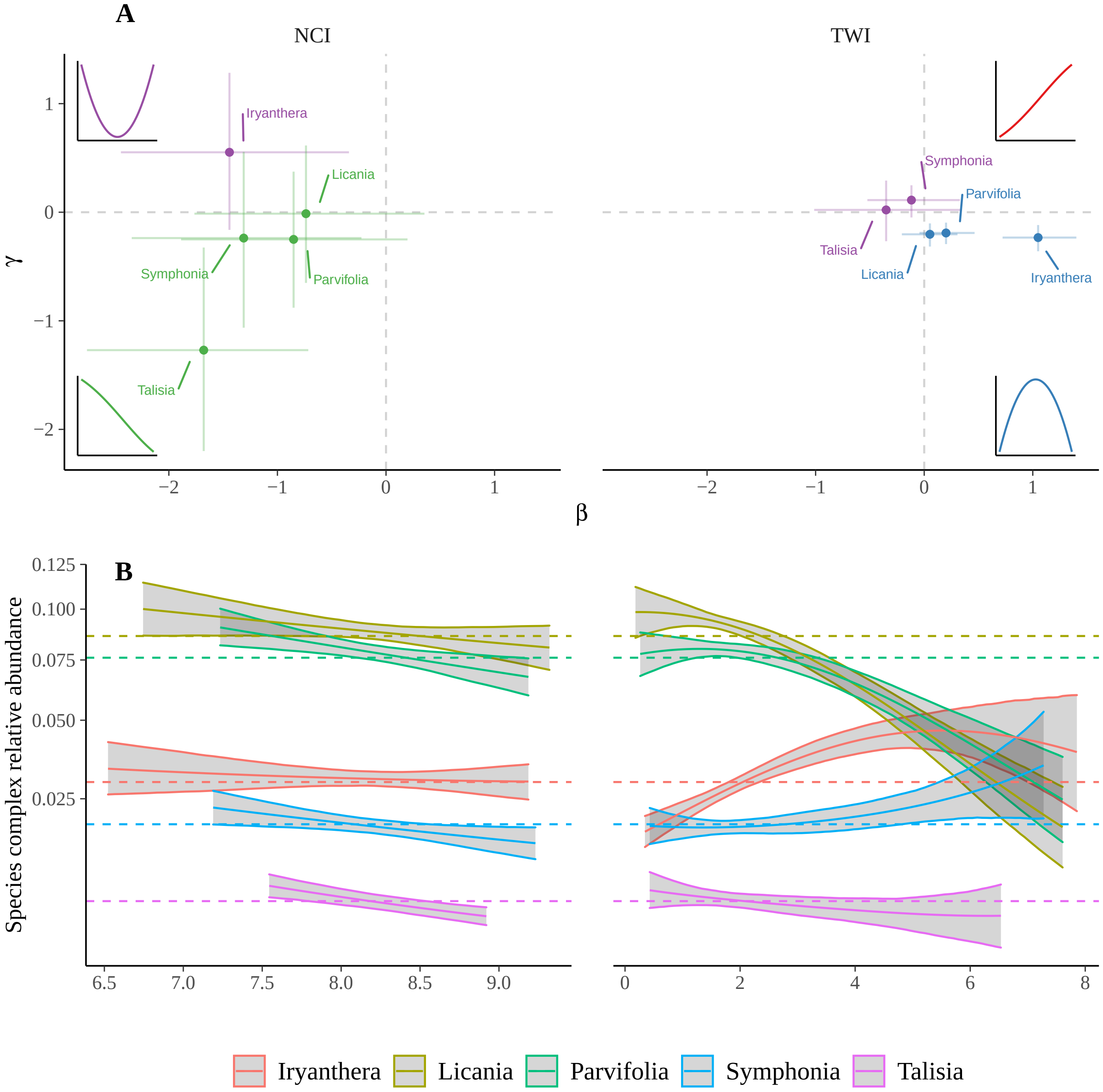

Figure 2: Parameters posteriors (**A**) and predicted relative abundance (**B**) for species complexes. Subplot **A** represent parameters posteriors for species complexes as their position in the β-γ space for each descriptor (TWI and NCI), with the point representing the mean value of the parameter posterior, thin lines the 80% confidence interval. The color indicates the sign of anddetermining the shape of the distribution represented by the 4 subplots with corresponding colors. Subplot **B**, represent species complex predicted relative abundance with solid line and area representing respectively the mean and the 95% confidence interval of projected relative abundance of species complexes depending on descriptors. The color indicates the species complex whereas the dashed lines represent the mean relative abundance of the complex in Paracou.

hostmanii, *E. coriacea*, and *S. globulifera* species relative abundances increased with water accumulation (TWI) when it decreased for *I. sagotiana*, *E. sagotiana*, and *S. sp1* within *Iryanthera*, *Eschweilera clade Parvifolia* and *Symphonia* species complexes respectively (Fig. 4). The change of relative abundance along the topography gradient even led to a shift of dominance between aforementioned species within *Symphonia*, *Eschweilera clade Parvifolia* and *Iryanthera* species complexes, revealing a strong effect of topography. Similarly, *L. membranacea*, *E. sagotiana*, and *S. sp1* species relative abundances increased with neighbour crowding (NCI) when it decreased for *L. alba*, *E. coriacea*, and *S. globulifera* within *Licania*, *Eschweilera clade Parvifolia* and *Symphonia* species complexes respectively (Fig. 4). Thus, two species complexes included species with opposed preference of TWI and NCI. For instance, *S. sp1* more tolerant to neighbor crowding grow preferentially in drier habitats such as plateaux when *S. globulifera* is more abundant with decreased neighbor crowding and dominates in wet habitat such as bottom-lands.

Discussion

Understanding the the eco-evolutionary processes creating and maintaining species complexes, such as how species within species complexes segregate in their ecological niche exploitation (Runemark et al. 2019), is paramount to further our knowledge of Neotropical diversification processes (Pinheiro et al. 2018). Nevertheless, the ecological processes governing species complexes distributions in the Neotropics have received relatively little attention (Baraloto et al. 2012b, Levi et al. 2019a, Steege et al. 2013). Here, we show that species complexes of Neotropical trees as a whole span all the topography and competition gradients and are thus widely spread across light, water, and nutrient habitats at fine-scale. Conversely, most species within species complexes show pervasive niche differentiation along topographic position, water accumulation, and competition gradients. Habitat preferences along topography and competition were coordinated among species within several species complexes: species more tolerant to competition for resources grow in drier and less fertile plateaux and slopes as opposed to wet and fertile bottom-lands, where species less tolerant to competition for resources are more frequently found. Consequently, if supported by as least partial ecological reproductive isolation of species, but with occasional adaptive introgression at the complex level, our results suggest that both widespread distribution of species complexes combined with habitat specialisation of species within species complex might explain the success of these Neotropical species complexes at the regional scale (Steege et al. 2013).

Species complexes are widely spread across habitats

The general null or weak effects of biotic and abiotic environmental variables considered here on species complexes distribution suggest that species complexes are widely spread across light, water, and nutrient habitats at the local-scale, and that the species complexes are

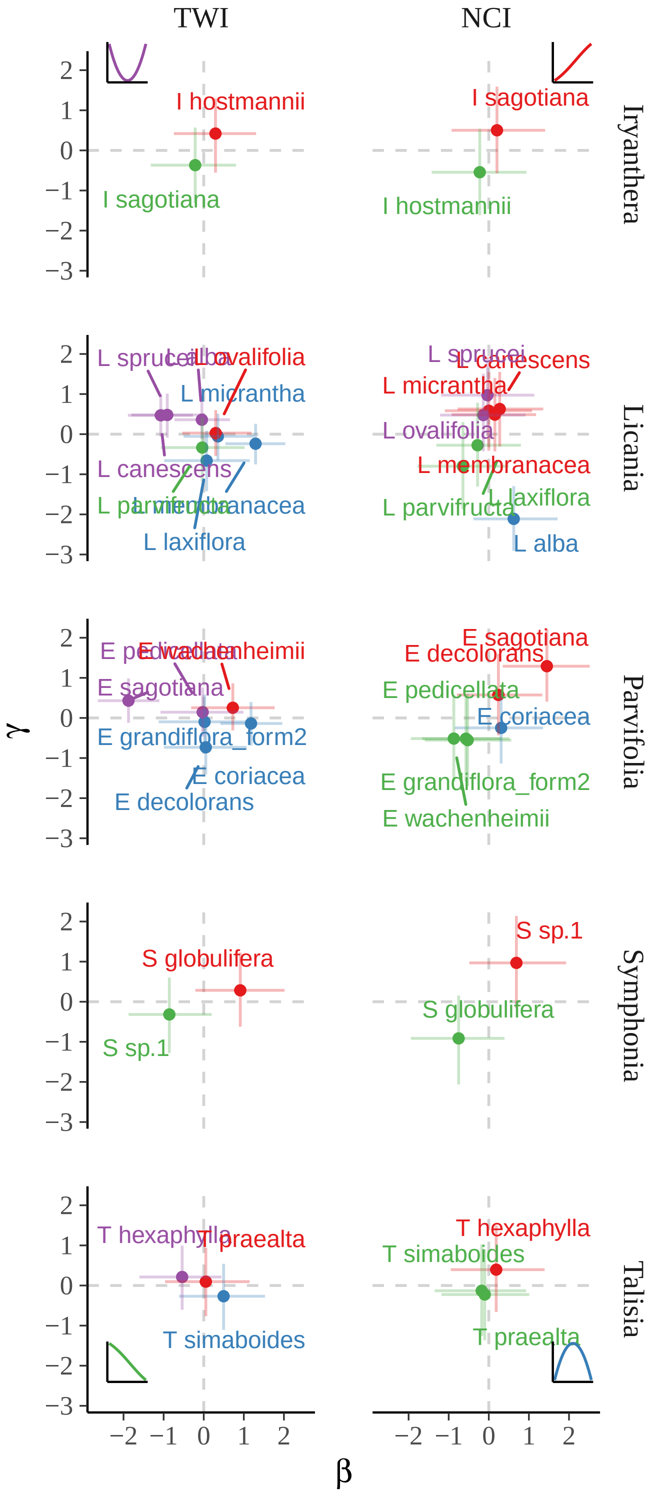

Figure 3: TWI and NCI effects on species relative distribution within species complexes. Parameters posteriors for species within species complexes is represented as their position in the β-γ space for each descriptor and each complex, with the point representing the mean value of the parameter posterior, thin lines the 80% confidence interval. The color indicates the sign of anddetermining the shape of the distribution represented by the 4 subplots with corresponding colors.

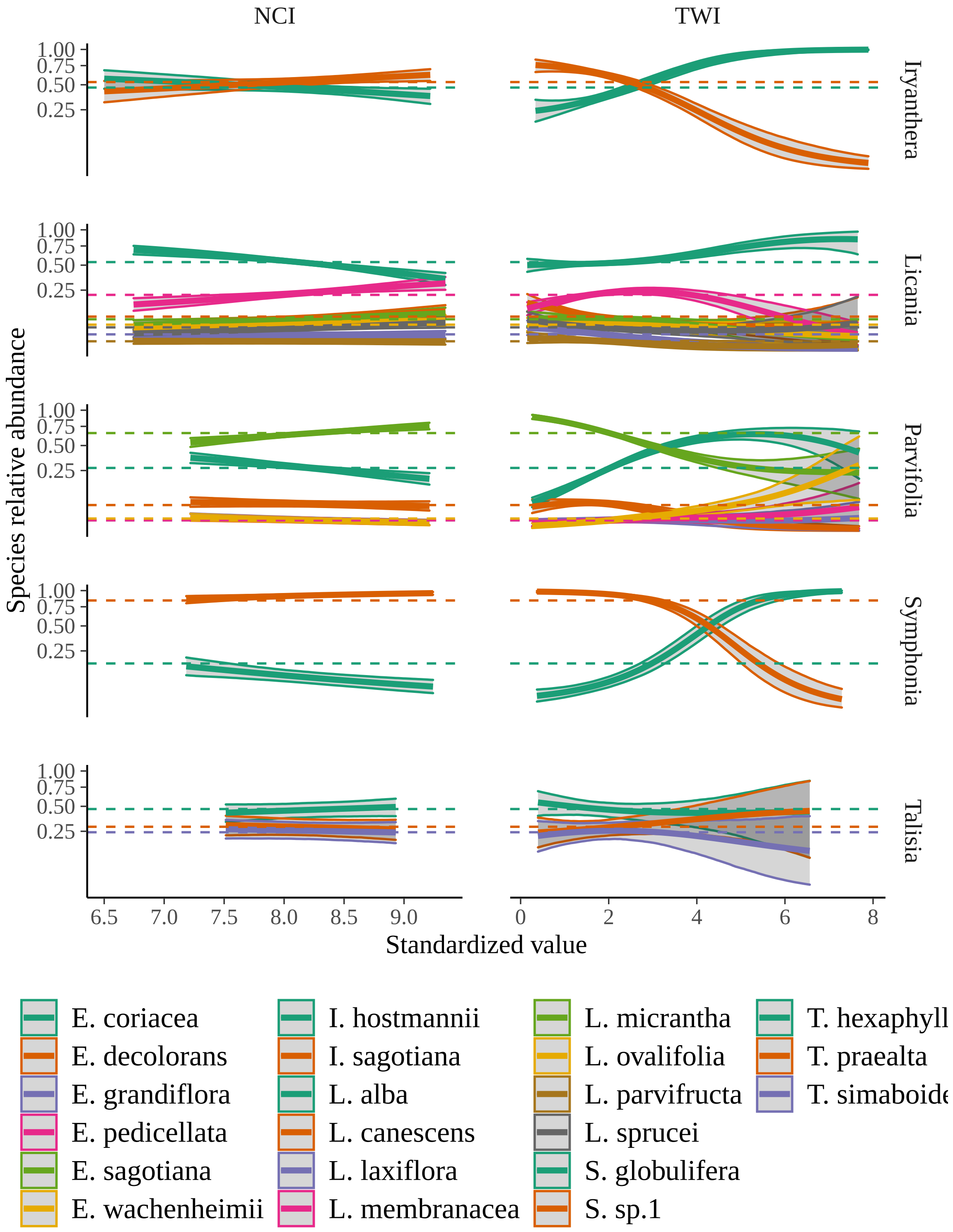

Figure 4: Relative abundance of species within species complexes. Predicted relative abundance of species within species complexes with dashed line indicating observed relative abundance of species within species complex in Paracou, and solid line and area representing respectively the mean and the 95% confidence interval of projected relative abundance of species complexes depending on descriptors. The color indicates the species complex.

capable of exploiting the whole range of environmental conditions studied here, supporting our hypothesis of widespread species complexes at the local scale. Topographic wetness index (TWI) indicates the topographic position where water accumulates. Neighbourhood crowding index (NCI) represents competition with neighbours and thus access to light, water, and nutrients. Consequently, TWI and NCI represent the combined effects of abiotic and biotic environment in defining local scale habitats for species and species complexes distributions. In our study, TWI and NCI had no effect on species complexes distribution, at the exception of a weak effect of TWI on *Iryanthera*, *Licania*, and *Eschweilera clade Parvifolia* abundances, emphasizing the generality of the widespread distribution of species complexes across local habitats. In a nutshell, species complexes span the whole light, water, and nutrients gradients with either segregated species with ecological preferences or generalist species.

The higher abundance of *Iryanthera* species complex in wet habitats has been already evidenced experimentally (Baraloto et al. 2007). Species complexes increased or decreased abundance at high TWI values might be due to variations in species complex-specific adaptations to a more constraining habitat such as anoxia.

Species show pervasive niche differentiation within species complexes

The repeated opposed response of species relative distribution within species complexes to biotic and abiotic environments showed a pervasive niche differentiation of species within four locally abundant species complexes. Indeed, species within *Iryanthera*, *Licania*, *Symphonia*, and *Eschweilera clade Parvifolia* species complexes are segregated along a gradient from wet to drier habitats and a gradient from low crowding to increased crowding.

Habitat segregation along topography and wetness gradients correspond to the well known bottomland to plateau gradient observed in Amazonia (Kraft et al. 2008, Ferry et al. 2010a). Species within species complexes segregate between seasonally flooded habitats resulting in anoxia but increased soil fertility and drier habitats more susceptible to suffering from drought and reduced fertility, besides few species growing preferentially in intermediate habitat (*e.g. Licania membranacea*, Fig. 3). Indeed, water-use strategies and edaphic conditions shape divergent habitat associations between congeneric species pairs (Baltzer et al. 2005). Our results are in agreement with previous evidence of species-habitat association with topography between sympatric congeneric species at local scale (Allié et al. 2015, Lan et al. 2016, Itoh et al. 2003, but see Baldeck et al. 2013a). But, we tested topography in our study but not edaphic properties. Besides covariation with topography, edaphic properties have independent effect on the species distribution (Baldeck et al. 2013b), which may increase species niche differentiation within species complexes.

Moreover, species within species complexes segregate also between high crowding resulting in decreased access to light, water, and nutrients and low neighboring with less competition for resources. (Yamasaki et al. 2013) already evidenced segregation with light access between two congeneric species at local scale, but growing in the same topography. In our study, at least four species showed more tolerance to competition for resources (*i.e.* high NCI) and grow in drier and less fertile habitats (*i.e.* low TWI), whereas species growing in wet habitats also grow preferentially with less competition for resources.

Conclusion

We found Neotropical tree species complexes to be widespread across habitats at local scale, while the species composing them showed pervasive habitat differentiation along topography and competition gradients. The pervasive niche differentiation among species within species complex might be related to repeated functional strategy adaptation to local environment (Baltzer et al. 2005, Baraloto et al. 2007) with several diversification events across taxa (*e.g.* (Fine et al. 2004) for Protiae). Habitat specialisation reduces competition among the species and thus helps the species gain reproductive isolation for their establishment within species complex (Runemark et al. 2019), especially in our study for animal dispersed species with reduced dispersion. Meanwhile, porous genomes allow for the transfer of adaptive genes through introgression that may benefit one or several species, allowing coevolution at the species complex level (Cannon and Lerdau 2015). Consequently, if habitat specialisation allow at least partial reproductive isolation and porous genomes allow adaptive introgression, our results suggest that both habitat specialisation of species within species complex and widespread distribution of species complexes might explain the success of these Neotropical species complex at the regional scale (Steege et al. 2013).

Acknowledgements

We thank the University of Bordeaux for a PhD grant to Sylvain Schmitt. We are grateful to Pascal Petronelli and the CIRAD inventory team for their work on tree inventories and botanical identification. This study was partially funded by an Investissement d'Avenir grant of the ANR: CEBA (ANR-10-LABEX-0025).

Authors' contributions

NT and SS conceived the ideas; SS, BH, and NT designed methodology; SS and BH analysed model outputs; SS, NT and MH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

TWI and spatial positions of individuals were extracted from the Paracou Station database, for which access is modulated by the scientific director of the station (https://paracou.cirad.fr).

Chapter 2: Topography consistently drives intra- and inter-specific leaf trait variation within tree species complexes in a Neotropical forest

Accepted in Oikos with doi 10.1111/oik.07488 (Schmitt et al. 2020)

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Abstract

Tropical forests shelter the highest species diversity worldwide, although genus diversity is lower than expected. In the species-rich genera, species complexes are composed of closely-related species that share large amounts of genetic variation. Despite the key role of species complexes in diversification, evolution, and functioning of ecological communities, little is known on why species complexes arise and how they are maintained in Neotropical forests. Examining how individual phenotypes vary along environmental gradients, within and among closely-related species within species complexes, can reveal processes allowing species coexistence within species complexes.

We examined leaf functional trait variation with topography in a hyperdiverse tropical forest of the Guiana Shield. We collected leaf functional traits from 766 trees belonging to five species in two species complexes in permanent plots encompassing a diversity of topographic positions. We tested the role of topography on leaf functional trait variation with a hierarchical Bayesian model, controlling for individual tree diameter effect.

We show that, mirroring what has been previously observed among species and communities, individual leaf traits covary from acquisitive to conservative strategy within species. Moreover, decreasing wetness from bottomlands to plateaus was associated with a shift of leaf traits from an acquisitive to a conservative strategy both across and within closely-related species. Our results suggest that intraspecific trait variability widens species' niches and converges at species' margins where niches overlap, potentially implying local neutral processes. Intraspecific trait variability favors local adaptation and divergence of closely-related species within species complexes. It is potentially maintained through interspecific sharing of genetic variation through hybridization.

Keywords

intraspecific variability; leaf traits; Paracou ; species complex; syngameon; tropical forests

Introduction

Tropical forests shelter the highest species diversity worldwide (Gaston 2000), although genus diversity is lower than expected (Cannon and Lerdau 2015). The species-rich genera can be the result of networks of partially interfertile and closely related species called syngameons (Cannon and Lerdau 2019). Indeed, interspecific hybrids occur in 16% of tree genera (Whitney et al. 2010) and many species-rich genera have higher levels of genetic polymorphism than species-poor genera, oftentimes sharing haplotypes among species, which is likely related to introgression between congeneric species (Caron et al. 2019). Syngameons respond to two contrasting evolutionary pressures, those acting at the species level maximizing local adaptation to a niche that reduces competition among species, and those acting at the syngameon level which benefit all constituent species. Syngameons as a whole might thus have a selective advantage in some cases, decreasing the overall risk of genus extinction, maximising population size, all the while increasing local adaptation of their distinct species and reducing competition among them (Cannon and Lerdau 2015).

More generally, species that share large amounts of genetic variation due to recent common ancestry and/or hybridization are defined as species complexes (Pernès and Lourd 1984). Species complexes can result from combination and reshuffling of genetic features in hybrid swarms leading to adaptive radiation and segregation among species along environmental gradients (Seehausen 2004). These processes may multiply the number of potential ecological niches, in turn reducing competition among the species and helping the species gain reproductive isolation (Runemark et al. 2019). Despite the key role of species complexes and syngameons in evolutionary processes in ecological communities (Pinheiro et al. 2018)), little is known about the reasons for their appearance and maintenance in Neotropical forests (Baraloto et al. 2012a, Levi et al. 2019b, Steege et al. 2013, Cannon and Petit 2019).

Examining individual fitness, for example through phenotypic trait variation, can shed new light on processes of species coexistence, particularly within species complexes, because changes in individual fitness may promote long-term coexistence of species (Clark 2010). For instance, variation in foliar traits is heritable and under selection, suggesting that foliar traits are linked to individual fitness (Donovan et al. 2011). Intraspecific variability can promote species coexistence when it increases niche differentiation or when it decreases fitness differences between species, thus shielding them from competitive exclusion (Turcotte and Levine 2016). This highlights the need to consider within-species variation to investigate ecological processes, for example by examining the variation in individual performance, phenotypic traits, and genes (Albert et al. 2010a, Violle et al. 2012). Phenotypic variation within species is shaped by genetic diversity in interaction with the abiotic and biotic environment, including its spatial and temporal heterogeneity (Whitlock et al. 2007), and is modulated by ontogeny (Wright and McConnaughay 2002). Describing the relative roles of these sources of variation among individuals within and among closely-related species within species complexes thus contributes to a better understanding of the ecological and evolutionary processes that underlie the maintenance of biological variation within species complexes at both levels of integration.

Functional traits reflect fundamental trade-offs determining the species' ecological niches along environmental gradients (Wright and Westoby 2002) and shape the structure (Paine et al. 2011) and dynamics (Hérault and Piponiot 2018) of sympatric species in conjunction with their environment (Kraft et al. 2008). Functional traits have been defined as phenotypic traits that impact fitness through their effect on individual performance, which is defined as the ability to recruit, grow, survive, and reproduce in a given environment (Violle et al. 2007). Functional traits covary among species (Díaz et al. 2016) and communities (Bruelheide et al. 2018) along distinct economics spectra of leaf (Osnas et al. 2013, Wright et al. 2004, but see Lloyd et al. 2013) and wood (Chave et al. 2009). The leaf economics spectrum opposes acquisitive ecological strategies, with high photosynthetic carbon assimilation, to conservative ones with high investment in leaf defense and durability. For instance, specific leaf area (i.e. area divided by dry weight) varies among species along gradients of soil fertility and exposure to light and represents a trade-off between resource acquisition by photosynthesis and investment in leaf defense and durability (Evans and Poorter 2001a, Hodgson et al. 2011). The leaf economics spectrum is under selection in the wild and is thus partially related to individual fitness (Donovan et al. 2011). The wood economics spectrum opposes fast growing to slow growing species (Chave et al. 2009). Nevertheless, some authors advocate a unique plant economics spectrum (Reich 2014b).

Large intraspecific variability has been documented in tree allometric relationships (Vieilledent et al. 2010) and in leaf and wood trait values(Hulshof and Swenson 2010a, Messier et al. 2010b, Poorter et al. 2018), and marked differences in variability have been detected among species within communities (Siefert et al. 2015a). Several studies have investigated the role of intraspecific variability in community assembly and evidenced effects of environmental filtering (Paine et al. 2011, Messier et al. 2010b), with shifts in trait values following environmental and resource gradients (Jung et al. 2010b, Siefert and Ritchie 2016). The articulation of plant trait responses to environmental gradients at the within-species vs. the between-species levels still remains poorly investigated. (Kichenin et al. 2013) documented responses of plant functional traits to topography that were either congruent or opposed at the intra- vs. the inter-specific levels.

In the present study, we assessed variation in leaf functional trait values of individual trees within and among closely-related species within species complexes, and addressed the effects of abiotic environment on this variation. We controlled for the effect of tree diameter, as a proxy of tree size and access to light, two factors known for their effect on intraspecific trait variation (Chazdon and Kaufmann 1993, Koch et al. 2004, Woodruff et al. 2007). We measured leaf traits on a large number of individuals (766 trees > 10 cm in diameter at breast height) belonging to five Neotropical tree species from two dominant species complexes in a highly diverse tropical forest site located within the Guiana Shield in the Amazon Basin. The site encompasses a diversity of micro-habitats through hydrologic and topographic variation ranging from seasonally flooded bottomlands to drier plateaus (Ferry et al. 2010a, Allié et al. 2015). Combining tree inventories, LiDAR-derived topographic data, and leaf functional traits, we used multivariate approaches and Bayesian modelling to address the following questions: (1) how do traits covary among individuals within tree species of tropical species complexes and (2) how does the abiotic environment influence individual leaf trait values among and within closely-related species within species complexes? Based on conservation of functional strategies both within plant communities and at the global level (Díaz et al. 2016, Bruelheide et al. 2018), we expected trait covariation to be maintained at the within-species level (but see Messier et al. 2016). We hypothesized that the abiotic environment shaped trait variation both among and within species in interaction with tree diameter and access to light (Roggy et al. 2005, Coste et al. 2009).

Material and Methods

Study site

The study was conducted in the Guiana Shield, at the Paracou field station (latitude 5°18'N and longitude 52°53'W) in the coastal region of French Guiana, northern South America. The site is characterized by an average annual rainfall of 3041 mm and a mean air temperature of 25.71 °C (Aguilos et al. 2018). Old tropical forest with an exceptional richness (i.e. over 200 woody species per hectare) dwells in this lowland area characterised by heterogeneous microtopographic conditions with numerous small hills generally not exceeding 45 m a.s.l in elevation, with a dominance of Fabaceae, Chrysobalanaceae, Lecythidaceae, and Sapotaceae (Gourlet-Fleury et al. 2004).

The site comprises 16 permanent plots (fifteen 6.25 ha plots plus one 25 ha plot) which have been censused (diameter at breast height >10 cm) every 1-2 years since 1984. Trees were mapped to the nearest meter. Nine of the plots were intentionally manipulated in 1986 with a range of disturbance intensities that created a variety of biotic environments (details on the experiment in Hérault and Piponiot 2018).

Plant material

Two sampling campaigns were led in 2017 and 2018 during the dry season, between September and December. Sampling was made for two species of *Symphonia* (Clusiaceae) in 2017 and for three species of *Eschweilera* (Lecythidaceae) in 2018 (Tab. 2). All three *Eschweilera* species belong to the Parvifolia clade (Mori et al. 2016, Huang et al. 2015) and represent the most abundant of eleven sympatric species in the clade recorded in the 2017 inventory. The three *Eschweilera* species and the two *Symphonia* species are Amazonian hyperdominant tree species (Steege et al. 2013) and are among the most abundant species in the Paracou station (e.g. *Eschweilera sagotiana* was the second most abundant tree species in the 2017 inventory in Paracou).

Table 2: Number of individuals sampled per genus and species and associated TWI values (mean value, 5th and 95th quantile in brackets).

Genus	Species	N	TWI
Symphonia	sp.1	232	1.97 [0.97- 4.12]
Symphonia	globulifera	170	4.24 [1.59- 6.31]
Eschweilera	sagotiana	156	1.97 [1.06- 3.52]
Eschweilera	coriacea	137	2.52 [0.96- 4.92]
Eschweilera	decolorans	71	1.9 [1.06- 2.78]

The genus *Symphonia* includes the well-recognised species *Symphonia globulifera* L.f (Clusiaceae) with two morphotypes, *S. globulifera sensu stricto* (S. globulifera hereafter) and *Symphonia sp.1*, occurring in sympatry but in differentiated habitats, with *S. globulifera* preferentially growing in valley bottoms and *S. sp1* preferentially exploiting a variety of drier habitats. Similarly, *Eschweilera sagotiana* and *E. coriacea* have been shown to exhibit a niche differentiation for topographic position (Allié et al. 2015). The genus *Symphonia* and the Parvifolia clade have been both highlighted as species complexes with low phylogenetic resolution and high levels of plastid DNA sharing among sister species (Baraloto et al. 2012a, Heuertz et al. 2020, Gonzalez et al. 2009, Huang et al. 2015, Torroba-Balmori et al. 2017). Moreover, *Eschweilera* species share haplotypes (Caron et al. 2019) and *Symphonia* shows introgression between species (S. Schmitt unpublished), suggesting interspecific gene flow characteristic of syngameons.

Individual trees with diameter at breast height larger than 10 cm (DBH $>$ 10cm) were randomly selected across all plots so as to represent the natural distribution of DBH and niche width in topographic gradients (see sample sizes in Tab. 2). For each tree five mature and healthy leaves were sampled at the top of the crown using a slingshot sampling device (BIG SHOT ® SHERILLtree), and kept in humidified ziplock bags with CO2-enriched air in darkness until measurement within the next 6 hours following a standard protocol (Pérez-Harguindeguy et al. 2013). Access to light for each sampled tree was assessed using the Dawkins index (Dawkins 1958).

Trait measurements

For each leaf, we measured five leaf functional traits that relate to resource investment strategies through light interception and carbon assimilation (Diaz et al. 1998, Wright et al. 2004), with known role in individual fitness (Donovan et al. 2011), and that can be measured on a large number of individuals (Tab. 3): leaf mass per area (i.e. leaf dry weight divided by leaf area, LMA, $g.cm^{-2}$), leaf dry matter content (i.e. leaf dry weight divided by fresh weight, LDMC, $g.g^{-1}$), leaf thickness (LT, μm), leaf area (LA, cm^2), and leaf chlorophyll content (CC,

$g.cm^{-2}$). The latter three traits were assessed on fresh leaves. Although LMA is a function of LDMC and LT (Vile et al. 2005), we chose to explore the distribution of the variation of the three interdependent traits within and among species, while always recognising their interrelation. The petiole was removed for all trait measurements. Leaf fresh weight was measured with an analytical balance of precision 0.001 g (Denver instruments, New York, USA), leaf thickness with a micrometer of precision 1 μm (Motionics, Austin, USA), leaf area was quantified using the ImageJ software (Schneider et al. 2012) on scanned images of fresh leaves with a precision of 0.01 cm^2, and leaf chlorophyll content was determined with a SPAD-502 instrument (Konica-Minolta, Osaka, Japan) converted with an allometric model (Coste et al. 2010). Leaf thickness and chlorophyll content measurements were repeated 3 times per leaf to account for intra-leaf variation and leaf traits were measured by a single person per genus. Leaves were then vouchered and oven-dried for at least 48 hours at 80°C before measurement of dry weight.

Table 3: Functional traits measured, with trait unit, abbreviation, intra-individual variation, and mean and standard error per species.

Trait	Unit	Abbreviation	*S.globulifera*	*S.sp.*1	*E.sagotiana*	*E.coriacea*	*E.decolorans*
Leaf Mass per Area	$g.m^{-2}$	LMA	106.66 ± 25.22	103.02 ± 28.1	145.32 ± 27.53	102.2 ± 20.37	101.57 ± 21.06
Leaf Dry Matter Content	$g.g^{-1}$	LDMC	0.33 ± 0.04	0.36 ± 0.04	0.46 ± 0.04	0.46 ± 0.05	0.44 ± 0.05
Leaf Thickness	μm	LT	325.74 ± 83.51	278.63 ± 76.18	325.13 ± 56.45	213.49 ± 44.13	236.98 ± 41.69
Leaf Area	cm^2	LA	33.43 ± 15.16	18.28 ± 7.68	80.9 ± 30.73	90.7 ± 33.18	66.95 ± 20.61
Chlorophyll Content	$g.cm^{-2}$	CC	73.54 ± 11.74	78.97 ± 11.6	75.07 ± 11.44	75.74 ± 12.62	74.78 ± 11.67

Phenotype descriptors

The topographic wetness index (TWI) was selected among several interdependent abiotic descriptors (supplementary material Fig. 30) as a proxy of water accumulation. TWI is defined by the cell catchment area (i.e. cumulative upslope areas draining through the cell) divided by local slope, and represents thus a relative measure of soil moisture availability (Kopecký and Čížková 2010), where a higher TWI represents a higher soil moisture availability. Waterlogging and topography have been identified as crucial for forest dynamics (Ferry et al. 2010a) and species habitat preference (Allié et al. 2015) at the Paracou study site. TWI was derived at a 1-m resolution from a 1-m resolution digital elevation model using SAGA-GIS (Conrad et al. 2015) based on a LiDAR campaign done in 2015. In order to distinguish inter- from intraspecific abiotic effects, we split TWI into TWI_s and $TWI_{i|s}$. TWI_s was the mean value across all the individuals within species s, and represented the interspecific abiotic effect. $TWI_{i|s}$ was the value of individual i minus the mean value of species s ($TWI_{i|s} = TWI_i - TWI_s$), and represented the intraspecific abiotic effect.

The diameter at breast height (DBH, cm) was chosen to control for tree size (O'Brien et al. 1995, Zhang et al. 2004), and access to light (evidenced with Dawkins index, supplementary material Fig. 31). DBH values of sampled individuals were retrieved from the 2017 inventory of the Paracou permanent plots (supplementary material Fig. 32).

Analysis

To examine covariation across traits independently of among-species differences, we assessed covariation in leaf functional traits across individuals by within-species principal component analyses (wPCA, Dolédec and Chessel 1994) using the `withinpca` function in R package `ade4` (Dray et al. 2007).

Then we used Bayesian modelling to test the role of topography on leaf functional trait variation among and within species. In our models, we controlled for the effect of diameter, for which an effect on intraspecific trait values through ontogeny and access to light has already been shown (Roggy et al. 2005, Coste et al. 2009, Spasojevic et al. 2014). Leaf trait (t) $Trait_{t,s,p,i}$ of individual (i) belonging to species $s \in [1;S]$ in plot $p \in [1;P]$ is explained by its DBH_i, using an equation with a Michaelis Menten form (more likely than a linear form, Supplementary Material Tab. 9), in interaction with an additive linear form of abiotic inter- (TWI_s) and intraspecific ($TWI_{i|s}$) effects:

$$
\begin{aligned}
Trait_{t,s,i} \sim \mathcal{N}\left(\frac{DBH_i}{\beta_{DBH_{t,s}} + DBH_i}.(\alpha_{t,s} + \beta_{TWI_t}.TWI_s + \gamma_{TWI_{t,s}}.TWI_{i|s}), \sigma_t^2\right) \\
with\ \alpha_{t,s} \sim \mathcal{N}(\alpha_t, \sigma_\alpha^2)\ and\ \delta_{t,p} \sim \mathcal{N}(0, \sigma_p^2)
\end{aligned}
\tag{4}
$$

In equation (4), $\alpha_{t,s}$ represents the maximum trait value expected at maximum DBH in species s and $DBH_{t,s}$ is the DBH of species s for which the trait reaches half of $\alpha_{t,s}$. $\alpha_{t,s}$ is integrated as a random effect centered on α, the mean maximum trait value expected among species, of variance σ_{α}^2. $\delta_{t,p}$ represents plot random effects (Supplementary Material Fig. 35), encompassing the potential effects of both past disturbance and microclimate (e.g. a given plot was sampled within a few days so we assumed that weather conditions were homogeneous for all sampled trees from a given plot), centered on 0 and of variance σ_p^2. Maximum trait value is also modulated by β_{TWI} and γ_{TWI_s} the slope of TWI effects on trait values among species and within the species s, respectively. Contrary to other traits, LA showed a decrease with increasing DBH so we used $\frac{1}{LA}$ instead of LA to allow for a positive covariation with DBH.

Traits, DBH, TWI_s and $TWI_{i|s}$ were all normalised to ease model inference and enable comparison of traits and covariates. A Bayesian method was used to build the models. We inferred parameters for each leaf trait t and each genus separately, resulting in 10 models, using stan language (Carpenter et al. 2017) and the `rstan` package (Stan Development Team 2018) in the R environment (R Core Team 2020).

Results

Almost seventy percent of the within-species variance in leaf trait values was explained by the first two axes of the within-species Principal Component Analysis (wPCA, Fig. 5. Globally, the wPCA highlighted the covariation of the five leaf traits on the first axis, which alone represented 46% of the total trait variation. This axis opposed large leaves (i.e. high LA) to high values for all other leaf traits: LT, LDMC, CC and LMA. Additionally, LT and LDMC were orthogonal to an axis opposing CC and LDMC to LA. As expected, we found a strong and significant correlation between LMA and the product of LT and LDMC ($LMA = 0.98 + 0.12.LT.LDMC$, $R^2 = 0.72$).

Taking into account the strong and expected effect of tree diameter (DBH, Tab. 4 and supplementary material Tab. 33), the parameterized models showed both inter- and intraspecific effect of topography (TWI) on leaf functional trait values, validating our hypothesis. The fitted models had substantial squared deviation with σ_t^2 around 0.8 (Fig.B 4). In *Symphonia*, TWI had a positive effect on LA and a negative effect on LMA, LDMC, and CC both among and within species, i.e. *Symphonia* trees in wetter habitat had larger and lighter leaves with less chlorophyll than those in drier habitat. This result was obtained within *S. globulifera* and within *S. sp1* and as well as *S. globulifera* and *S. sp1* (Fig. 6 and Table 4). In *Eschweilera*, TWI had a positive effect on LA and CC and a negative effect on LT and LDMC both among and within species, i.e., *Eschweilera* trees in wetter habitat had thinner and larger leaves with higher chlorophyll content but overall lower dry matter content. For LMA, the effect of TWI was negative among *Eschweilera* species and within *E. decolorans* and *E. coriacea*, but weakly positive within *E. sagotiana*. Essentially, eight out of ten models showed congruence of inter- and intraspecific effects of TWI on leaf functional traits in the two species complexes

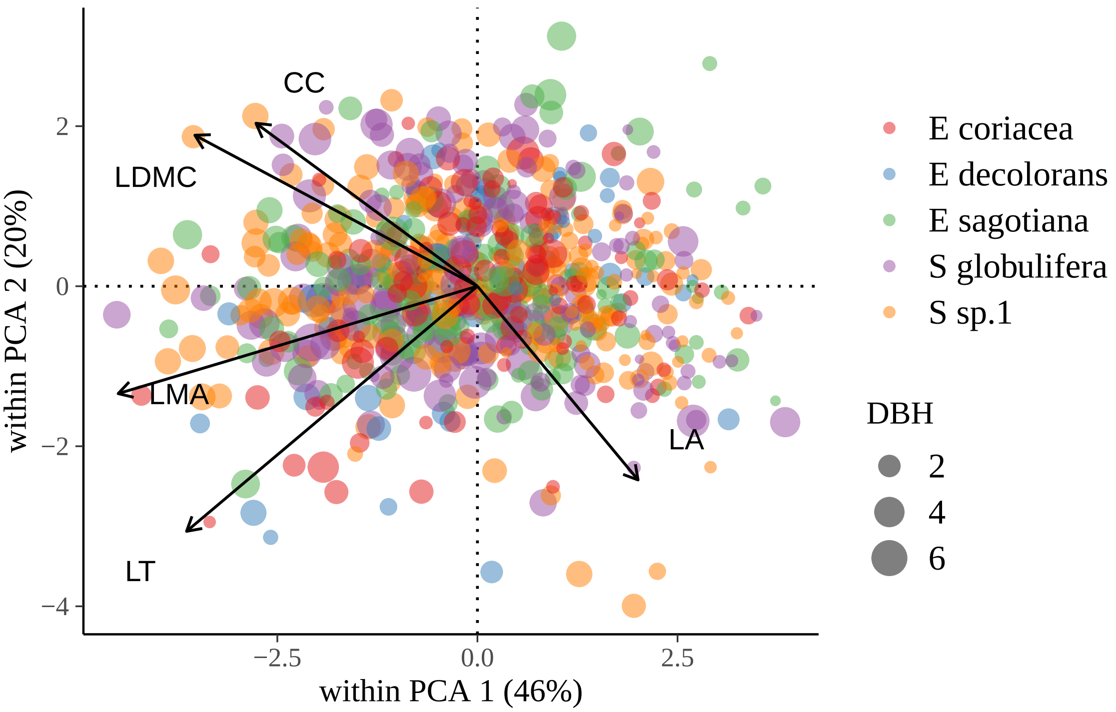

Figure 5: Within-species Principal Component Analysis (wPCA) of leaf traits across individuals in five Neotropical tree species. Circle colors indicate the species, whereas size of circles indicates individual diameter at breast height. See Tab. 3 for abbreviation of traits.

examined, although large uncertainties were associated with many effects (especially LT in *Symphonia* and LMA in *Eschweilera*, see Figure 6). The two complexes diverged, however, in the covariation of traits: the responses of LMA, LDMC, and LA to TWI was similar for both complexes, whereas CC and LT responded in opposite ways in *Symphonia* vs. *Eschweilera*.

Table 4: Model estimated parameters for genera, species and traits. α is the species intercept, whereas β_{DBH} is the value of DBH for which the trait accounts for half of its plateau value and β_{TWI} and γ_{TWI} are the slope of TWI inter- and intraspecific effects, respectively. See Tab. 3 for abbreviation of traits.

Genus	Parameter	Species	LMA	$LDMC$	LT	$\frac{1}{LA}$	CC
Eschweilera	α	All	6.564	6.975	5.271	1.351	6.347
Eschweilera	β_{DBH}	E coriacea	0.269	0.038	0.108	0.238	0.055
Eschweilera	β_{DBH}	E decolorans	0.680	0.068	0.427	0.382	0.076
Eschweilera	β_{DBH}	E sagotiana	0.283	0.069	0.215	0.934	0.057
Eschweilera	β_{TWI}	All	-0.678	-0.013	-0.585	-0.275	0.091
Eschweilera	γ_{TWI}	E coriacea	-0.011	-0.035	-0.003	-0.020	0.195
Eschweilera	γ_{TWI}	E decolorans	-0.162	-0.214	-0.108	-0.014	0.259
Eschweilera	γ_{TWI}	E sagotiana	0.006	-0.021	-0.071	-0.020	0.235

Genus	Parameter	Species	LMA	$LDMC$	LT	$\frac{1}{LA}$	CC
Eschweilera	$\sigma^2_{Species}$	All	0.698	0.349	0.813	0.305	0.426
Eschweilera	σ^2_{Plot}	All	0.443	0.198	0.365	0.029	0.124
Eschweilera	σ^2_{Trait}	All	0.713	0.659	0.570	0.193	0.992
Eschweilera	log-likelihood	All	-61.250	-30.319	17.361	437.283	-176.361
Symphonia	α	All	5.445	6.260	4.632	5.627	7.614
Symphonia	β_{DBH}	S globulifera	0.450	0.178	0.349	0.409	0.200
Symphonia	β_{DBH}	S sp.1	0.822	0.173	0.571	1.235	0.191
Symphonia	β_{TWI}	All	-0.221	-0.181	0.007	-0.812	-0.130
Symphonia	γ_{TWI}	S globulifera	-0.051	-0.070	0.047	-0.146	-0.131
Symphonia	γ_{TWI}	S sp.1	-0.050	-0.084	0.135	-0.133	-0.042
Symphonia	$\sigma^2_{Species}$	All	0.736	0.759	0.750	0.771	0.738
Symphonia	σ^2_{Plot}	All	0.252	0.149	0.958	0.265	0.276
Symphonia	σ^2_{Trait}	All	0.753	0.503	0.644	0.729	0.900
Symphonia	log-likelihood	All	-75.262	92.664	-34.137	-63.308	-150.485

Discussion

Despite the key role of species complexes in Neotropical forest ecology, diversification, and evolution, little is known of the ecological drivers creating and maintaining diversity within Neotropical species complexes. Here, we show that individual leaf traits covary from acquisitive to conservative strategy within species that belong to species complexes, mirroring what has been previously observed among species and communities (Wright et al. 2004, Bruelheide et al. 2018). Specifically, decreasing water availability through higher topographic position, e.g. from bottomlands to plateaus, resulted in a shift of leaf traits from acquisitive to conservative strategies both across and within species. We discuss these results in the context of co-existence of closely related species within species complexes.

Covariation of leaf traits within species follows the leaf economics spectrum

All sampled leaf functional traits show substantial variation among individuals within species along the leaf economics spectrum (Wright et al. 2004), suggesting a conservation at the within-species level of functional strategies previously acknowledged at the among-species level (Wright et al. 2004). The first wPCA axis opposed individuals with small leaves (LA) with high thickness (LT), rich in dry matter (LDMC) and chlorophyll content (CC) and with high LMA, to individuals with large leaves (LA) with small leaf thickness (LT), poor in dry matter (LDMC) and chlorophyll content (CC) and with low LMA, within species. Covariation of

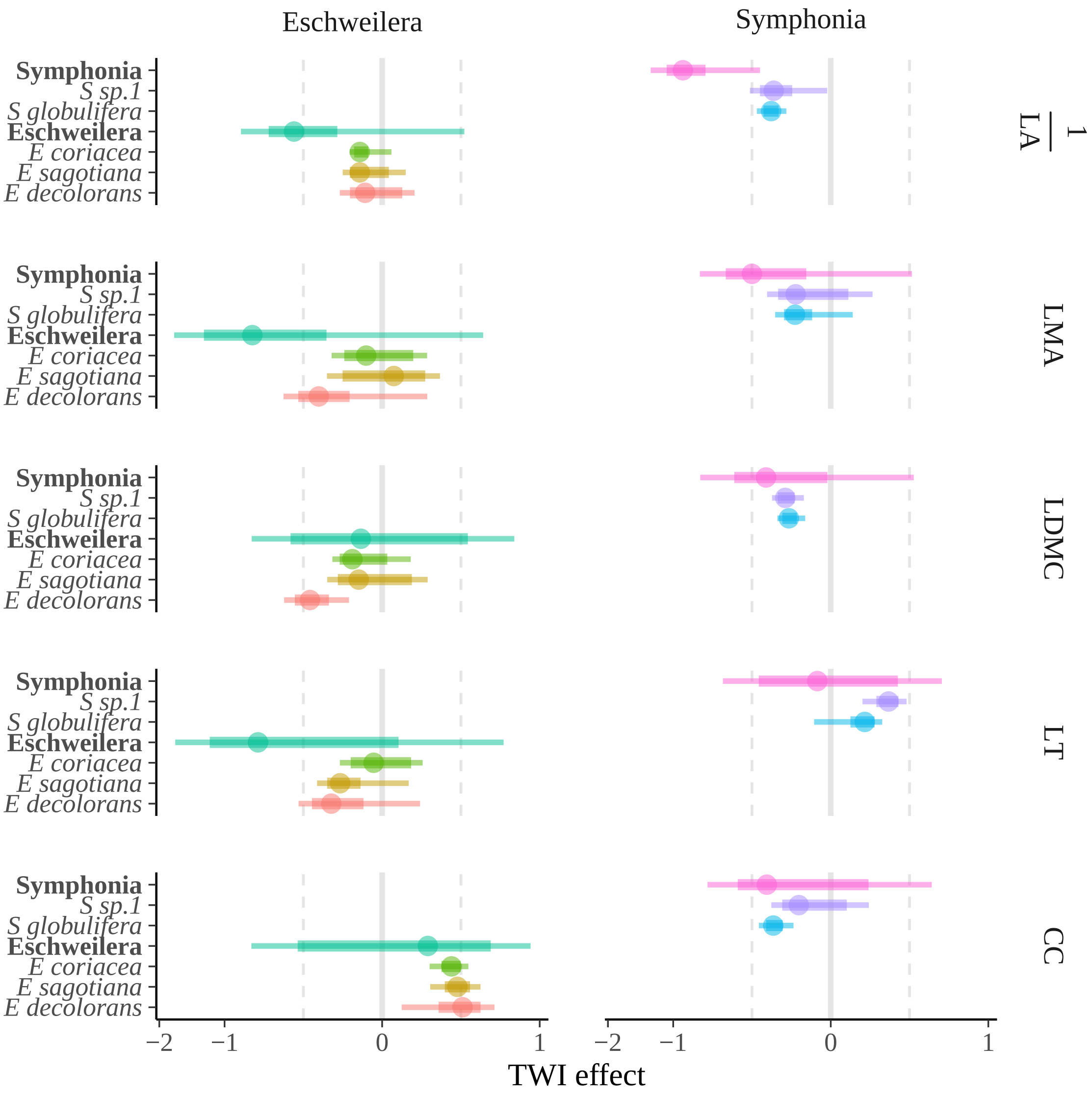

Figure 6: Inter- and intraspecific effect of topographic wetness index (TWI) on each trait for both *Symphonia* and *Eschweilera.* The effect of TWI was estimated as the posterior distribution of the slope parameters β and γ representing respectively inter- and intraspecific effects (see Materials and Methods) using Bayesian inference. Circles represent the mean estimate, thick lines the 50% confidence interval, and thin lines the 95% confidence interval, and colour the corresponding genus for the interspecific effect or species for the intraspecific effect. See Tab. 3 for abbreviation of traits.

LMA, LDMC, and LT across species has already been linked to a trade-off between resource acquisition by photosynthesis and investment in leaf defense and durability (Vile et al. 2005, Baraloto et al. 2010b, Hodgson et al. 2011, Evans and Poorter 2001b). In our study, LA was negatively correlated with LMA, LDMC, and LT at the intraspecific scale, whereas previous studies showed a positive correlation of LA with LMA, LT and LDMC at the interspecific scale (Fortunel et al. 2012, Poorter et al. 2018). The functional role of LA remains a subject of debate (Nicotra et al. 2011) especially regarding its contribution to common leaf functional trade-offs between species (Ackerly et al. 2002). Our results suggest that within species increasing LA contributes to a more acquisitive strategy among individuals. Individual light interception scales with both LA and the number and distribution of leaves in the crown. As individuals have more similar crown shapes within than among species, LA might be related to acquisitive strategy within species and not among species due to high variation in crown shape.

Intraspecific trait variability widens species niche

We observed a consistent response of leaf functional traits to abiotic environment both within species and among closely-related species belonging to species complexes. Topographic wetness index (TWI) characterises topographic position where water accumulates. TWI is a marker of habitat features where wetter habitats associated with increased fertility and faster demographic turnover (i.e. tree recruitment, growth, and mortality) in seasonally flooded bottomlands are opposed to nutrient-poor habitats with slower turnover at higher topographic position (Ferry et al. 2010a, Allié et al. 2015). In our study, TWI had a negative effect on LDMC and LMA, and a positive effect on LA both among and within species, i.e., sites with higher water availability were associated both with trees and species that had larger leaves with lower mass and dry matter content.

Consequently, higher topographic positioning (i.e. decreasing TWI) resulted in a shift from acquisitive to conservative functional strategy both within and among species in our study. Similar results have been found among species, where more conservative strategies were associated with drier or less fertile habitats: (i) on higher topographic position, e.g. ridge-tops (Kraft et al. 2008, Méndez-Toribio et al. 2017), (ii) with decreasing climatic water availability (Gotsch et al. 2010), and (iii) with decreased precipitation and phosphorous (Cunningham et al. 2007). Conversely, the increased fertility and water availability and faster turnover of lower elevation habitats can explain that individuals growing there show a more acquisitive strategy (Hodgson et al. 2011).

The among-species relationship between functional trait variance and the abiotic environment heterogeneity is mirrored within-species belonging to species complexes, where we find the same signatures between intraspecific trait variation and the abiotic environment (but see Kichenin et al. (2013) for opposed effects). Thus, intraspecific trait variability is widening species' niches allowing individuals to grow in environmental conditions where their species' average functional trait values would not have allowed them to survive (Violle et al. 2012).

Wide niches result in an increased niche overlap among closely-related species within species complexes. For instance, *S. sp1* grows in drier sites, on average, than *S. globulifera*, but the wet limit of *S. sp1* transgresses the dry limit of *S. globulifera* (mean and 95th percentile of TWI for *S. sp1* are 1.97 and 4.12, respectively, whereas 5th percentile and mean of TWI for *S. globulifera* are 1.59 and 4.24, respectively, Tab. 2). Consequently, this increases functional similarity at the margin of species' ecological niches, once individual size and species effects are accounted for (respectively, β_{DBH} and $\sigma^2_{species}$, Tab. 4). This convergence may result from genetic exchange among sister species through hybridization specific to syngameons. If, as expected, leaf functional traits related to resource-acquisition impact individual fitness (Violle et al. 2007, Donovan et al. 2011), functional convergence at species margins may drive the fitness of individuals belonging to different species to similar values, which would support neutral coexistence processes (Hubbell 2001) between functionally-similar individuals (Hérault 2007).

Our results concerned two Amazonian basin-wide hyperdominant (Steege et al. 2013) and locally abundant species complexes. Nevertheless, other congeneric pairs of species have been shown to grow in contrasting topography and soil type (Allié et al. 2015, Lan et al. 2016, Itoh et al. 2003), and many closely-related species within abundant species complexes are segregated along topography in Paracou (Schmitt et al. in prep). In addition, studied species here encompassed a broad range of niche breadth along the topographic wetness index (ΔTWI from 1.7 to 4.7, Tab. 2) close to the niche breadth observed across all species in Paracou (ΔTWI from 1 to 5, Supplementary Material Fig. 34). Consequently, although our results are limited to species complexes, we expect similar patterns of individual functional response to topography within many species of the community. Indeed, other studies showed a similar shift from acquisitive to conservative functional strategies within species for grassland plants (Liancourt et al. 2013, Jung et al. 2014) and forest trees (Umaña and Swenson 2019) along topographic, drought, and elevation gradients among species not necessarily belonging to a species complex. In addition, the consistency of the functional response to topography within and between species suggests that the response is environmentally controlled, and should therefore be consistent outside of species complexes.

Within species complexes, local adaptation to fine-scale heterogeneity of abiotic environments may favor divergence of closely-related species in sympatry (Seehausen 2004). While local adaptation favors divergence, hybridization may help the transfer of genetic variability responsible for conserved leaf trait responses to topography within and among species, a hypothesis that can be tested in the future using ongoing genomic data production. Hybridization among closely-related species from species complexes has been suggested to accelerate adaptation to rapidly changing environments (Cronk and Suarez-Gonzalez 2018), and can thus contribute to increasing the adaptive potential of species in the context of growing anthropogenic disturbances (Harte et al. 2004), such as increased drought risk in the Amazon basin due to global climate change (Davidson et al. 2012).

Acknowledgements

We thank the University of Bordeaux for a PhD grant to Sylvain Schmitt and acknowledge the support of a grant from Investissement d'Avenir grants of the ANR (CEBA:ANR-10-LABX-25-01) and from the GUYAMAZON program (LECYTOMICS project). We are grateful to Pascal Petronelli and the CIRAD inventory team for their work on tree inventories and botanical identification. Special thanks go to Josselin Cazal, Ilke Gelaldi, Fabien Lehuede, Adeline Adam, Agathe Benfredj Zaleski, Numa Faucherre, and David Zipper for their assistance during sampling in Paracou station.

Authors' contributions

SS, GD, BH, ED, and AB conceived the ideas; SS, GD, BH, and AB designed the methodology; SS and GD analysed model outputs; SS, GD and MH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Functional traits data have been submitted to TRY initiative (Kattge et al. 2020) under the name ParacouITV. DBH, TWI and spatial positions of individuals were extracted from the Paracou Station database, for which access is modulated by the scientific director of the station (https://paracou.cirad.fr).

Chapter 3: Topography drives microgeographic adaptations of closely-related species in two tropical tree species complexes

Submitted the 16th of August 2020 and under review in New Phytologist

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Summary

- Closely-related tree species that grow in sympatry are abundant in rainforests. However, little is known of the eco-evolutionary processes that shape their niches and allow their local coexistence. Here, we assessed genetic species delimitation in closely-related sympatric species belonging to two Neotropical tree species complexes and investigated their genomic adaptation to a fine-scale topographic gradient with associated edaphic and hydrologic features.
- Combining LiDAR-derived topographic data, comprehensive tree inventories, and single nucleotide polymorphisms (SNPs) from gene capture experiments, we explored genome-wide population genetic structure, covariation of environmental variables, and genotype-environment association to assess microgeographic adaptations to topography within the species complexes *Symphonia* (Clusiaceae), and *Eschweilera* (Lecythidaceae) with three species per complex and 385 and 257 individuals genotyped, respectively.
- Within species complexes, closely-related tree species had different realized optima for topographic niches defined through the topographic wetness index or the relative elevation, and species displayed genetic signatures of adaptations. *Symphonia* species were differentially adapted to water and nutrient distribution, whereas *Eschweilera* species avoided hydromorphic soils and were differentially adapted to soil chemistry.
- Our results suggest that varied topography represents a powerful driver of tropical forest biodiversity, driving differential adaptations and stabilizing local coexistence of closely-related tree species within tree species complexes.

Keywords

Ecological niche; French Guiana; relative elevation; species coexistence; syngameon; topographic wetness index; tropical forests

Introduction

Closely-related tree species are abundant at the local and regional scales in Neotropical forests (Gentry 1988, Steege et al. 2013, Pinheiro et al. 2018). The five thousand tree species botanically identified in Amazonia belong to only height hundred ten genera (Steege et al. 2013), many of which thus contain multiple related species. Even at the local scale, tropical forests shelter up to several hundred tree species per hectare (Gentry 1988), including genera with multiple closely-related species growing in sympatry (Caron et al. 2019). Closely-related species are expected to share similar niche and functional strategies due to phylogenetic constraints (Wiens et al. 2010). Such similar strategies can lead to increased competition between species, and a heightened risk of local competitive exclusion (Turcotte and Levine 2016). The abundance of sympatrically growing closely-related tropical tree species represents thus an intriguing paradox that warrants the investigation of the eco-evolutionary forces that shape their ecological niches and allow their local coexistence.

Genetic studies have shown that species in species-rich genera have a higher level of genetic polymorphism (Caron et al. 2019) and hybridize more often between congeners (Whitney et al. 2010) than those in species-poor genera. Species-rich genera thus frequently contain species complexes, defined as clades of morphologically similar species and/or species that share large amounts of genetic variation due to recent common ancestry and/or hybridization (Pernès and Lourd 1984). Species-rich genera also frequently contain syngameons, defined as species connected by limited, but recurrent, interspecific gene flow (Suarez-Gonzalez et al. 2018). Syngameons are evolving at two contrasting taxonomic levels, they maximize each species adaptation to its ecological niche, and they evolve at the syngameon level which benefits all the constituent species through adaptive introgressions. The syngameon is thus unlikely to just represent a transitional stage before complete speciation; instead it is probably a successful evolutionary strategy that maximizes adaptive evolution while decreasing the overall risk of extinction (Cannon and Lerdau 2015, Cannon and Petit 2019). Species complexes and syngameons frequently include sympatric species coexisting at local scales (Gonzalez et al. 2009, Caron et al. 2019, Cannon and Petit 2019), but how these species remain distinct and persist in sympatry despite phylogenetic constraints and inter-specific gene flow remains poorly known.

The local coexistence of ecologically and phenotypically similar, closely-related species is governed by ecological and evolutionary processes, contingent on the history of speciation and niche differentiation (Weber and Strauss 2016). Once in contact, ecologists consider foremost the competition for resources and the resulting niche differentiation (Chesson 2000a, Turcotte and Levine 2016), whereas evolutionary biologists are more interested in the level of reproductive isolation (Weber and Strauss 2016). For stable coexistence, niche theory evokes that species maximize ecological niche differences (Weiher and Keddy 1995, Lortie et al. 2004b), while the “emerging similarity theory” reconciles niche and neutral theories by suggesting coexistence of distinct groups of species that are functionally similar within groups (Scheffer and Van Nes 2006). Functionally similar species must have similar fitness as an additional condition for stable coexistence (Chesson 2000a), and recently diverged species must have evolved sufficient reproductive isolation to avoid the break-down of differences and their genetic homogenization upon secondary contact (Levin et al. 1996, Taylor et al. 2006, Abbott et al. 2013).

The heterogeneity of resource distribution in space and time defines fine-scale habitat structure where species can coexist. In tropical forests, topography explains the local spatial distribution of water and nutrient availability, showing a strong association with soil nitrogen, carbon, and phosphorus content (Ferry et al. 2010b). Topography has been shown to explain pervasive differentiation in habitat preference among species (Gunatilleke et al. 2006, Engelbrecht et al. 2007, Kraft et al. 2008, Allié et al. 2015). In particular, soil nutrients, also influenced by topography through hydromorphy, directly shape the spatial distribution of forest tree species (John et al. 2007). Topography has also been shown to drive functional responses among and within species (Schmitt et al. 2020). Topography, for example measured through the topographic wetness index (Schmitt et al. 2020) or relative elevation (Allié et al. 2015), is thus a proxy of numerous habitat features related to the distribution of nutrients and water. Therefore, fine-scale mapped topography is a good candidate factor that may explain adaptation and local coexistence of closely-related species in Neotropical tree species complexes.

Closely-related species growing in sympatry in differentiated ecological niches are frequently the product of an adaptive radiation (Seehausen 2004), such as Darwin's finches in the Galapagos (Grant and Grant 2019). Evolutionary history behind sympatric species in adaptive radiations falls within a continuum from sympatric ecological speciation to secondary contacts of species ecologically specialised in allopatry or parapatry (Rundell and Price 2009, Weber and Strauss 2016). In particular, species complexes can result from adaptive radiations and species segregation along environmental gradients. Species complexes may combine and reshuffle genetic features among species in hybrid swarms (Grant and Grant 2019, Seehausen 2004), thus multiplying the number of potential ecological niches and helping species to achieve reproductive isolation (Runemark et al. 2019). A certain degree of reproductive isolation is necessary to prevent hybrid or derived species from becoming an evolutionary melting pot. Nevertheless, species-specific adaptations can be maintained or even maximised under gene flow, especially with selective pressures varying in space and or time (Tigano and Friesen 2016). For instance, the European white oaks form one of the best known syngameons (Cannon and Petit 2019) with extensive hybridisation (Petit et al. 2002), but each species has a unique ecological niche concerning tolerance to drought, cold, and alkaline soils (Leroy et al. 2019, Cannon and Petit 2019). The coexistence of the different species is partly due to the genes that allow them to survive in different, adjacent, ecological niches (Leroy et al. 2019). To our knowledge, only few studies have reported genetic evidence for differential adaptation to topography or abiotic habitats in tropical tree clades (Pillon et al. 2014, Paun et al. 2016, Fine et al. 2004). At the within-species level though, topography has been highlighted as a driver of genetic divergence (Brousseau et al. 2015).

In the present study, we assessed genetic species delimitation and genotypic diversity of closely-related sympatric tree species belonging to two Neotropical species complexes, the genus

Symphonia (Clusiaceae) and the clade *Parvifolia* of the genus *Eschweilera* (Lecythidaceae). We addressed fine-scale spatial adaptation along a topographic gradient associated with nutrient and water distribution. Combining LiDAR-derived topographic data, comprehensive tree inventories, and single nucleotide polymorphisms (SNPs) from gene capture experiments, we explored genome-wide population genetic structure, covariation of environmental variables and genotype-environment association to address the following questions:

1. How is genetic diversity structured among and within species of Neotropical tree species complexes ?
2. How are soil water and nutrients distributed at fine spatial scale along the topographic gradient exploited by the species complexes?
3. Are tree species and individuals adapted to the fine-scale topographic gradient?

We hypothesized species to be delineated into gene pools corresponding to already described taxonomic morphotypes. We expected misidentifications due to overlapping intraspecific morphological variability and the difficulty to access reproductive material (Mori et al. 1990). In this context, gene pool delimitation based on molecular data can reveal cryptic species or lead to the merging of taxa previously thought to be distinct (Ewédjè et al. 2020). We hypothesized relative elevation and topographic wetness to explain the distributions of water and nutrients at fine scale (Allié et al. 2015, Ferry et al. 2010b). We expected genetic variation among and within species to be structured along the topographic gradient and to detect genetic signatures of adaptation, following preliminary evidence of topography determining species' ecological niches [Schmitt et al., in prep]. However, countering this process, interspecific gene flow could reduce neutral and adaptive signatures of differentiation among species within the species complexes (Tigano and Friesen 2016).

Material and Methods

Study site

The study was conducted in the Paracou field station, in the coastal forests of French Guiana, South America. The site is characterized by an average of 3,041 mm annual rainfall and a mean air temperature of 25.71 °C (Aguilos et al. 2018). Old tropical forest with an exceptional richness (i.e. over 750 woody species) grows across the succession of small hills of this area, which rise to 10–40 m a.s.l. (Gourlet-Fleury et al. 2004). The site comprises 16 permanent plots (fifteen 6.25 ha plus one 25 ha) which have been censused (DBH>10) every 1-2 years for more than 35 years. Nine of the plots were logged and subjected to human-induced disturbance in 1986 (details on the experiment in Hérault and Piponiot 2018).

Plant material

Four hundred and two individuals of *Symphonia globulifera* (Clusiaceae) and 417 individuals belonging to the clade *Parvifolia* of the genus *Eschweilera* (Lecythidaceae, Huang et al. 2015, Mori et al. 2016) were sampled in 2017 and 2018 during the dry season (i.e. from September to December) in Paracou (Fig. 7). Both genera are locally abundant and some species within them are Amazonian hyperdominants (Steege et al. 2013). *Symphonia globulifera* L.f (Clusiaceae) was previously recognized as composed of two morphotypes in French Guiana (Sabatier et al. 1997, Molino and Sabatier 2001, Baraloto et al. 2007). *Symphonia globulifera sensu stricto* and *Symphonia sp.1* occur in sympatry but in differentiated habitats, with *S. globulifera* preferentially growing in valley bottoms with an acquisitive functional strategy and *S. sp1.* preferentially exploiting a variety of drier habitats with a conservative functional strategy (Allié et al. 2015, Schmitt et al., in prep; Schmitt et al. 2020). Reciprocal transplantation experiments of Symphonia seedlings have shown that survival and growth performance of each morphotype is better in their home environment than in the opposite environment, showcasing how the two morphotypes are differently adapted to their respective environments (Tysklind et al., 2020). Similarly, *Eschweilera sagotiana* Miers, *E. decolorans* Sandwith, and *E. coriacea* (DC.) S.A.Mori exhibit niche differentiation, differential responses to water stress, and different functional traits along topography (Allié et al. 2015, Schmitt et al., in prep; Baraloto et al. 2007, Schmitt et al. 2020). The genera *Symphonia* and *Eschweilera* have been highlighted as species complexes with low (phylo-)genetic species resolution and high levels of plastid DNA sharing among closely related species (Baraloto et al. 2012a, Heuertz et al. 2020, Gonzalez et al. 2009, Huang et al. 2015, Torroba-Balmori et al. 2017, Caron et al. 2019). In addition, outgroups for genetic analysis in *Symphonia* were comprised of 13 individuals of *Symphonia globulifera* from Africa (Sao Tome, Gabon, Cameroun, Congo, Benin, Liberia, Ivory Coast, and Ghana), seven *Symphonia globulifera* from South America (Brazil, Costa Rica and Panama), two *Symphonia nectarifera* Jum. & H. Perrier from Madagascar, two *Symphonia urophylla* (Decne. ex Planch. & Triana) Benth. & Hook.f. ex Vesque from Madagascar, five *Pentadesma butyracea* Sabine from Benin and Cameroon and one *Pentadesma grandifolia* Baker f. from Cameroon. For *Eschweilera*, outgroups were selected from other *Eschweilera* and *Lecythis* clades in Paracou (*Lecythis persistens* Sagot, *E. simiorum* (Benoist) Eyma, and *E. chartacea* (O.Berg) Eyma). Leaves were collected from the 864 individuals (402 *Symphonia* + 30 outgroups; 417 *Eschweilera* + 15 outgroups) and dessicated using silica gel.

Sequence capture

Design of probes sets

We designed in *silico* two sets of 20,000 80-mer probes for sequence capture, one for *Symphonia globulifera*, and a second one compatible with both *Eschweilera sagotiana* and *Eschweilera coriacea* (Fig. 36, Fig. 37).

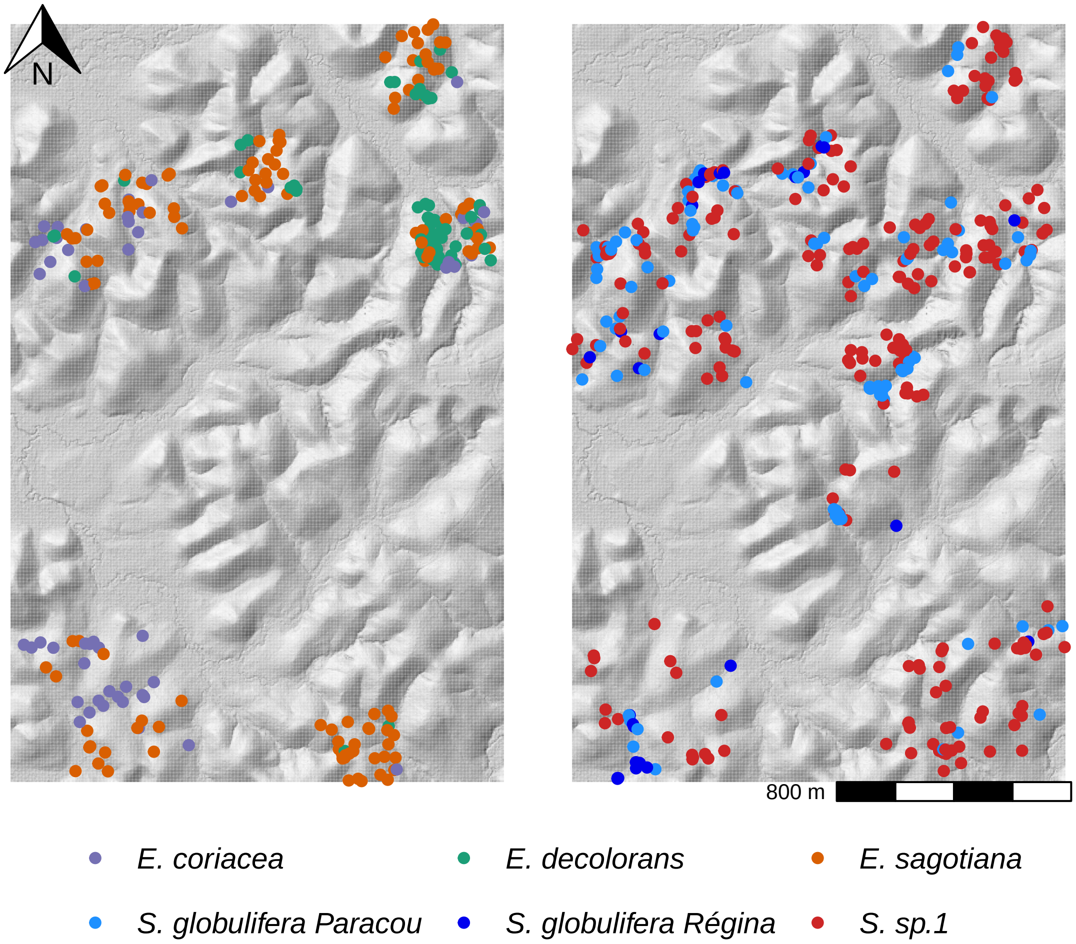

Figure 7: Map of sampled individuals for species complexes *Symphonia* and *Eschweilera* clade *Parvifolia*. Colours represent species determined based on the genetic structure of capture datasets, which was not necessarily in agreement with original botanical identification. Grey level represents hill shading to visualize topography.

For *Symphonia globulifera*, the genomic and transcriptomic resources used for the design were comprised of a published low-coverage draft genome obtained from an individual from Cameroon (Olsson et al. 2017), an unpublished draft genome from an individual from French Guiana [Scotti et al., in prep], an unpublished transcriptome from 20 juveniles from French Guiana [Tysklind et al., in prep], and reduced-representation genomic sequence reads of individuals from French Guiana [Torroba-Balmori et al., unpublished]. Details on the design of the probes set for *Symphonia* are given in Method S1.

For *Eschweilera*, we used transcriptomes from *Eschweilera sagotiana* and *Eschweilera coriacea* (Vargas et al. 2019), and unpublished reduced representation genomic reads of *E. coriacea*, *E. sagotiana*, and *E. decolorans* (M. Heuertz pers. com.). Details on the design of the probes set for *Eschweilera* are given in Method S2.

Genomic libraries and sequence capture

Genomic DNA was extracted from 5 mg of dried leaf tissue with a CTAB protocol (Doyle and Doyle 1987). DNA extracts were digested with 'Ultra II FS Enzyme Mix' (new England Biolabs Inc, MA, USA) for a target size of 150 bp, and libraries built with the 'NEBNext Ultra II FS DNA Library Prep kit for Illumina' (New England Biolabs Inc, MA, USA). We amplified and tagged libraries using 5 μL of adaptor-ligated DNA, 8.3 μL of 'NEBNext Ultra II Q5 Master Mix' (new England Biolabs Inc, MA, USA), 2x 1.6 μL of Index Primer i5 and i7 from 'NEBNext Multiplex Oligos for Illumina (Dual Index Primers Set 1 and Set 2)' (new England Biolabs Inc, MA, USA). Initial denaturation (98°C for 30 s) was followed by 8 cycles (98°C for 10 s and 65°C for 1 min 30 s) and a final extension (65°C for 5 min). We pooled libraries in four equimolar multiplexes for each genus. We used a custom made set of 20,000 80-mer probes for each genus (myBaits Custom 1-20K, Arbor Biosciences, MI, USA) and conducted the capture experiments using the corresponding myBaits V4 protocol with a hybridization time of 80 hours. We pooled the four multiplexes and sequenced them in two lanes of an Illumina HiSeq 4000 instrument obtaining 2x150bp pair-end reads for each genus.

SNP calling, filtering and annotation in Symphonia

We assessed the quality off raw reads using `multiqc` (Ewels et al. 2016) and trimmed them with `trimmomatic` (Bolger et al. 2014). We kept only pair-end reads without adaptors and a phred score above 15 in a sliding window of 4. Seventy percent of trimmed reads mapped off-targets using `bwa` (Li and Durbin 2009). We thus mapped trimmed reads on the hybrid reference built for the sequence capture experiment using `bwa` (Li and Durbin 2009), `picard` (Broad Institute 2018), `samtools` (Li et al. 2009) and `bedtools` (Quinlan and Hall 2010). We called variants for each individual using `HaplotypeCaller`, aggregated variants using `GenomicsDBImport` and jointly-genotyped individuals using `GenotypeGVCFs` all in `GATK4` software (Auwera et al. 2013). We filtered biallelic SNPs with a quality above 30, a quality by depth above 2, a Fisher strand bias below 60 and a strand odds ratio above 3 using `GATK4` (Auwera et al. 2013). Finally, we filtered individuals and SNPs for missing data with a maximum of 95% and 15% of missing data per individual and SNP permitted, respectively, using `plink2` (Chen et al. 2019). We obtained 454,262 biallelic SNPs over

385 individuals, without outgroups, for population genetic analysis. Since low-frequency alleles and linkage disequilibrium (LD) will bias the number of fixed loci and increase the number of false-positives in genomic scans for outliers (Foll and Gaggiotti 2008), we built a second dataset for outlier and environmental association analysis, filtering variants with a minor allele frequency (MAF) above 5% (18 individuals) and with LD $r^2 < 0.99$. We further removed admixed individuals (<90% gene pool membership, see Genetic species delimitation) and retained 70,737 biallelic SNPs over 372 individuals. We used the genome-transcriptome alignments built for the design of probes sets to annotate called SNPs (Method S1).

SNP calling and filtering in Eschweilera

We conducted quality control and trimming of sequence reads as described for *Symphonia*. We kept only trimmed reads that mapped on-targets using `bwa` (Li and Durbin 2009). Because of problems with paralogs in *Eschweilera* clade *Parvifolia* due to a strong signature of a past genome duplication (Heuertz et al. 2020), we decided to build a *de novo* reference of successfully mapping reads using `ipyrad` with a very strict sequence similarity threshold of 0.95 for clustering within and across individuals (Eaton and Overcast 2020). We automatically tested numerous values of missing data and outgroup filtering, and kept strict filters with population structure congruent with botanical identification but keeping a maximum of individuals (Fig. 38, Fig. 39). We filtered individuals and SNPs for missing data allowing a maximum of 99% of missing data per SNP and at least 5 individuals represented per SNP using `plink2` (Chen et al. 2019). Outgroups were automatically filtered out by clustering individuals in two groups using K-means in a genomic principal component analysis (Fig. 40). We obtained 418,793 biallelic SNPs over 257 individuals.

Analyses

Genetic species delimitation For genetic species delimitation in the *Symphonia* species complex, we investigated population genetic structure using `admixture` (Alexander and Lange 2011), using 10 repetitions of K genetic groups with K varying from 1 to 10 and assessed the number of gene pools with cross validation. We defined individuals with a membership to gene pools below 90% as admixed and the remaining individuals as genetically pure. We further investigated admixture with the `introgress` R package (Gompert and Alex Buerkle 2010), using genetically pure individuals as parental populations and all individuals as the hybrid population. Due to an excess of missing data, `admixture` failed to infer genetic custers in *Eschweilera*. We thus used principal component analysis and K-means clustering to delimit *Eschweilera* species. We assessed the number of gene pools using the within-group sum of squares. We validated gene pool delimitation in *Symphonia* and *Eschweilera* by comparison with botanical identifications using a confusion matrix, and we conducted a second blind-identification of every collected individual of Symphonia in November 2019.

We used the genomic scan approach implemented in `bayescan` (Foll and Gaggiotti 2008) to detect high-differentiation outlier SNPs between the different *Symphonia* gene pools using the dataset of 70,737 MAF and LD-filtered SNPs with an *a priori* odds ratio of ten. We considered as outliers those SNPs for which the p-value corrected for multiple testing by false discovery rate was below 5%. We tested genic outlier SNPs for enrichment in gene ontology with the R package `clusterProfiler` (De La Cruz and Raska 2014).

Topography as a proxy for the distribution of soil water and nutrients We used two relatively-independent topographic variables, the topographic wetness index (TWI) and the relative elevation (RE, orthogonality shown in Fig. 10), as proxies of the distribution of soil water and nutrients availability in Paracou. Waterlogging and topography have been highlighted as crucial for forest dynamics (Ferry et al. 2010b), species-habitats relationships (Engelbrecht et al. 2007), and phenotypic variation of *Symphonia* and *Eschweilera* (Schmitt et al. 2020). TWI and RE were derived from a 1-m resolution digital elevation model using SAGA-GIS (Conrad et al. 2015) based on a LiDAR campaign of the whole Paracou field station done in 2015. Principal component analysis (PCA) was further used to characterize the distribution of variables summarizing soil water and nutrients along TWI and RE in Paracou interpolating previous studies: we specifically assessed the co-variation in organic matter, carbon, nitrogen and phosphorous content, exchangeable cation charge (Soucémarianadin 2004, Roelens in press), water table depth (Gourlet-Fleury et al. 2004), hydromorphy, and waterlogging (Cantet 2004).

Topography effect on neutral and adaptive genetic variation We did environmental association analyses (Rellstab et al. 2015) in each complex using general linear mixed models developed for genome wide association studies (GWAS). We used topographic wetness index (TWI) or relative elevation (RE) as the response variable and genetic structure (i.e. gene pools representing species) and relatedness (i.e. kinship matrix) as explanatory variables, as it is common practice (Rellstab et al. 2015). This analysis assumed that the topographic conditions where individuals have grown above 10-cm DBH are strongly correlated to the individual heritable phenotypes (e.g. Eckert et al. 2010). We used genetic species and individual kinship in an animal model (Wilson et al. 2010) to estimate genetic variance associated with topography. We used a lognormal likelihood given that distributions of environmental variables were positive and skewed. We defined species based on the gene pools identified with `admixture` and inferred individual kinship using KING (Manichaikul et al. 2010), as the method is robust to population structure. We set negative kinship values to null as they were confounding with population structure, and we further ensured that the matrix was positive-definite using the `nearPD` function from the R package `Matrix`. The environment $y_{s,i}$ where individual i in species s grows was inferred with a lognormal distribution with the following formula:

$$\begin{gathered} y_{s,i} \sim logN(log(\mu_s.a_i), \sigma_1^2) \\ a_i \sim MVlogN_N(log(1), \sigma_2^2.K) \end{gathered} \tag{5}$$

where μ_s is the mean environment of species s, a_i is the breeding value of individual i and σ_1^2

is the shape parameter of the lognormal distribution. Individual breeding values a_i are defined following a multivariate lognormal law $\mathcal{MV}\updownarrow\wr\}\mathcal{N}$ of co-shape matrix defined as the product of the kinship matrix K with estimated individual genotypic variation σ_2^2. To estimate variances on a normal scale, we log-transformed species fixed effects, genetic additive values, and we calculated conditional and marginal R^2 (Nakagawa and Schielzeth 2013). A Bayesian method was used to infer parameters using `stan` language (Carpenter et al. 2017, code available in Model S1) and `rstan` package (Stan Development Team 2018) in the R environment (R Core Team 2020) using the No-U-Turn Sampler alogirthm (NUTS, Hoffman and Gelman 2014), which performs better for estimating genetic parameters and breeding values (Nishio and Arakawa 2019).

Results

Symphonia globulifera was previously recognized as composed of two morphotypes in French Guiana, but cross validation of admixture analyses for different levels of clustering advocated for K = 3 different gene pools (Fig. 8a, Fig. 41, Fig. 42). The three gene pools correspond to the two previously identified morphotypes (70-80% of match), *S. globulifera* and *S. sp.1*, where the *S. globulifera* morphotype itself comprises two gene pools. These two gene pools correspond to two locally defined sub-morphotypes herafter called *S. globulifera type Paracou* and *S. globulifera type Régina* (Fig. 8b). *Symphonia sp.1* grows preferentially in drier plateaux and slopes (Schmitt et al., submitted) and has a light grey thin and smooth bark associated with smaller leaves, flowers, and fruits (Fig. 8b). *Symphonia globulifera type Paracou* grows in wet habitats of bottomlands, but drier than those of *S. globulifera type Régina*, and has a dark bark that is intermediate between that of the other morphotypes with respect to thickness and rugosity (Fig. 8b). *Symphonia globulifera type Régina* grows in the wettest bottomlands of Paracou and has a thick and lashed bark (Fig. 8b). The second blind-identification correctly assigned the difference between all *S. globulifera type Paracou* and *S. globulifera type Régina* and reclassified correctly 87% of previous mismatches between gene pools and previous botanical identification. Among the three populations, 25 individuals (7%) showed admixed genotypes, 15 between *S. globulifera type Régina* and *S. sp.1* and 10 between *S. globulifera type Paracou* and *S. sp.1*, whereas no admixed individuals were found between *S. globulifera type Régina* and *S. globulifera type Paracou* (confirmed with `introgress` R package, Fig. 43). Admixed individuals were removed from subsequent analyses.

Genomic scans for *Symphonia* revealed high-differentiation outliers among gene pools (5.7% of SNPs, Fig. 44), and outliers were enriched in the gene ontology term “response to water deprivation” ($p = 0.01106$). Based on our results, *Symphonia globulifera* is locally and genetically structured in three sympatric species, corresponding to three distinct morphotypes (Fig. 8). *Eschweilera* clade Parvifolia was locally and genetically structured in three genepools separated based on a principal component analysis. The gene pools corresponded to botanical species *E. coriacea*, *E. sagotiana*, and *E. decolorans* (65-80% of match, Fig. 9, Tab. 10). Symphonia and Eschweilera gene pools showed intermediate genetic differentiation, $F_{ST} = 0.15$

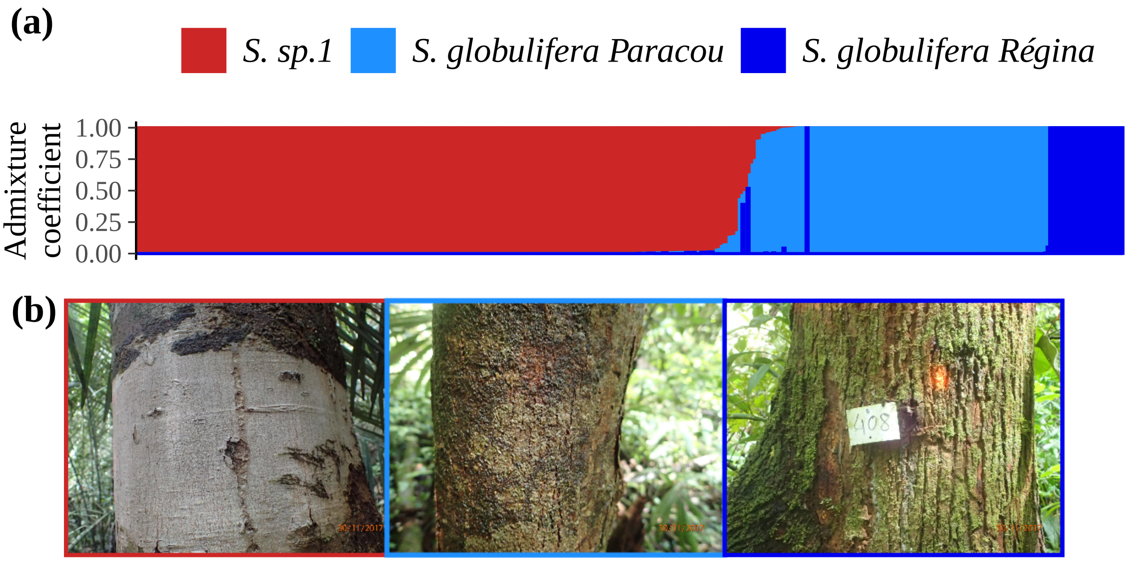

Figure 8: Admixture plot **(a)** of *Symphonia* individuals for the best K, K = 3 and corresponding trunk morphology **(b)**. The three morphotypes are identified with their bark with *S. sp.1* (left, red) having a light grey thin and smooth bark, the *S. globulifera type Paracou* (center, light blue) having a dark that is intermediate between that of the other morphotypes with respect to thickness and rugosity and the *S. globulifera type Régina* that has a thick and lashed bark (right, dark blue).

and $F_{ST} = 0.35$, respectively.

We confirmed topographic wetness index (TWI) and relative elevation (RE, Fig. 11) as descriptors of microenvironmental variation along the topographic gradient exploited by the two species complexes in Paracou. Topographic wetness index (TWI) was related to soil water distribution, opposing water tables deeper than 100 cm to those between the surface and 100 cm deep, which corresponded to hydromorphic soils with the most pronounced waterlogging (variable waterlog5, Fig. 10). Relative elevation (RE) was related to the distribution of nutrients, opposing hilltop soils with the lowest degree of waterlogging (waterlog1) and increased soil organic compounds (soil carbon, nitrogen, organic matter, exchangeable cation charge) to those further down the slopes with intermediate levels of waterlogging and higher soil fertility (higher availability of phosphorus) (Fig. 10).

The distribution of *Symphonia* and *Eschweilera* species along the topographic gradient suggested that both topographic wetness index (TWI) and relative elevation (RE) drove individual survival across gene pools ($0.06 < R^2_m < 0.39$, Fig. 11, Tab. 5). The spatial distribution of *Symphonia* species was driven by both the topographic wetness index (TWI, Fig. 11**c**, Tab. 5), especially between *S. globulifera type Régina* and *S. globulifera type Paracou*, and the relative elevation (RE, Fig. 11**d**, Tab. 5), especially between *S. sp.1* and the two other species. The spatial distribution of *Eschweilera* species was more driven by relative elevation (RE, Fig. 11**b**, Tab. 5) than by topographic wetness index. Variance partitioning revealed that the total genetic variance for topographic position was higher in *Symphonia*

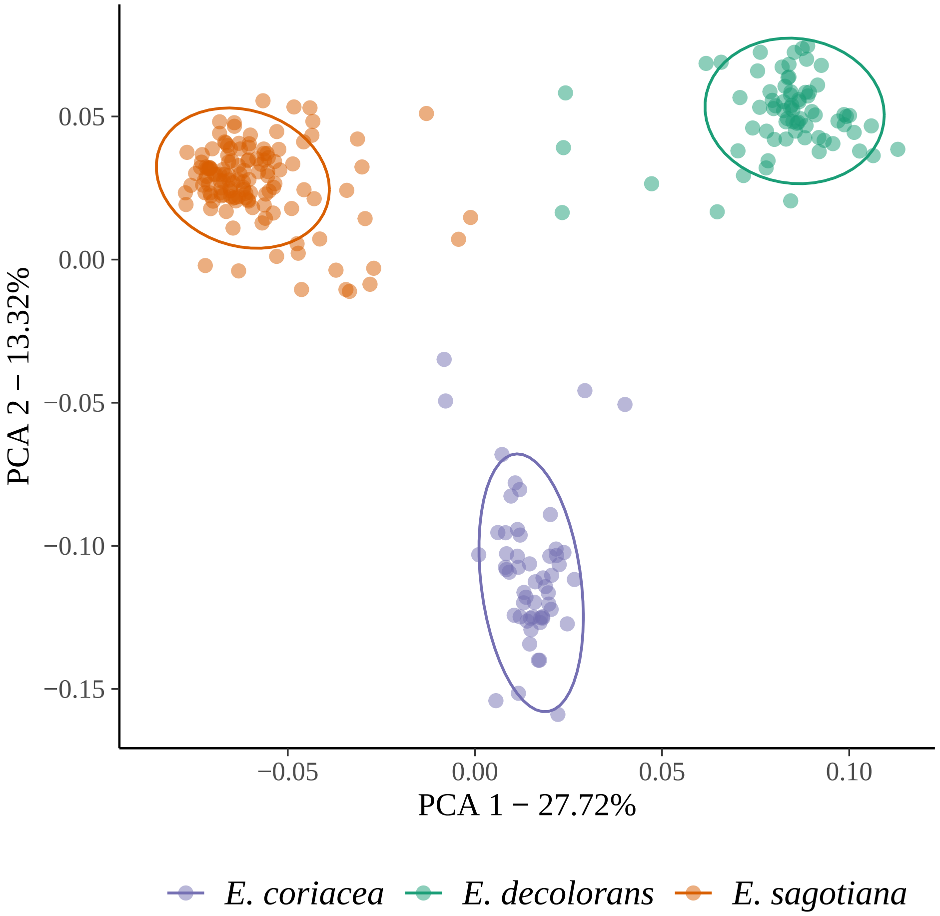

Figure 9: Principal component analysis (PCA) of single nucleotide polymorphisms (SNP) from *Eschweilera* clade *Parvifolia.* The colours represent the clusters detected with Kmeans for the best K, K = 3.

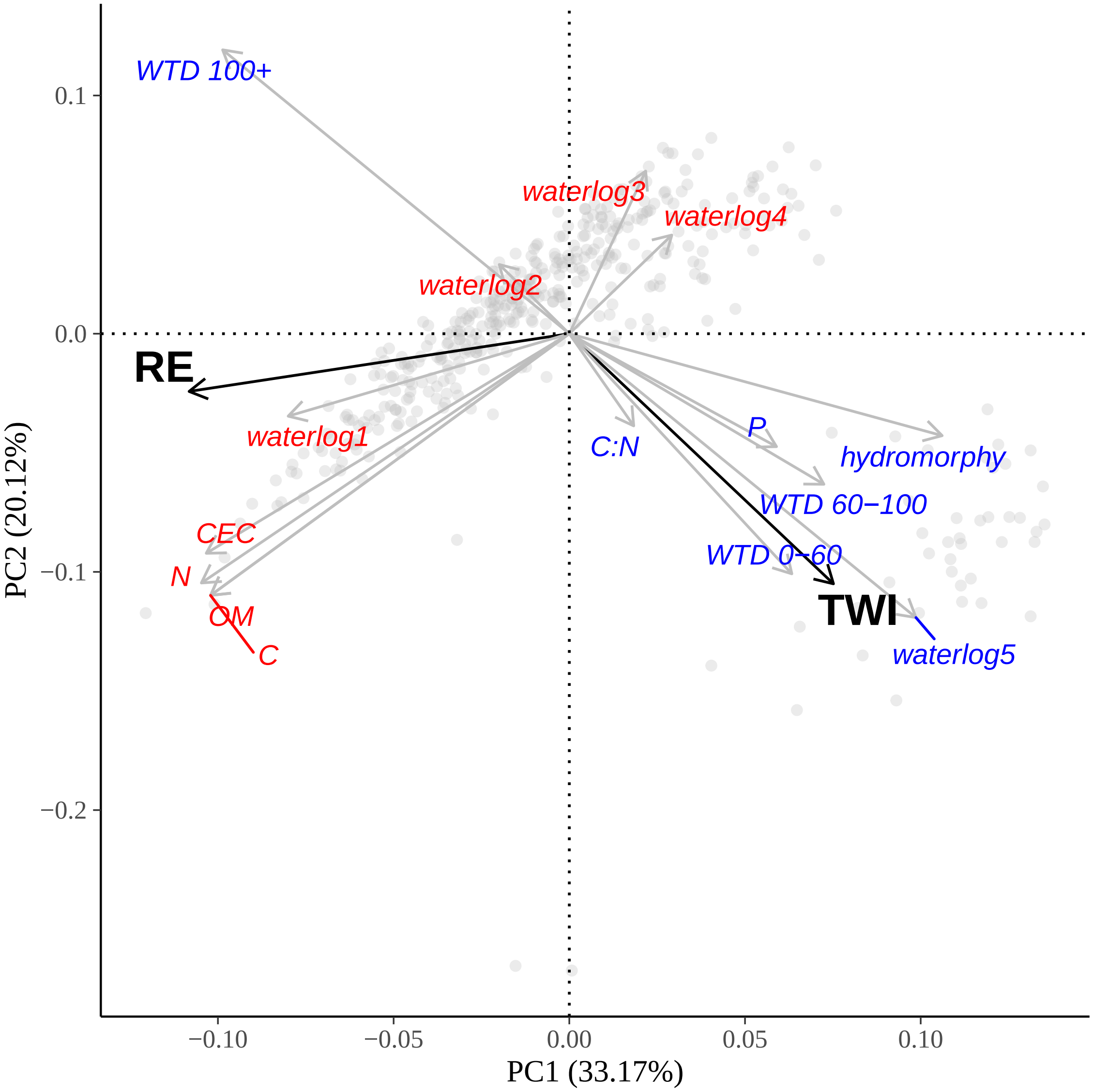

Figure 10: Principal component analysis (PCA) of topographic wetness index (TWI), relative elevation (RE) with edaphic and hydrological properties. Edaphic and hydrological properties include organic matter (OM), carbon (C), nitrogen (N), exchangeable cation charge (C) (Soucémarianadin 2004, Roelens in press), water table depth (WTD in cm, Gourlet-Fleury et al. 2004), hydromorphy and waterlogging (waterlog in 5 classes, Cantet 2004)). Data were obtained through interpolation of soil sample data on TWI and RE from LiDAR data.

(44 and 46% for TWI and RE, respectively) than in *Eschweilera* (27 and 25%, respectively) and that the variance component corresponding to species was much higher in *Symphonia* (35 and 39%) than in *Eschweilera* (6 and 13%, respectively). Within-species additive genetic variance explained between 7 and 21% of total variance in topographic position in all models of the two species complexes.

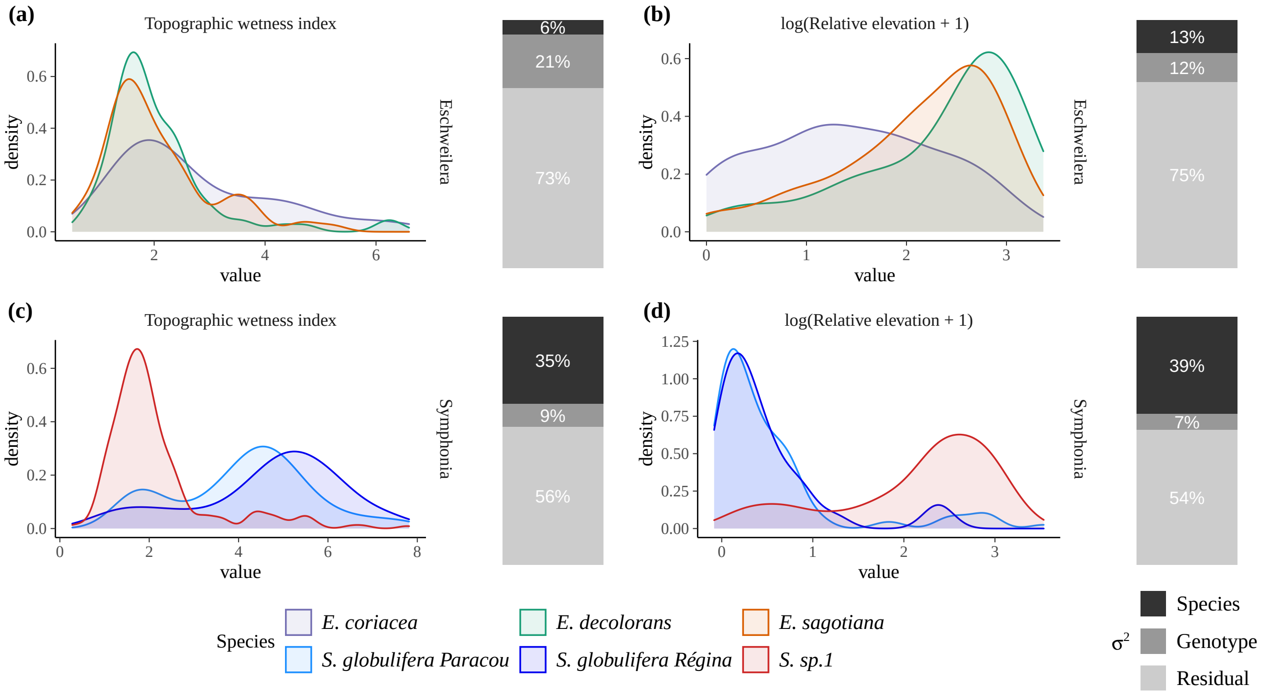

Figure 11: Species distribution and individual variance partitioning along topography. Each subfigure shows density of individuals per species (density plot) against the variable considered (topographic wetness index (TWI, left subfigures) or the logarithm of relative elevation (log(RE+1), right subfigures) and the partitioning of individual variation in the positioning along topography (barplot) partitioned with the Animal model into among-species (dark grey), among-genotypes (intermediate grey) and residual (light grey). Species complexes correspond to *Eschweilera* clade *Parvifolia* (top subfigures) and *Symphonia* (bottom subfigures). Colours represent species determined based on the genetic structure of capture datasets, which was not necessarily in agreement with original botanical identification.

Table 5: Parameters and associated standard deviation of the animal model for *Symphonia* and *Eschweilera* with topographic wetness index (TWI) and relative elevation (RE). Parameters include species mean (μ_s), variance ($V_{species}$), genotype variance ($V_{genotype}$), and residuals variance ($V_{residuals}$). Parameters have been infered with bayesian modelling of the animal model (Model S1) independently for the two species complexes and the two topographic variables.

Species complex	Variable	Parameter	Species	Estimate	Standard deviation
Symphonia	TWI	μ_s	S. globulifera Paracou	1.076	0.056
Symphonia	TWI	μ_s	S. globulifera Régina	1.302	0.115
Symphonia	TWI	μ_s	S. sp.1	0.570	0.021
Symphonia	TWI	$V_{species}$		0.111	0.013
Symphonia	TWI	$V_{genotype}$		0.038	0.031
Symphonia	TWI	$V_{residuals}$		0.171	0.029
Symphonia	RE	μ_s	S. globulifera Paracou	1.153	0.038
Symphonia	RE	μ_s	S. globulifera Régina	1.109	0.068
Symphonia	RE	μ_s	S. sp.1	1.916	0.047
Symphonia	RE	$V_{species}$		0.063	0.006
Symphonia	RE	$V_{genotype}$		0.014	0.012
Symphonia	RE	$V_{residuals}$		0.086	0.012
Eschweilera	TWI	μ_s	E. coriacea	0.998	0.059
Eschweilera	TWI	μ_s	E. sagotiana	0.775	0.030
Eschweilera	TWI	μ_s	E. decolorans	0.772	0.041
Eschweilera	TWI	$V_{species}$		0.012	0.006
Eschweilera	TWI	$V_{genotype}$		0.055	0.049
Eschweilera	TWI	$V_{residuals}$		0.133	0.050
Eschweilera	RE	μ_s	E. coriacea	1.376	0.059
Eschweilera	RE	μ_s	E. sagotiana	1.742	0.048
Eschweilera	RE	μ_s	E. decolorans	1.928	0.072
Eschweilera	RE	$V_{species}$		0.015	0.005
Eschweilera	RE	$V_{genotype}$		0.021	0.023
Eschweilera	RE	$V_{residuals}$		0.077	0.023

Discussion

Despite the local abundance of closely-related tree species growing in sympatry in the Neotropics, little is known of the eco-evolutionary forces that shape their niches and allow their local coexistence. Here, we show that within tree species complexes, closely-related species have different realized optima for topographic niches and we provide evidence for genetic adaptations of species and of genotypes within species for the topographic position where they occur. *Symphonia* species are adapted to the distribution of water and nutrients captured through the topographic wetness index and the relative elevation, hence they coexist locally through exploiting a broad gradient of local habitats. Conversely, *Eschweilera* species are differentially adapted to soil chemistry, captured foremost through the relative elevation, and avoid the wettest, hydromorphic habitats. The greater adaptive signature to topographic position in *Symphonia* than in *Eschweilera* suggests that topographic niche differentiation may be the main factor explaining sympatric coexistence of *Symphonia*, while additional factors related to niche and/or fitness may be necessary to explain coexistence of *Eschweilera* species. Overall, our results suggest that genetic adaptations to different characteristics of topography stabilize local coexistence of species through reducing competition among closely-related species within the two tree species complexes.

Three species of *Symphonia* adapted to topography coexist in sympatry

We identified three distinct species within *Symphonia globulifera sensu lato* with different morphologies, distinct gene pools, and topographic niches. For the purpose of the study, we named the three species *S. sp.1*, *S. globulifera type Paracou*, and *S. globulifera type Régina* in reference to already existing morphotypes and local names. The three species showed a low but significant genetic differentiation ($F_{ST} = 0.15$), as shown previously at the local scale between the two previously recognized morphotypes, *S. globulifera sensu stricto* and *S. sp.1* ($F_{ST} = 0.114$ for genic SSRs; Olsson et al. 2017). Evidence for adaptive genetic differentiation among species was revealed by 5.7% of SNPs identified as high-differentiation outliers, with an enrichment in genes implicated in response to water deprivation.. Topography has already shown to be a driver of the distribution of the two previously recognized morphotypes (Allié et al. 2015) with *S. globulifera* growing in low-elevation and wet bottomlands and *S. sp.1* growing in drier slopes and plateaux. In addition, our study revealed the existence of two *Symphonia globulifera* morphotypes segregated within wet areas, with *Symphonia globulifera type Régina* growing in the wettest bottomlands, such as swamp characterized by increased wetness and anoxia. Similar ecotypic differentiation with a designated swamp ecotype has been suggested in Africa (Budde et al. 2013). Individual topographic positions had a large plastic component (54-56% of variation) but genetics explained the remaining variation, with a ca. five-fold larger inter- than intra-specific component (Fig. 11). Thus, finescale topographic variation among individuals was driven by adaptive processes, revealing local adaptation to topography within and among the three species at the hectare-scale. Further studies at a broader regional scale are needed, but our results advocate for the definition of three distinct taxonomic species with differences in morphology (Fig. 8), habitat preference (Fig. 11), functional traits and growth trajectories (S. Schmitt unpublished results).

Three species of *Eschweilera* adapted to soil chemistry coexist in sympatry

Eschweilera species avoided hydromorphic soils and were differentially adapted to soil chemistry. At least three distinct species of *Eschweilera* clade *Parvifolia* with different morphologies, gene pools, and topographic niches coexist in sympatry. *Eschweilera coriacea* preferentially grows in fertile and phosphorus-rich valley bottoms but has a broad topographic niche, and *E. sagotiana* and *E. decolorans* preferentially exploit slopes and plateaus, characterized by low levels of waterlogging and soils rich in organic compounds (Fig. 11; Allié et al. 2015). Topography, through the dissolution of iron oxides, litter- and tree-fall transfers and waterlogging, shape soil nutrient distribution in tropical forests (Ferry et al. 2010a, John et al. 2007). The lack of power of *Eschweilera* data prevented us from detecting the less abundant *Eschweilera* species of the *Parvifolia* clade (e.g. *E. grandiflora* (Aubl.) Sandwith, *E. wachenheimii* (Benoist) Sandwith), but our results do not question their botanical definitions. Topographic position within *Eschweilera* was mainly plastic (73-75% of residual variation), but concerning genetic variation, relative elevation best captured differences among species (52%) whereas the topographic wetness index best captured genetic variation among genotypes (78%, Fig. 11).

Species niche differentiation and coexistence within species complexes

The interaction between topography and genes shapes the microgeographic genetic structure among and within species in the studied tropical tree species complexes. We found genomic evidence for a functional response to water deprivation between *Symphonia* species, confirming the role of water availability as a driver of the topographic niches in the complex. Similarly to European white oaks, *Symphonia* holds coexisting species with differential genetic adaptations that allow them to thrive in different ecological niches despite interspecific hybridization (Leroy et al. 2019). In *Eschweilera*, we evidenced a genomic signature of topographic niche differentiation but the low resolution of our data did not allow us to demonstrate hybridization. Although the regional-scale evolutionary history and the specific roles of interspecific hybridization and introgression remain unknown for both species complexes, our study shows that inter- and intra-specific adaptive processes to topographic niches stabilize local coexistence of species in these tropical tree species complexes, similarly to what is observed in the European white oaks syngameon. *Symphonia* and *Eschweilera* clade *Parvifolia* might thus represent syngamons (Cannon and Petit 2019) of tropical trees. It remains to be shown that interspecific gene flow benefits their constituent species, through adaptive introgression, or through preventing local extinction of congeners by enabling reproductive assurance and increasing their effective population size (Cannon and Lerdau 2015).

The distribution of *Eschweilera* species along the topographic gradient was more influenced by plasticity than in *Symphonia* and the role of intra-specific adaptive processes was stronger in *Eschweilera*, with intra-specific genotypic effects stronger or equal to inter-specific effects. As compared to *Symphonia*, *Eschweilera* exhibited globally a weaker role of topography on the structuring of its genetic variation, its species had a more marked topographic niche overlap, and the intra-specific adaptive signature to topography was larger. These patterns may be a consequence of the evolutionary history of the complex. *Eschweilera* species, despite similar morphology, have a higher genetic differentiation and their phylogenetic constraints may thus be relaxed as compared to Symphonia (Wiens et al. 2010), allowing greater topographic niche overlap possibly in conjunction with niche differentiation along other ecological gradients, e.g., related to root depth or light access (Rüger et al. 2009). But *Eschweilera* species may also coexist through a decrease in fitness differences among species allowing them to persist in a shared niche (Turcotte and Levine 2016). This explanation is plausible in a species complex like Eschweilera in which the risk of hybridization and consequent breakdown of inter-specific divergence may be more limited than in more closely-related, recently diverged species (Tobias et al. 2014). Furthermore, the signature of within-species genotypic adaptations to topographic niche may be associated with broad niches for TWI. Schmitt et al. (2020) showed that *E. coriacea* and the two major previously recognized *Symphonia* morphotypes had broader niches for TWI than the majority of tree species in Paracou. To further improve our understanding on the eco-evolutionary drivers of coexistence in these tropical tree species complexes, future work should improve our knowledge on the evolutionary history of both complexes, including aspects of interspecific gene flow and introgression, as well as consolidate knowledge on the factors that shape the niche space of both species complexes at broader geographic scale.

The literature includes numerous examples of niche differentiation among closely-related species growing in sympatry, along fine-scale topography (Gunatilleke et al. 2006, Engelbrecht et al. 2007, Kraft et al. 2008, Allié et al. 2015) or along other local ecological niche variables (Yamasaki et al. 2013, Itoh et al. 2003). On a larger scale, topography is also a driving force for tropical species diversity on the Andes (Mutke et al. 2014). In Paracou, several species complexes have been shown to present differentiated niches along topography [Schmitt et al. in prep]. Combined with our results, this abundant evidence of niche differentiation among closely related species calls into question the more general role of topography in the genetic adaptation and diversification of tropical tree species complexes, even for small topographic gradients such as those found in French Guiana. Our results suggest that ecological speciation as demonstrated along steep gradients, such as soil types or soil metal content (Paun et al. 2016, Fine et al. 2004), could possibly occur at a fine spatial scale with gradual habitat variation. Our work emphasizes the potential role of species complexes and syngameons in the origin and maintenance of Neotropical forest diversity.

Acknowledgements

We thank the University of Bordeaux for a PhD grant to Sylvain Schmitt. We are grateful to Pascal Petronelli and the CIRAD inventory team for their work on tree inventories and botanical identification. This study was funded through an Investissement d'Avenir grant of the ANR: CEBA (ANR-10-LABEX-0025), the "projet innovant" LOCOCAP granted through INRA and the LECYTOMICS project granted through the IRD-GUYAMAZON program.

Authors' contributions

All authors conceived the ideas and designed methodology; SS, MH, and NT sampled individuals; SS and MH performed the gene capture experiments; SS, MH and BH analysed outputs; SS and MH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Supporting information

Method S1. Design of the probes set for *Symphonia*.

Method S2. Design of the probes set for *Eschweilera*.

Model S1. Stan code for the animal model

Tab. 10. *Eschweilera* botanical species and genetic clusters

Fig. 36. Target selection for the capture experiment of *Symphonia*

Fig. 37. Target selection for the capture experiment of *Eschweilera*

Fig. 38. SNP abundance per library for *Eschweilera*

Fig. 39. Library abundance per SNP for *Eschweilera*

Fig. 40. Outgroup detection for *Eschweilera*

Fig. 41. Cross-validation for *Symphonia* population structure

Fig. 42. *Symphonia* population structure using admixture

Fig. 43. *Symphonia* population structure using hybrid index

Fig. 44. Outlier SNPs among *Symphonia* species

CHAPTER 4: FOREST GAP DYNAMICS: AN UNDEREXPLORED FACTOR THAT DRIVES DIVERGENT ADAPTIVE GROWTH STRATEGIES WITHIN TROPICAL TREE SPECIES

In preparation for the Proceedings of the National Academy of Sciences of the United States of America (PNAS)

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Keywords: genotypic adaptation | neighbor crowding index | *Symphonia globulifera*

Abstract

In tropical forests, natural gap dynamics is a primary driver of ecosystem functioning by triggering a wide variety of ecological growth and survival strategies of trees. These strategies have long been studied *among* species, neglecting individual variation in demographic responses *within* species. Variation in demographic response is facilitated by overlapping generations which maintain the genetic diversity necessary for temporally-variable but strong selection acting on specific life stages. Tropical trees are long-lived and produce many seedlings whose growth and survival is shaped by forest gap dynamics. Here, we provide evidence that genotypic adaptive growth strategies allow forest tree species to grow in a mosaic of light and competition environments, or successional niches, shaped by time since the last tree fall. Consequently, the successional niche selects individuals with the most suitable adaptive growth strategy to reach the canopy, with fast-growing *hares* in forest gaps and slow-growing *turtles* in shaded closed-canopy patches.

Significance Statement

The natural gap dynamics from falling trees is one of the main drivers of ecosystem functioning in tropical forests. Trees respond to forest gap dynamics by a wide variety of ecological strategies, but these strategies have long been studied among species, neglecting genetic variability within species. Here we provide genetic evidence for diverse adaptive growth strategies of individuals within mature forest tree species that allow them to grow in a diversity of light and competition environments that vary with time since the last tree fall. We show that the fine spatio-temporal dynamics of forest gaps is a previously neglected factor that, along with others, contributes to maintaining tropical tree within-species genetic diversity, the raw material of evolution.

Introduction

The heterogeneity of resource distribution in space and time defines the fine-scale habitat structure where species and individuals can grow and coexist (Weiher and Keddy 1995, Lortie et al. 2004a). For instance, the spatial distribution of water and nutrients varies strongly along topographic gradients in tropical forests (Ferry et al. 2010a). Therefore, topography drives pervasive differentiation in habitat preference among tree species (Engelbrecht et al. 2007) and in functional responses among and within species (Schmitt et al. 2020). In natural tropical forests, competition for light due to forest gap dynamics (Hubbell et al. 1999, Molino and Sabatier 2001) is often greater than the effect of competition for water and nutrients, even in early successional stages (Breugel et al. 2012). Forest gap dynamics is characterised by a mosaic of light and competition environments, or successional niches, shaped by time since the last treefall. Forest succession contrasts a bright environment with reduced competition from adult trees after a treefall with a variety of more shaded environments in which competition from tall trees increases as they fill with vegetation. Successional niches trigger a wide variety of demographic responses associated with ecological strategies of individuals and species (Rüger et al. 2009, Herault et al. 2010). Pioneer species with fast growth, thanks to productive leaf tissue and light wood, rapidly colonize treefall gaps whereas late successional species with slower growth and more conservative tissue progressively establish in more shaded environments (Craven et al. 2015).

But “nothing in biology makes sense except in the light of evolution” (Dobzhansky 1973). Spatial habitat heterogeneity has been shown to drive differential adaptations of tree species, in the case of adaptive radiations (Pillon et al. 2014, Paun et al. 2016), and within tree species, with microgeographic adaptations within the dispersal neighbourhood of an individual (Richardson et al. 2014, Brousseau et al. 2013, 2015). However, the role of temporal habitat heterogeneity as a driver of adaptive evolution has been much less explored. Forest gap dynamics is a spatio-temporal process that has a strong impact on tree ecology (Breugel et al. 2012), however, to our knowledge, no studies have explored its role as a driver of adaptation within species.

The assumption that evolution and ecology operate at very different time scales may have impeded such studies (Pelletier et al. 2009), however, evidence is accumulating showing that evolutionary processes can be fast enough to impact ecological processes on a contemporary time scale (Hairston et al. 2005, Rudman et al. 2017). Theoretical work demonstrated that biological systems with overlapping generations can maintain genetic variation in long-lived stages in which selection is relaxed and which provide diversity for specific, young stages, on which strong temporally variable selection can act (Ellner and Hairston Jnr 1994). For instance, overlapping generations with oscillation between short high-recruitment periods and long population-decline periods explain the spatial genetic structure of the Neotropical tree Jacaranda copaia (Jones and Hubbell 2006).

In tropical forests, the dynamics of forest gaps strongly determines the survival and recruitment of non-mature trees through competition for access to light. Once in the canopy, adult trees with full access to light are free from the light-driven selection of forest gap dynamics. Adult trees can therefore act as a reservoir of genotypes against the hazards of fine spatio-temporal dynamics of forest gaps. Generations of tropical trees broadly overlap, for instance late-successional tree species start reproducing around 20cm of diameter at breast height (DBH), while they may grow up to 1m DBH (Hardy et al. 2005) and live more than a century (O'Brien et al. 1995).

Tropical trees thus disperse many seedlings over time into a mosaic of light conditions that fluctuates spatially and temporally due to the dynamics of forest gaps. Individual offspring encounter mainly shady and sometimes bright environments in which they face competition and must grow to survive. Since forest gap dynamics opposes rapid growth in a bright environment to slow growth in a shaded environment, we hypothesize that individual genotypes within species would be adapted to divergent growth strategies between bright and shaded environments. Adaptation to slow growth in shade would allow individuals to persist with conservative tissues, whereas adaptation to fast growth in a bright environment would allow individuals to outgrow other seedlings and maintain access to light through an acquisition strategy with cheaper tissues but with less defence against herbivores and pathogens (Fine et al. 2006). Consequently, we hypothesize that forest gap dynamics is a major driver of the spatial and temporal structuring of genotypic diversity within tropical tree species.

Following our hypothesis, we expect that the divergent adaptive growth strategies of individuals would be spatially structured according to the mosaic of successional niches created by the past fine-scale gap dynamics. We also expect the divergent adaptive growth strategies to be structured in time. Because of strong light and competition-mediated selection on sapling stages (Lewis and Tanner 2000), genotypic adaptations to growth in different light conditions are expected to be more pronounced in intermediate life stages. Seedlings may be mostly affected by very stochastic survival. Conversely, older stages maintain diversity as they have been recruited from diverse past successional niches and, once in the canopy, they are free from the light-driven selection of forest gap dynamics.

In the present study, we assessed genotypic diversity within closely-related sympatric tree species belonging to the widespread tropical tree species complex *Symphonia globulifera*. We addressed the fine-scale spatial and temporal genetic adaptations of individuals through differential growth strategies in response to forest gap dynamics. We finally compared the breadth of successional niches encountered by *Symphonia* species to other locally abundant species. Combining tree diameter censuses, indirect measures of light environment of the recent past and present, and single nucleotide polymorphisms (SNPs), we used population genomics, environmental association analyses, genome wide association and growth modelling to address the following questions:

- Are individual genotypes structured by the mosaic of light and competition environments resulting from forest gap dynamics?
- Is the growth of individuals determined by genotypes?
- Is there an association between genotypic adaptations to gap dynamics and to growth?

- How are genotypic adaptations to gap dynamics and to growth structured in time, i.e., across life stages?
- Are breadths of successional niches for Symphonia species wider than those of other locally abundant species?

Results

Symphonia globulifera was locally composed of three sympatric species corresponding to three different gene pools with associated morphotypes and differentiated topographic niches (Schmitt et al., in prep). Individual tree genotypes explained a significant variation in individual neighbourhood crowding, an indirect measure of competition and light access during the last three decades, (18%) and in individual growth potential (43%, Fig. 12). This indicates an adaptive genetic response of *Symphonia* genotypes to successional niches and an adaptive component to growth potential. Genotypic adaptations to successional niches and individual growth potential were spatially structured on a similar scale, with higher than average genotypic similarity found up to 47m for both adaptations ($Moran's\ I, p-value < 0.01$, Fig. 13). The adaptive responses to successional niches and to growth potential were significantly correlated, and, as predicted based on our hypothesis, the correlation was strongest for intermediate life stages: a significant negative correlation (Pearson's $R = -0.3$, $p = 4.5.10^{-9}$) was observed between genotypic values for neighbourhood crowding and those for individual growth potential across diameter classes (Fig. 14), with a stronger and a more significant signal for individuals in intermediate diameter classes, from 14 to 46cm DBH, than for individuals with smaller or larger DBH. These results suggest that individual genotypes within *Symphonia* species are adapted to successional niches that trigger adaptive growth strategies: a fast growth potential in response to a preference for low competition and bright environments, or a slower growth potential in response to a preference for higher competition and more shaded environments, structured in space and in diameter classes. The breadths of successional niches for *Symphonia* species (92 for botanically defined *S. globulifera*, which contains two biological species, and 103 for *S. sp1*) are representative of those of locally abundant species (97 ± 10, Fig. 15).

Discussion

In agreement with our hypothesis, we found that individual tree genotypes are differentially adapted to regenerate and thrive in response to the fine spatio-temporal dynamics of forest gaps. Divergent adaptive growth strategies are found under different light conditions and the adaptive genetic signature is spatially structured into patches the size of a typical gap opened by a treefall. The adaptive genetic signature is also structured in time across life stages, with a stronger effect in the intermediate stages, than in either young stages under diverse selection pressures (Tysklind et al. 2020) or in older stages recruited in diverse past environments and

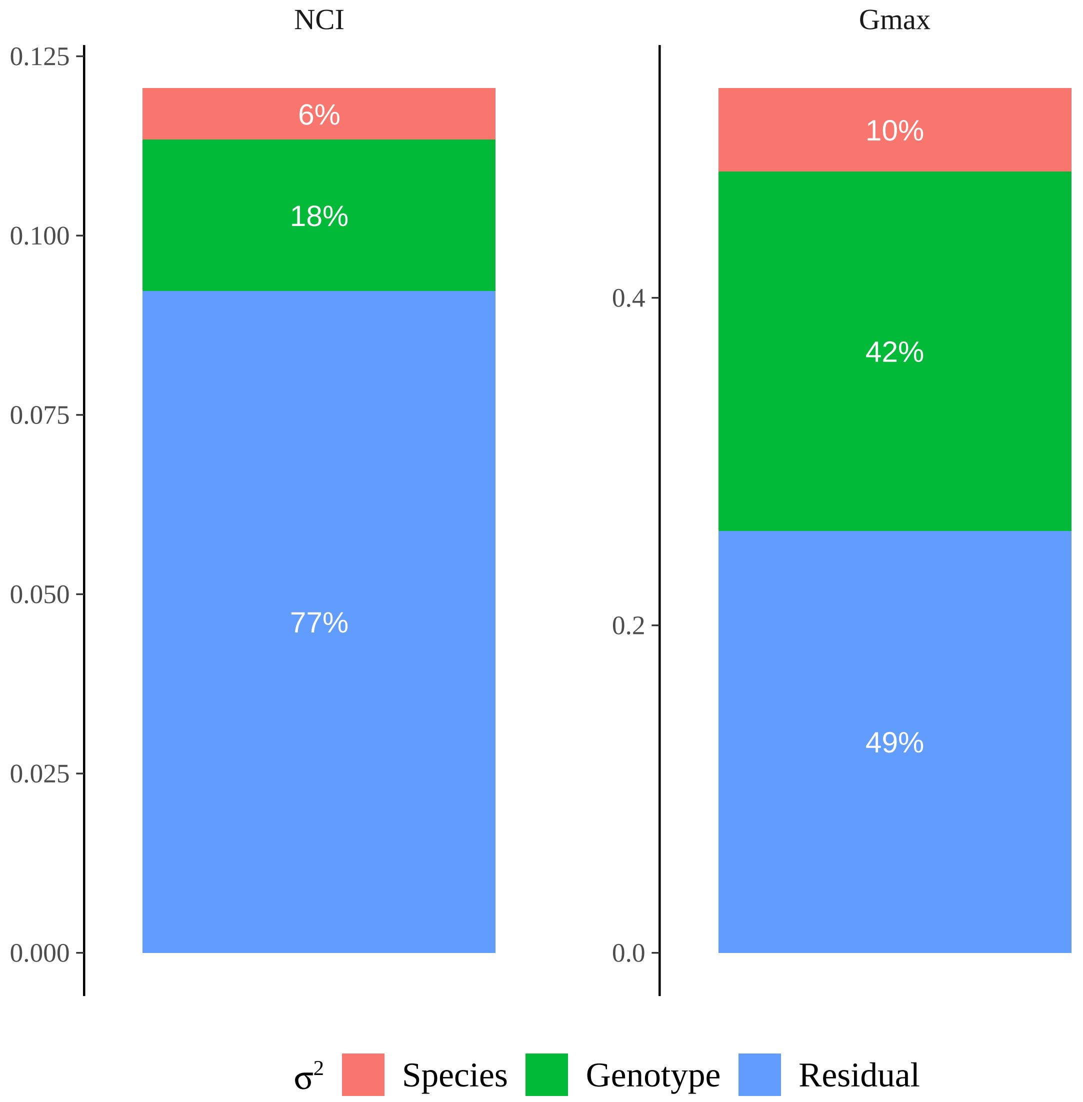

Figure 12: Variance partitioning for neighbourhood crowding index (NCI), an indirect measurement of access to light, and for individual maximum growth potential (Gmax). Variation of each variable has been partitioned into among-species (red), among-genotype (green), and residual (blue) variation.

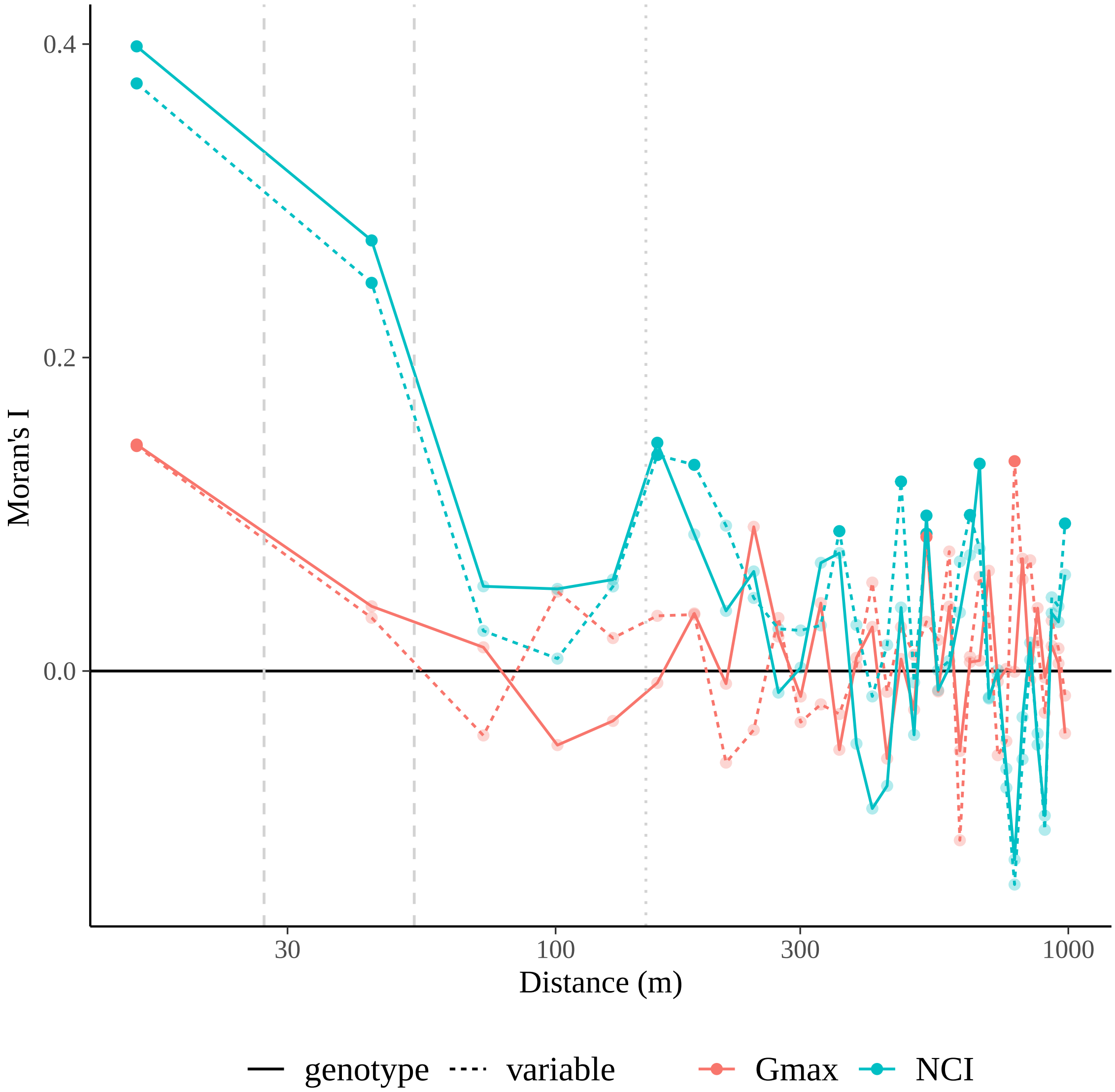

Figure 13: Spatial autocorrelogram for raw variable and genotypic values of neighbourhood crowding index (NCI), an indirect measurement of access to light, and individual maximum growth potential (Gmax). The spatial autocorrelogram shows Moran's I value for different distance classes with significant values represented by filled circles vs. empty circles for non-significant values. Colours of lines and points represent neighbourhood crowding index (blue) and individual maximum growth potential (red). Line type represents raw variable (dashed) and associated genotypic values (continuous).

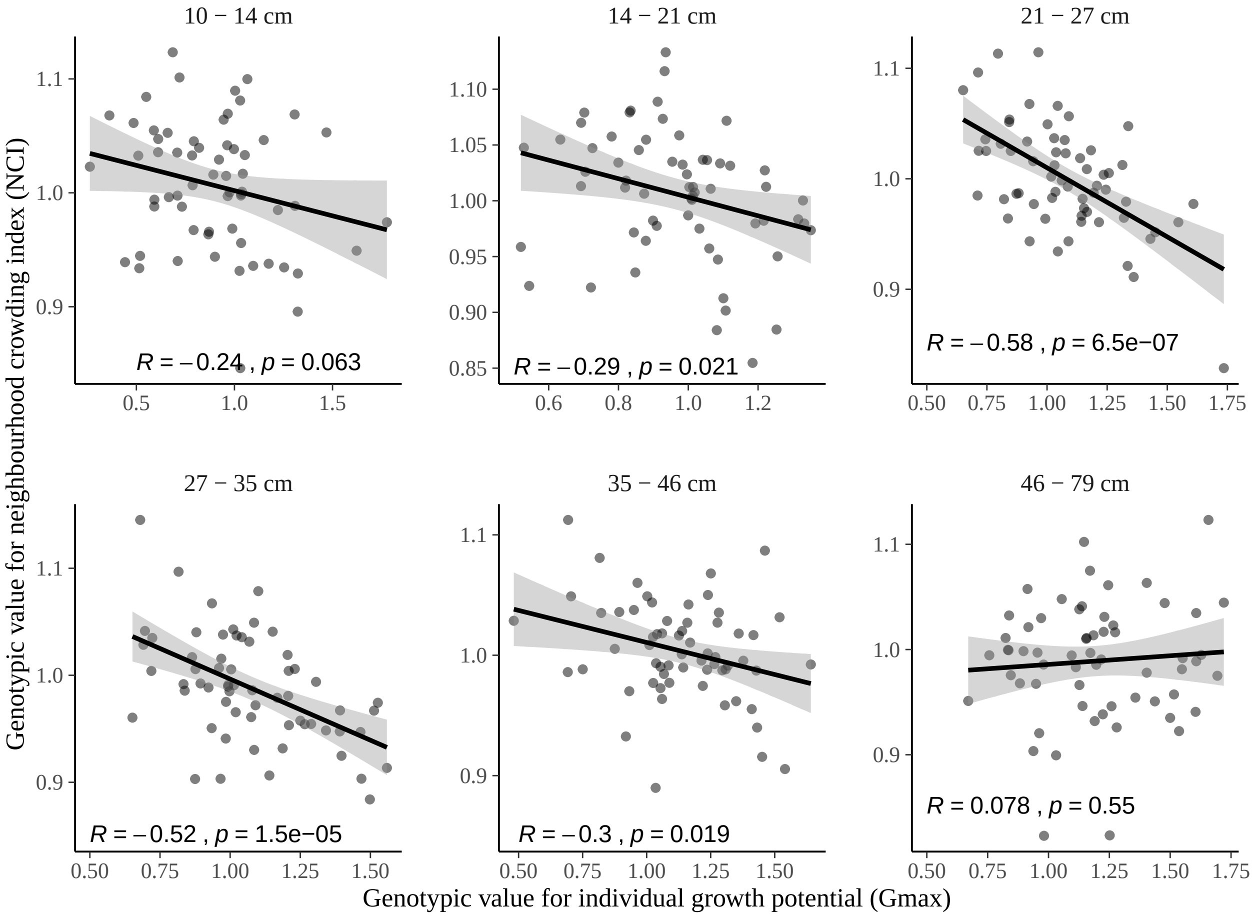

Figure 14: Correlations between genotypic values for individual growth potential (Gmax) and neighbourhood crowding index (NCI), an indirect measurement of access to light, for different classes of tree diameters. Regression lines represent a linear model of form y ~ x. Annotations give for each diameter class the Pearson's R correlation coefficient and the associated p-value.

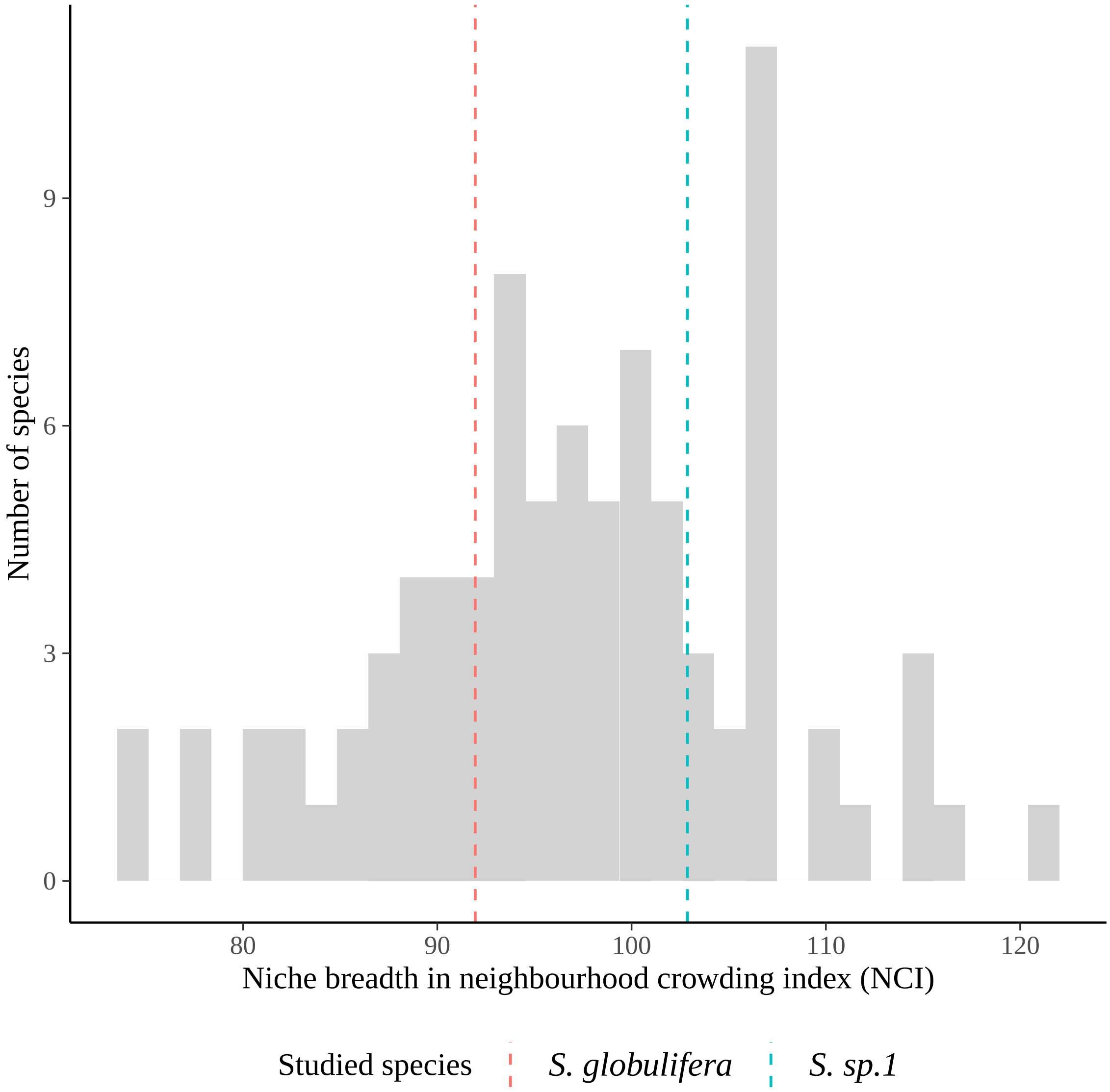

Figure 15: Niche breadth in neighbourhood crowding index (NCI) for tree species abundant in the study site (Paracou). Niche breadth is defined by the difference between the 95th and 5th quantiles of neighbourhood crowding index (NCI) for individuals with a diameter at breast height between 10 and 20 cm. Niche breadth has been calculated for species with at least fifty individuals meeting previous criteria. The analyses used only control inventory plots, and not human disturbed plots. Dashed lines represent niche breadth for Symphonia globulifera (red) and Symphonia sp. 1 (blue).

currently free from the light-driven selection of forest gap dynamics. Therefore, *Symphonia* species use genetically differentiated growth strategies that allow its individuals to grow in a diversity of successional niches, thanks to these divergent adaptive growth strategies to forest gap dynamics, decreasing the overall risk of a stochastic local extinction. Our results thus demonstrate that the effect of forest gap dynamics on growth and survival strategies among tropical tree species (Herault et al. 2010, Rüger et al. 2020) is maintained at the within-species level in the *Symphonia globulifera* species complex .

Our results observed in the *S. globulifera* species complex which contains three species reveal the influence of forest gap dynamics on genotypes of tree species in tropical forests. Breadths of successional niches for Symphonia species are similar to those of most of the locally abundant species (Fig. 15). As forest gap dynamics broadly affects the tree species in a tropical forest community, we can assume that genotypic adaptations to this process are not specific to *Symphonia* species, or species complexes, but are likely to be present in numerous tree species of tropical mature forests. Indeed, locally abundant species could only adapt to such broad successional niches through plasticity, if not through genotypic adaptations. The strength of competition for light due to forest gap dynamics (Breugel et al. 2012) advocates more for varied and complex genotypic adaptations than for a single genotype superior across a wide variety of successional niches (Ellner and Hairston Jnr 1994), likely due to physiological or adaptive constraints.

Forest gap dynamics of natural (Scotti et al. 2015) or anthropogenic (Leclerc et al. 2015) origin was evidenced as a driver of genetic diversity and structure within tree species, with varying effects depending on the disturbance intensity. However, to our knowledge, no studies have investigated genotypic adaptations to forest gap dynamics until now. Temporal dynamics and spatial stochasticity may have been an impediment to the hypothesis of selection based on forest gap dynamics, but patches with varying successional stages and steady-state are abundant, while disturbance events are episodic (Chambers et al. 2013). Our study, linking genotype distribution to forest gap dynamics, was only possible thanks to a long-term and large-sized study site that allows us to study the eco-evolutionary dynamics of a complex phenotype: the individual growth trajectory. The relative temporal stability of forest patches and the strength of forest gap dynamics on ecosystem functioning probably make it a major driver of the distribution of diversity from genes to species in tropical forests.

The existence of a few taller individuals growing all the way to the canopy, i.e. the *winners*, and relegating a group of *losers* to the understory has already been demonstrated in tropical forests (Farrior et al. 2016). Our analyses revealed that the *winners* are not determined entirely at random but may result from a subtle match between the light environment produced by the forest gap stage and the relevance of individual genotypic adaptations to such an environment. Therefore, the *winners* are not necessarily the fastest growing individuals, i.e. with the strongest vigor sensu Aubry-Kientz et al. (2015a), but slow-growing individuals might also represent *winners* in shaded closed-canopy patches. To conclude, genetic adequacy with forest gap dynamics determines successful individuals reaching the canopy through divergent growth strategies, with *hares* in forest gaps and *turtles* in more shaded closed-canopy patches.

Material and methods

Study design. The study was conducted in the Guiana Plateau region, at the Paracou field station in French Guiana. The site is made of 16 permanent plots which have been censused (diameter at breast height over 10cm) every 1-2 years for more than 35 years. Nine of the plots were logged and subjected to human-induced disturbance in 1986. We sampled leaf tissue from 402 individuals previously morphologically identified as *Symphonia globulifera* or *Symphonia sp. 1* in November and December 2017 (*SI Materials and Methods*).

Sequence capture. We designed in silico 20,000 80-mer probes for sequence capture on *Symphonia globulifera*. The genetic resources used for the design consisted of two draft genomes, a transcriptome, and reduced-representation genomic sequence reads. We prepared and pooled libraries for each individual including a few replicates, captured sequences by hybridization with probes, and sequenced them in two lanes of an Illumina HiSeq 4000 instrument, following standard protocols. We called, filtered and annotated single nucleotide polymorphisms (SNPs) of sequenced libraries against the references used to build the experiment with standards used in quantitative genomics(*SI Materials and Methods*).

Genetic analyses. We investigated population genetic structure using `admixture` (Alexander and Lange 2011) and the `introgress` R package (Gompert and Alex Buerkle 2010). We validated species delimitation with a second blind-identification of every collected individual in November 2019. Population genetics is further described in Schmitt et al. (in prep) and *SI Materials and Methods*. We inferred individual kinship using `KING` (Manichaikul et al. 2010), as the method is robust to population structure. We set negative kinship values to null as they were confounding with population structure, and we further ensured that the matrix was positive-definite using the `nearPD` function from the R package `Matrix`.

Neighbour crowding index. We used mean neighbourhood crowding over the last 30 years as an indirect measurement of access to light and forest gap dynamics, defined as follow:

$$NCI_i = \overline{\sum_{j|\delta_{i,j}<20m} DBH_{j,t}^2 . e^{-\frac{1}{4}\delta_{i,j}}}$$

with $DBH_{j,t}$ the diameter of the neighbouring tree j in year t and $\delta_{i,j}$ its distance to the individual tree i. NCI_i is computed for all neighbours at a distance $\delta_{i,j}$ inferior to the maximum neighbouring distance of 20 meters. The power of neighbours $DBH_{j,t}$ effect was set to 2 to represent a surface. The decrease of neighbours diameter effect with distance was set to -0.25 to represent trees at 20 meters of the focal trees having 1% of the effect of the same tree at 0 meters. NCI_i is computed as the mean of yearly $NCI_{i,t}$ over the last 30 years denoted by the overline.

Individual maximum growth potential. The individual growth of individual i in population p between individual recruitment y_0 and 2017, correspond to the difference of diameter at breast height DBH between the two years, and is defined with a hierarchical model in a lognormal distribution as follow:

$$DBH_{y=2017,p,i} - DBH_{y=y0,p,i} \sim logN(log[\sum_{y=y0}^{y=2017} AGR(DBH_{y,p,i})], \sigma_1^2)$$

where the difference of $DBH_{y=2017,p,i} - DBH_{y=y0,p,i}$ is defined with a lognormal distribution located on the logarithm of the sum of annual growth rates AGR during the period y_0 to 2017 and of shape σ_1^2. The annual growth rates AGR for individual i in population p at year y with a diameter of $DBH_{y,p,i}$ is defined following a Gompertz model (Gompertz 1825), already identified as the best model for growth-trajectories in Paracou (Hérault et al. 2011):

$$AGR(DBH_{y,p,i}) = Gmax_i.exp(-\frac{1}{2}[\frac{log(\frac{DBH_{y,p,i}}{Doptp})}{Ksp}]^2)$$

where $Gmax_i$ is the maximum growth potential (maximal AGR during individual life) for individual i further used in association analyses, $Dopt_p$ is the population optimal diameter at which the individual reaches its maximum growth potential, and Ks_p is the population kurtosis defining the width of the bell-shaped growth-trajectory (see figure 1 in Hérault et al. 2011). To ease model inference population optimal diameter $Dopt_p$ and kurtosis Ks_p were defined as a random population effect centered on a genus $Dopt$ and Ks with corresponding variances σ_{Dopt}^2 and σ_{Ks}^2.

Genotypic values estimate and associations. We used population and individual kinship in an homemade bayesian Animal model with a lognormal distribution to estimate genetic variance associated to the neighbourhood crowding where individual grow and individual maximum growth potential. The Animal model was directly inferred with neighbourhood crowding, while the Animal model was nested in a hierarchical model to describe individual maximum growth potential $Gmax_i$ in the previous growth model (*SI Materials and Methods*). To estimate variances on a normal-scale, we log-transformed population fixed effect, genetic additive values, and we calculated conditional and marginal R^2 (Nakagawa and Schielzeth 2013) to partition observed variance. We investigated the relationships between genotypic associations to neighbourhood crowding and individual maximum growth and their structure in space and time with respectively spatial autocorrelogram, using the `pgirmess` R package (Giraudoux et al. 2018), and decomposed relations over diameter classes.

Acknowledgments

We thank the University of Bordeaux for a PhD grant to Sylvain Schmitt. We are grateful to Pascal Petronelli and the CIRAD inventory team for their work on tree inventories and botanical identification, and to Christophe Plomion for comments on an early version of the manuscript. This study was funded through an Investissement d'Avenir grant of the ANR: CEBA (ANR-10-LABEX-0025), and the INRAE ECODIV department, through "projet innovant" LOCOCAP.

Authors' contributions

All authors conceived the ideas and designed methodology; SS, MH, and NT sampled individuals; SS and MH realized the gene capture experiment; SS, MH and BH analysed outputs; SS, MH and BH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DISCUSSION

Despite the key role of species complexes in Neotropical forest ecology, diversification, and evolution, little is known of the eco-evolutionary forces creating and maintaining diversity within Neotropical species complexes. Here, we showed that the species complexes of Neotropical trees cover most local gradients of topography and competition and are therefore widespread in the study site whereas most of the species within them exhibit pervasive niche differentiation along these same gradients. Specifically, in the species complexes *Symphonia* and *Eschweilera* clade *Parvifolia*, the decrease in water availability due to higher topographic position, e.g., from bottomlands to plateaus, has led to a change in leaf functional traits from acquisitive strategies to conservative strategies, both among and within species. *Symphonia* species are genetically adapted to the distribution of water and nutrients, hence they coexist locally through exploiting a broad gradient of local habitats. Conversely, *Eschweilera* species are differentially adapted to soil chemistry and avoid the wettest, hydromorphic habitats. Last but not least, individual tree genotypes of *Symphonia* species are differentially adapted to regenerate and thrive in response to the fine spatio-temporal dynamics of forest gaps with divergent adaptive growth strategies along successional niches. Consequently, topography and the dynamics of forest gaps drive fine-scale spatio-temporal adaptations of individuals within and among distinct but genetically connected species within the species complexes *Symphonia globulifera* and *Eschweilera* clade *Parvifolia*. Fine-scale topography drives genetic divergence and niche differentiation with genetic adaptations among species; while forest gap dynamics maintains genetic diversity with variable adaptive strategies within species, at least for *Symphonia* species. I suggest that adaptations of tree species and individuals to topography and dynamics of forest gaps promote coexistence within and among species within species complexes, and perhaps among forest tree species outside species complexes. I further stress the potential role of the eco-evolutionary structure of Neotropical tree syngameons in their local and regional success, and their potential role in shaping the exceptional diversity of Neotropical forests. I discuss the limitations of the low-cost capture approach to study the evolution of non-model species complexes in nature. I further emphasize the need to merge ecology and evolution in an interdisciplinary approach and I present an exploration of future simulation approaches to address the conditions of coexistence of tree species given the joint effects of topography and forest gap dynamics. Overall, I defend the primordial role of individuals within species in tropical forest diversity, suggesting that we should develop a theory of community ecology starting with individuals, because interactions with environments happen after all at the individual level.

Topography and forest gap dynamics drive fine-scale spatio-temporal adaptations of individuals within and among species from two Neotropical tree species complexes.

Symphonia globulifera and *Eschweilera* clade *Parvifolia* include distinct but connected species

We identified six distinct species in the two species complexes based on differences in morphologies, gene pools (chapter 3) and topographic niches (chapter 1), with overlapping but different functional traits (chapter 2) and growth trajectories (Fig. 18); which were maintained despite the existence of an interspecific gene flow with hybridization (chapter 3). Genetic analyses of population structure revealed the existence of three species growing in sympatry within the *Symphonia globulifera* species *sensu lato* (Fig. 8a), previously recognized as structured in two morphotypes, *S. globulifera sensu stricto* and *S. sp.1* (Sabatier et al. 1997, Molino and Sabatier 2001, Baraloto et al. 2007). Similarly, genetic analyses of population structure revealed the existence of at least three abundant species of *Eschweilera* clade *Parvifolia* (Fig. 9), corresponding to the botanical species *Eschweilera coriacea*, *E. sagotiana*, and *E. decolorans*. A lack of power in genomics data prevented us from detecting less abundant species of *Eschweilera* clade *Parvifolia*. Species from the two species complexes showed distinct morphotypes (Fig. 8b), despite blurred limits due to intermediate morphologies and ontogenetic effects on morphology. Species showed pervasive niche differentiation along topography and to a lesser extent with competition (Fig. 4 and Fig. 11), notably along a variation in the distribution of water and nutrients with topographic wetness index and relative elevation (Fig. 10). Niche differentiation between species is associated with a differentiation of functional traits (Fig. 17) and growth trajectories (Fig. 18). Nevertheless, the overlap between species niches, functional traits and growth trajectories emphasizes the importance of individual variation within closely-related species within the two species complexes. Finally, genetic analyses of population structure revealed interspecific gene flow with high levels of hybridization among *Symphonia* species (around 5%, Fig. 43). A lack of power in genomics data prevented us from exploring gene flow in *Eschweilera* clade *Parvifolia*, but previous studies already suggested interspecific hybridization (Heuertz et al. 2020, Caron et al. 2019).

The history of Symphonia species in the Neotropics might be more complex than previously thought

Symphonia globulifera colonized the Americas from Africa ca 18-16 Ma (Dick et al. 2004). Despite morphological variation and genetic differentiation observed across 13 populations from Costa Rica, Panama, Ecuador, and French Guiana, *S. globulifera* was never split into more than one Neotropical species (Dick and Heuertz 2008). Our results are mainly limited to the local scale (chapter 3), and further studies are needed on a broader regional scale, but they do support the definition of three distinct Neotropical taxonomic species of *Symphonia*. Site frequency spectra (SFS, Fig. 19) revealed a population in expansion with an excess of rare alleles in each population, as suggested in a previous study involving a population from the Guiana Shield and on from the Western Amazon (Dick and Heuertz 2008), although Barthe et al. (2017) concluded on population demographic stability in the two Symphonia morphotypes in French Guiana based on genetic data.

Moreover, genotyped outgroups of *Symphonia globulifera* were used to build a pantropical phylogeny of *Symphonia* populations using `treemix` (Pickrell and Pritchard 2012). The phylogeny revealed a high likelihood of at least one migration event between *S. sp.1* and the two *S. globulifera* populations in Paracou (20). The phylogeny was in agreement with a previous topology (S.C. González-Martínez pers. com.) with an ancestral population in Madagascar, and Sao Tome as the intermediate population between African and American populations. Interestingly, in our phylogeny, *S. sp1* was closer to the population of Brazil and the two *S. globulifera* populations were closer to the population of Costa Rica. Our results suggest a possible more complex biogeographic history of *Symphonia globulifera* in the Neotropics, but they call for further analyses before extrapolating.

New insights in intraspecific trait variability advocate for their role in local adaptation and divergence of closely-related species

We found a co-variation of leaf functional traits within species (Fig. 5), that corresponds to the co-variation, previously identified in the literature, among species and among communities (Bruelheide et al. 2018). Leaf functional strategy observed among species and communities is thus conserved within species. Moreover, the response of intraspecific leaf trait variability to topography was consistent across intra- and inter-specific levels (Fig. 6). Intraspecific trait variability thus widens species' niches, with individuals matching their idiosyncratic environments in parallel with the niche spectrum (Umaña and Swenson 2019). Intraspecific trait variability converges at species' margins where niches overlap, potentially implying local neutral processes (Hubbell 2001) with a decrease in fitness differences among species (Turcotte and Levine 2016), if investigated traits affect individual fitness. Interspecific gene flow with hybridization may maintain intraspecific trait variability through introgressions (Tigano and Friesen 2016), thus favouring the maintenance of the whole syngameon. Interspecific gene flow can lead both to intermediate and transgressive phenotypes (Rieseberg et al. 2003). Transgressive phenotypes can either hinder intraspecific variability at the shared margins of species or improve intraspecific variability at the extreme margins of species where species do not overlap. Interspecific gene flow can also result in reproductive interference, discussed later, with a risk for species to become an evolutionary melting pot.

Ontogeny and plasticity can strongly impede the use of leaf functional traits

I used genetic species identity, individual kinship, individual diameter at breast height, and plot identification to estimate genetic variance decomposition associated with leaf functional traits (Fig. 21). Most of the trait variation was residual, associated with tree size, or with weather (illustrated in part by plot effect, see chapter 2 material and methods). Species identity had a strong effect only on leaf area, used to determine species in the field. Genotype effect was always null or non significant. The measured leaf functional traits were thus mainly plastic and lacked a clear adaptive signature. Consequently, ontogeny, access to light, topography and weather (Fig. 23, Schmitt et al. in prep) were the main drivers of the functional trait variation measured on the sampled leaves. A strong intra-individual variation in functional traits has already been highlighted previously, for leaf thickness, transfusion tissue, and mass per area with leaf height within the tree (Oldham et al. 2010, Koch et al. 2004), and on leaf vein density, stomatal pore index and hydraulic conductance with shoot length (Leigh et al. 2011). Moreover, leaf functional traits had no or non-significant effects on individual growth potential (Fig. 22), as already evidenced in the literature (Umaña and Swenson 2019).

Functional traits have been defined as traits which impact fitness indirectly through their effect on performance (Violle et al. 2007). But my results do not suggest an adaptive signal of leaf functional traits, questioning their effect on fitness, nor an effect of leaf functional traits on individual growth, questioning their effect on individual performance. This observation underlines the need to control variation in leaf traits, including sampling date, leaf position in the crown, and ontogeny variation in order to collect trait values that would represent the typical leaf functional strategy of an individual. But is there a typical leaf functional strategy at the individual level? Leaf functional traits may be mainly plastic and wide proxies under environmental control, not representative of individual functions nor associated individual eco-evolutionary strategies, but may rather only represent the functioning of a few specific leaves within an individual.

Nevertheless, my sampling within species can guide further sampling among species. Resampling 5 mature individuals with a DBH > 30 cm, as advised in a standard protocol (Pérez-Harguindeguy et al. 2013), I was able to show that estimation of the species mean trait value can vary from 5 to 15% percent (Fig. 24); while the increase in the number of individuals sampled to 10 almost reduced the variation from the estimate of the mean value of the species' traits by two folds. In addition, improving ontogeny and habitat control in the sampling help better estimate species mean trait values. I also advocate for an accurate sampling of individual leaves within the tree in future trait-based study of intraspecific variation, controlling for instance for the architectural development stage and the position of the sampled branch and leaf, despite the tremendous work it represents.

Topography drives species niche divergence

Pervasive niche differentiation along topography (Fig. 4) was driven by genetic divergence and adaptation (Fig. 11) within and among closely-related species within species complexes. *Symphonia* species specifically displayed genomic signatures of adaptations to water gradients along topography (chapter 3). In detail, species are adapted to the distribution of water and nutrients captured through the topographic wetness index and the relative elevation. These results comfort the numerous examples of niche differentiation among closely-related species growing in sympatry, along fine-scale topography (Gunatilleke et al. 2006, Engelbrecht et al. 2007, Kraft et al. 2008, Allié et al. 2015), and reveal possible adaptive forces at play behind these examples. Adaptive radiations demonstrated along steep gradients in tree caldes (Paun et al. 2016, Fine et al. 2004) could thus occur also at a fine spatial scale with gradual habitat variation.

Forest gap dynamics maintains individual genetic diversity within species

Symphonia species can grow in a diversity of successional niches with genotypic adaptive growth strategies to the fine spatio-temporal dynamics of forest gaps (Fig. 14). Fast-growing genotypes grow in forest gaps, in a bright environment with low competition, and slow-growing genotypes grow in shaded closed canopies, with little access to light and high competition. The fine spatio-temporal dynamics of forest gaps thus contributes to promoting genetic diversity within tropical tree species (chapter 4).

Eschweilera clade *Parvifolia* species showed also genotypic adaptations to individual neighbourhood crowding, an indirect measure of competition for light during the last three decades, and to individual growth potential (Fig. 25). But, I did not find a significant association between genotypic values for neighbourhood crowding and those for individual growth potential, thus unlike in *Symphonia*, I did not find evidence for growth strategies matching successional niches. This lack of evidence could be due to methodological issues or to the ecology of *Eschweilera* species. After filtering the genomic data, less than two thirds of the sampled individuals were maintained in the data set and these showed a particular spatial structuring with neighbourhood crowding (absence of positive autocorrelation on a short scale), which the repeated random sampling of the same number of *Eschweilera* individuals in Paracou did not reproduce. In addition, the lack of individuals and the poor resolution of genomic data may have added noise and brought a lack of statistical power. But, the ecology of *Eschweilera* is particular compared to that of *Symphonia* with a very slow growth varying little from one individual to another on a short time scale (Fig. 18). Thus, *Eschweilera* could be following a different strategy in response to forest gap dynamics, through the specialization for a specific successional niche. Or individual age is less related to diameter in *Eschweilera* than *Symphonia* due to slow growth, and may result in a greater decoupling of the current successional niche from the successional niche at the time of recruitment of the individual.

Do adaptations of tree species and individuals to topography and forest gap dynamics promote coexistence within and among species within species complexes ?

Significance of species complexes and syngameons in Neotropical forests

We tried to identify species complexes in the Paracou community based on evidence for low (phylo)-genetic resolution or plastid DNA sharing among species (chapter 1). We identified five species complexes belonging to Lecythidaceae, Chrysobalanaceae, Myristicaceae, Clusiaceae, and Sapindaceae (Baraloto et al. 2012a, Heuertz et al. 2020, Gonzalez et al. 2009, Huang et al. 2015, Torroba-Balmori et al. 2017, Caron et al. 2019), which illustrates the phylogenetic diversity of species complexes in the Angiosperms. But, all tropical tree species, genera, and families do not have numerous genetic resources and detailed phylogenies available. Detailed genetic studies often detect cryptic species in widespread and abundant, supposedly well-known, tropical tree species, e.g. in *Symphonia* in chapter 3 or in three genera from the African flora (Ewédjè et al. 2020). Our knowledge on the frequency and abundance of tree species complexes in the Neotropics is thus limited. However, the identified species complexes include species that are locally abundant and hyperdominant at the regional level (Steege et al. 2013), illustrating their significant role in the Neotropics.

The eco-evolutionary roles of species complexes and syngameons in the tropics are subject to debate (Cannon and Lerdau 2019, Levi et al. 2019a, b), despite their recognized importance in South America (Pinheiro et al. 2018). Levi et al. (2019a) suggested that Janzen-Connell effects, in which natural enemies restrict the recruitment near conspecific adults, were sufficient to explain the maintenance of tropical biodiversity. Cannon and Lerdau (2019) responded by underlining the possible neglected role of syngameons to account for processes left out by Levi et al. (2019a), such as the effect of demographic processes on species survival or the phylogenetic distribution of diversity. Interestingly, Levi et al. (2019b) point to the lack of literature on syngameons in tropical forests while recognizing their potential importance in maintaining biodiversity: "virtually the entire literature on hybridization between tree species is based on temperate models, often at range boundaries or on steep environmental gradients". Indeed, knowledge on syngameons is mainly concentrated on temperate forests, and even historically on oaks (Cannon and Petit 2019). However, chapters 1 to 3, together with previous literature (Pinheiro et al. 2018), confirm the presence of syngameons in the Neotropics along subtle gradients, and a few studies in the Paleotropics show or suggest syngaemons in plants (Caujapé-Castells et al. 2017), fishes (Seehausen 2006) and even the genus *Homo* (Holliday 2006). Absence of proof is not proof of absence: our results contribute to answering the assertion of Levi et al. (2019b).

Tree species complexes distributed along large habitat gradients include species with pervasive niche differentiation

Fine-scale topographic variations drive differential adaptations of closely-related species within tree species complexes. Topography promotes the coexistence of closely-related species through niche differentiation within tree species complexes. Our genomic analyses were limited to *Symphonia* and *Eschweilera* clade *Parvifolia*, but we found similar niche partitioning in other species complexes from Paracou, which suggests similar processes in other clades. Indeed, chapters 1 and 3 suggest that the evolutionary response is environmentally controlled, and should therefore operate also outside of the studied species complexes. Pervasive effects of local topography observed pantropically (Kraft et al. 2008, Ferry et al. 2010a, Allié et al. 2015, Lan et al. 2016, Itoh et al. 2003), and related nutrients and water distribution (Baltzer et al. 2005, Baldeck et al. 2013a), could drive differential adaptations between observed closely-related species, promoting their local coexistence. Adaptive divergence could evolve both in species complexes or in more differentiated sister species. Sufficient adaptive divergence seems especially important for the coexistence of weakly differentiated species in species complexes (Tobias et al. 2014), since phylogenetic proximity and incomplete reproductive isolation increase the risk of hybridization and consequent breakdown of inter-specific adaptive divergences. On the other hand, more differentiated sister species could also coexist through emerging neutrality, e.g. by participating in a distinct group of species that are functionally similar and have similar fitness in a given environment (Scheffer and Van Nes 2006).

Forest gap dynamics, also identified as a driver of niche differentiation among closely-related tree species (Yamasaki et al. 2013), could drive differential adaptations among species in addition to its effect on within-species variation. Chapter 4 suggested a limited role of the successional niche on the divergence of *Symphonia* species (6%, Fig. 12). But we found the three *Symphonia* species to grow across a wide variety of successional niches (Fig. 15); whereas species exploiting a specific niche in the succession, such as pioneers species, could show more specific adaptations, and thus higher adaptive divergence from related species specialized on other successional niches. Similarly, abundant species with a wide topographic niche should have within-species genotypic adaptations. Indeed, chapter 3 showed important genotypic variation related to topography within species of *Eschweilera* clade *Parvifolia* (Fig. 11). Consequently, abiotic environments with topography and biotic environments with forest gap dynamics are both driving adaptations and genetic diversity within and among tree species.

Does the eco-evolutionary structure of Neotropical tree syngameons explain their local and regional success?

The local coexistence of closely-related species is governed by ecological and evolutionary processes, contingent on the history of speciation and niche differentiation (Weber and Strauss 2016). I focused on the competition for resources and the resulting niche differentiation in the previous paragraphs (Chesson 2000a, Turcotte and Levine 2016), but reproductive isolation is primordial to explain the coexistence of closely-related species in sympatry (Weber and Strauss 2016). Species must have evolved sufficient reproductive isolation to avoid the break-down of differences and their genetic homogenization through reproductive interference (Levin et al. 1996, Taylor et al. 2006, Abbott et al. 2013). Differences in phenology, e.g. flowering (Gentry 1974), or pollen dispersal, e.g. pollinators (Kay 2006), can increase reproductive isolation.

The way we perceive the role of genetic connectivity among species is changing. Despite the homogenizing power of gene flow, species-specific adaptations may be maintained or even maximised despite high levels of gene flow, especially if selective pressures are spatially and/or temporally variable (Tigano and Friesen 2016). Species adaptations and partial reproductive isolation can be maintained despite gene flow through: (i) linkage with an already diverged locus, (ii) increased resistance to gene flow following secondary contact, (iii) competition among genomic architectures, e.g. reducing recombination (Tigano and Friesen 2016). Consequently, adaptive introgression using gene flow among species diverging along the environment may imply species coevolution, or evolutionary mutualism, at the syngameon level (Cannon and Petit 2019). Gene flow among species can insure reproductive assurance by hybridization, lowering the risk of local extinction, and allow species to share innovation that benefits the whole syngameon (Cannon and Lerdau 2015). This subtle equilibrium between species adaptations and gene flow may be a powerful eco-evolutionary strategy leading to local and regional success of tropical tree syngameons (*Symphonia* and *Eschweilera* include Amazonian hyperdominant tree species (Steege et al. 2013) and some of the most abundant species in Paracou).

Do tree syngameons shape the exceptional diversity of Neotropical forests?

We found topography and forest gap dynamics to drive diversity within and among tree species within species complexes promoting their coexistence. I hypothesized the syngameon to be a subtle and fragile but evolutionary successful stage, which raises the question of the temporal dynamics of syngameons. Syngameons may not be restricted to transitions toward complete speciation of the species composing it, but syngameons may represent a temporally stable stage (Cannon and Petit 2019), with species interbreeding stably over time or with syngameons that are stable over time but changing in species composition, with some species reaching complete speciation while others emerge. Reproductive isolation, although partial, can evolve very slowly to complete isolation with little selection against hybridization, or hybridization could be favored during critical environmental disturbances. If it represents a temporally stable stage, the *Symphonia* syngameon shows considerable gene flow (chapter 3) despite a stable environment, which argues for the hypothesis of a slow evolution towards complete isolation. Anyway, as a temporally stable stage or as a transitional stage toward complete speciation, syngameons seem to represent a successful evolutionary strategy promoting the coexistence of sympatric closely-related species. Consequently, syngameons, and more generally species complexes, could play a key role in creating and maintaining the tremendous diversity of tropical forests by promoting the coexistence of phylogenetically and functionally similar species (Cannon and Lerdau 2019). Syngameons could participate generating biodiversity, i.e., in the ‘cradle’ (Eiserhardt et al. 2017) of the tropical forest, with their speciation through complete reproductive isolation , or they could preserve biodiversity as a tropical forest ‘museum’ (Eiserhardt et al. 2017) with a temporal stability that reduces the risk of local extinction.

Beyond species complexes: do adaptations to topography and forest gap dynamics promote coexistence within and among tree species from mature forests ?

Importance of intraspecific trait variation in the forest community

Chapter 2 revealed a consistent response of leaf functional traits to topography within and between tree species, suggesting an environmental control of leaf functional strategies. Topography similarly affects functional traits in species complexes and in fully differentiated species, so the functional response to topography within and between species should apply also outside species complexes. The only limit to a differential functional response would be a specific role of shared genetic variation through gene flow or the recent common ancestry, to conserve a similar functional strategy in species complexes but not in fully differentiated species. Indeed, once isolated, species may lose genetic diversity and individual plasticity. But the absence of effect of genotypes on functional traits (Fig. 21) strongly questions the role of shared genetic variation in the consistent functional response, unless observed trait plasticity is genetically promoted (Ghalambor et al. 2007) through recent divergence or inter-specific gene flow. Therefore, I hypothesize that environmental gradients, such as topography and associated nutrient and water distributions (Chapter 3), have a consistent effect on the variability of functional traits within and between species, widening their niches and leading to an emerging neutrality in their overlap (Chapter 2) for many species in the forest community.

Fine-scale topography is a powerful driver of tree species diversity that promotes species coexistence in tropical forests

Chapters 1 to 3 revealed the effect of gradual habitat variation through fine-scale topography on ecological divergence of species with differentiation of niches and phenotypes. But evolutionary history behind adaptive radiations falls within a continuum from sympatric ecological speciation to secondary contacts of species ecologically specialised in allopatry or parapatry (Rundell and Price 2009). Pairwise site frequency spectrum of *Symphonia* species (Fig. 19) did not help decipher between sympatric speciation or character displacement after a secondary contact. Demographic history modelling is still needed to establish the history of the evolution of *Symphonia* (Hoban et al. 2012), but a broader regional sampling may be necessary for a better understanding. In both cases, it can be assumed that the extreme competition between species in hyperdiverse communities pushes species towards fine-scale habitat specialization along stable spatio-temporal environmental gradients. Topography has been highlighted to drive differences among species at early plant life stages, which contribute to the maintenance of tropical forest diversity (Metz 2012). On the other hand, spatio-temporally unstable forest gap dynamics contribute only a little to differences between species (Chapter 4). Hence, fine-scale topography can locally represent a “species pump” in tropical forests, i.e. a cradle for species, such as the Andes on a regional scale (Mutke et al. 2014).

The studied species showed large topographic niches with areas of overlap in the Paracou community (chapter 2), which implies that neutral processes, by decreasing differences in fitness, also favour the coexistence of species via a jack-of-all-trades strategy (Turcotte and Levine 2016). Topography could thus also give rise to “superspecies”, i.e. allopatric taxa that are known or thought to have evolved to the species level (Amadon 1966).

Forest gap dynamics are a powerful driver of individual diversity in tropical forests that promotes species coexistence

Chapter 4 showed for the first time that forest gap dynamics drives individual diversity and growth adaptations within *Symphonia* species. Genetic adequacy with forest gap dynamics determines which individuals are successful in reaching the canopy through divergent growth strategies, with *hares* in forest gaps and *turtles* in more shaded closed-canopy patches. Because of the similar broad successional niches observed in many other species of the Paracou community (Fig. 15), we hypothesized the process underlying genotypic adaptations not to be specific to *Symphonia* or species complexes, but to be conserved in many tropical forest tree species, probably thanks to physiological or adaptive constraints (Ellner and Hairston Jnr 1994). Nevertheless, phenotypic plasticity remains a major process that may explain large successional niches of species (Gao et al. 2018, Goulet and Bellefleur 1986, Chevin et al. 2010) that we cannot rule out until further research is carried out. In both cases, large successional niches can promote species coexistence through emergent neutrality (Scheffer and Van Nes 2006), although forest gap dynamics also select for species with narrow successional niches such as pioneer species (Dalling and Hubbell 2002). Interestingly, Bazzaz and Carlson (1982) found late-successional species to be less plastic to light access than pioneer species, and Zangerl and Bazzaz (1983) revealed more adaptation to successional niches among genotypes in late-successional than in pioneer species. Indeed, late-successional species showed the widest breadth of traits and grew in more heterogeneous environments in space and time than pioneers in forests in Venezuela (Kammesheidt 2000). Together with the results of chapter 4, these studies argue in favour of forest gap dynamics driving genotypic adaptations with divergent growth strategies in species previously called “late-successional”, which in fact encounter a diversity of light environments and competition as seedlings.

In order to study treefall conditions, I examined the local basal area distribution prior to basal area loss, i.e. the successional stage of the forest patch before a treefall occurs. Unfortunately, studying treefalls ideally requires both large spatial and temporal coverage due to the episodic nature of treefalls (Chambers et al. 2013). Despite the huge amount of work behind the monitoring of dynamics of the forest gaps at Paracou (Hérault and Piponiot 2018), I was not able to obtain a clear pattern. Although most treefalls seem to occur when the local basal area is high, e.g. at the end of forest succession, also called climax, my results could not rule out the existence of treefalls occurring at a low local basal area during the early stages of succession (Fig. 26). These early-successional treefalls could be due to stochasticity, but a bold hypothesis would be the existence of niche-hiking pioneer species that create these early-successional treefalls. Niche-hiking results from genotypes favouring local niche construction (Schwilk and Kerr 2002), such as flammability favouring open spaces after a fire for the offspring of fire-adapted trees. In the case of treefall, one could imagine the existence of an adaptation to falls for genotypes or species that grow in forest gaps. Indeed, one could imagine fast-growing genotypes or species in forest gaps are mechanically more prone to fall once in the canopy. But, niche-hiking in forest gaps remains a bold hypothesis that needs to be tested further.

Joint effect of topography and forest gap dynamics on tropical diversity

We identified two orthogonal factors promoting diversity and coexistence among closely-related species with different characteristics and affecting different diversity levels. Topography, spatio-temporally stable, mainly affects trees among species and promotes coexistence with niche partitioning (Chapter 3). Forest gap dynamics, varying in space and time, mainly affect trees within species and promote species coexistence with emergent neutrality (Chapter 4). Anticipating their joint effect on species coexistence and tropical diversity is therefore not straightforward. Simulation approaches, discussed in the next section, can help test hypotheses on spatial and temporal scales that experimental studies on tropical forests cannot achieve.

From a static temporal point of view, the topography and dynamics of forest gaps both favour the coexistence of species with divergent processes on orthogonal niches. Consequently, genotypic adaptations within species decrease the risk of a stochastic local extinction while species adaptations stabilize local coexistence. But the limits arise with temporal variation, which questions the origin of the system, the stability of genotypic adaptations to the dynamics of forest gaps, the stability of species via divergence along topography despite gene flow, and the strength of niche differences and emerging neutrality to avoid competitive exclusion. Indeed, we showed overlapping niches along the topography despite niche differentiation and a low level of differentiation among species along successional niches despite genotypic adaptations (Chapters 3 and 4). Consequently, we do not know to what extent the neutrality of the distribution margin of the species, for example with the convergence of functional traits (Chapters 2), and along the successional niches, with the genotypic adaptations of the species, will make it possible to overcome competitive exclusion (Turcotte and Levine 2016). Similarly, the adaptive genetic component of topographic position in which individuals grow is not negligible (chapter 3) and may suggest evolution towards and increased differentiation of species niches (Hoffmann and Merilä 1999), but the interference of reproduction with gene flow could disrupt the divergence of species with topographic niches and hinder the coexistence of sympatric species (Hochkirch et al. 2007). This highlights the need to further document the processes responsible for partial reproductive isolation in our models. In addition, we do not know the stability of genotypic adaptations to the dynamics of forest gaps, and one could imagine the evolution of species, or even a speciation with barriers to reproduction among genotypes, towards a specialized niche of succession (Lenormand 2012). Finally, the ideal would be to be able to explain the conditions of emergence of this subtle eco-evolutionary dynamics. We need to explain how a genotype can rise to increased frequency in the population in response to the spatio-temporal dynamics of forest gap dynamics, such as, for example, the characterisation of the conditions for the stable existence of a flammability genotype in a forest undergoing fire dynamics (Schwilk and Kerr 2002). And we need to explain how species diverged along the topography with partial reproductive isolation despite gene flow, either with reinforcement after secondary contact (Haavie et al. 2004) or with sympatric speciation (Savolainen et al. 2006). The preceding points underline the importance of the temporal dynamics of our system, but we have limited our analyses and discussions to the sympatric and microgeographic scale, and we may need to explore larger spatial domains (Estes et al. 2018), such as the regional scale, especially considering the large spatial dynamics of forest gaps (Chambers et al. 2013).

Limits and future directions to address eco-evolutionary dynamics of tropical tree coexistence

Stochasticity and neutrality are of paramount importance in merging ecology and evolution in an interdisciplinary approach

I argue that stochasticity and neutrality are neglected, especially by non-specialists and scientists from other disciplines, in understanding the coexistence of species in ecology and evolution, especially with regard to the neutral theory of molecular evolution (Kimura 1968) and the unified neutral theory of biodiversity (Hubbell 2001). From an evolutionary point of view, considering adaptations without drift and gene flow prevents the full exploration of species coexistence, forcing a deterministic view of evolution towards an easy establishment of species coexistence. Andrews et al. (2012) revealed the many misconceptions about genetic drift among biology undergraduates. Similarly, from an ecological point of view, the partitioning of niches without considering the emergence of neutral processes prevents the complete exploration of the coexistence of species, forcing a deterministic vision of ecology towards the predominance of species niches. To my knowledge, no study has addressed the misconceptions about the unified neutral theory of biodiversity among undergraduate students, but I have little doubts on their existence (B. Hérault pers. com.). Finally, at the crossroads of ecology and evolution, considering niche differentiation and emerging neutrality without reproductive isolation also prevents the full exploration of species coexistence (Weber and Strauss 2016). I do not claim that specialists in one field neglect neutral processes in their field, but that specialists in one discipline often neglect neutral processes in the other field, despite their common origin, preventing the good development of interdisciplinarity in ecology and evolution. Overall, I think the lack of appreciation or understanding of stochastic and neutral processes in ecology and/or evolution is an obstacle to the development of a good interdisciplinary approach, but may result from a deterministic teaching of both disciplines when simplifying the discourse. I thus plead for a good appreciation of the complexity of ecology and evolution in order to avoid neglecting the cryptic eco-evolutionary dynamics (Kinnison et al. 2015).

Limits of local-scale low-cost sequence capture to study the evolution of non-model species complexes in the wild

My PhD thesis was the opportunity to contribute to the development of low-cost sequence capture for the study of eco-evolutionary processes with the financial support of the innovative LOCOCAP project granted by INRA in 2019. Our goal was to develop affordable tools for genomic studies, i.e., produce a few mega base pairs of sequence data, in non-model species, such as tropical trees, a necessary step for the successful completion of my PhD project. My results have revealed new affordable avenues opened up by these techniques, including population genomics, environmental association analyses and genome-wide association studies, while my experience has pointed to some methodological problems that may be encountered and that will need to be taken into account in future gene capture experiments. The first limit is the existing preliminary genetic resources needed to design the target sequences. We benefited from diverse genetic resources for *Symphonia* [Olsson et al. (2017); Scotti et al., in prep; Tysklind et al., in prep; Torroba-Balmori et al., unpublished], including both genomes and transcriptomes, compared to the reduced availability of genomic resources in the more complex *Eschweilera* model [Vargas et al. (2019); M. Heuertz pers. com.]. The cross-validation of genetic resources for *Symphonia* could explain in part the better success of the gene capture experiment compared to the one of *Eschweilera* with the resulting high quality of targeted sequences (chapter 3). Indeed, the probes design of *Symphonia* was more complex and based on better-quality reference data than the one of *Eschweilera*. But apart from the importance of the preliminary bioinformatics steps, I believe that the wet laboratory steps were the most involved in the difference in success between the gene capture experiments of *Symphonia* and *Eschweilera*. The issue of unequal read abundance among sequenced libraries was a big impediment to *Eschweilera* analyses, resulting in a lot of missing data despite low levels of reads sequenced off-targets compared to *Symphonia*. I blame a bad balance of libraries in pools during the wet lab for this problem of the representativeness of the libraries. Low-cost capture was enabled by a reduction in reaction volumes coupled with increased library indexing, which may have amplified pipetting errors. Finally, post-capture bioinformatics revealed two other issues explaining discrepancies between the gene capture experiments of *Symphonia* and *Eschweilera*: sequencing quality and paralogs. *Eschweilera* clade *Parvifolia* species are diploid but some include a strong signature of a past genome duplication (Heuertz et al. 2020). The past genome duplication may explain the inconsistencies of the SNP call in *Eschweilera* when using the *Symphonia* pipeline. We therefore had to use a strict SNP call for the *Eschweilera* data in order to guarantee the reliability of the SNPs, while favouring missing data. Local sampling also limited the inference of population evolutionary history due to short scale sampling of widespread species without phylogeny and range-wide niche characterization. Local sampling has been associated with the sampling of a cryptic species in *Symphonia* and more generally with the lack of good sampling of "genetically pure" populations compared to "hybrid" populations, which has prevented a good exploration of adaptive introgression with the various current methodologies (Gompert and Buerkle 2009, Burgarella et al. 2019, Pfeifer et al. 2019, Racimo et al. 2018). Despite the enormous sampling effort of hundreds of mature trees in tropical forests, the limited number of individuals per species and the associated population structure decreased the statistical power of our analyses and limited the detection of markers in genome-wide association studies (GWAS; Korte and Farlow 2013) while preventing the convergence of Markov chains in the Bayesian inference of polygenic genomic signals (Zhou et al. 2013) (although X. Zhou pers. com. considered our results as still valid). In conclusion, future gene capture experiments should consider: (i) the spatial scale, population structure and number of individuals, (ii) the existing preliminary genetic resources and the particularities of the evolution of the model, such as past duplication of the genome, (iii) the wet lab protocol with emphasis on library balance in capture pools, and (iv) the pipeline used for SNP call in post-sequencing analysis.

Promising directions in evolutionary studies of forest tree coexistence

Chapters 3 and 4 have pointed to several evolutionary areas and concepts, which I consider to be under-explored and promising in future studies of the coexistence of forest trees. Microgeographic adaptations point to a small and local spatial scale for evolution (Richardson et al. 2014) where sympatric coexistence of forest trees occurs. The hypothesis that evolution and ecology play at very different spatial scales may have been an obstacle to understanding the role of microgeographic adaptations (Pelletier et al. 2009), but previous studies (Brousseau et al. 2015) and chapters 3 and 4 have revealed the importance of microgeographic adaptation in the coexistence of trees within and between species in tropical forests, highlighting its importance in future studies. Similarly, overlapping generations are not exploited in evolutionary studies of tropical trees with widely overlapping generations (chapter 4), despite their importance in evolutionary theories (Ellner and Hairston Jnr 1994). Chapter 4 provides, to our knowledge, the first evidence for the role of forest gap dynamics on adaptation within tropical tree species. But our results are limited to three species in one species complex, and they open a quantity of new research avenues, such as the bold hypothesis of niche-hiking species in forest gaps (Schwilk and Kerr 2002). Studies on the genomics of forest gap dynamics need the previously highlighted concepts and may redefine the importance of forest gap dynamics in eco-evolutionary dynamics of tropical forest ecosystems, as forest gap dynamics is already recognized in ecology as a driving force of sylvogenesis. Microgeographic adaptations and overlapping generations played both a role in adaptation to forest gap dynamics detected in *Symphonia*. They highlight the fine spatio-temporal dynamics of forest gap dynamics. I thus more generally think that a promising direction in evolutionary studies of forest tree coexistence is a better understanding of the spatial and temporal domains of modern ecology and evolution (Estes et al. 2018). My PhD focused on a smaller spatial scale than usual with perhaps a larger temporal scale than usual, at least in ecology. This focus on specific spatial and temporal study scales has led to the uncovering of under-studied processes. However, these processes will still need to be included into regional spatial and longer temporal study scales, so as to further establish and characterize their role in the coexistence of species within the Amazon basin.

Simulation approaches to address the joint effects of topography and forest gap dynamics on the conditions for tree species coexistence

Eco-evolutionary observational studies on the coexistence of species in tropical forests are limited in forest stand inventories due to a lack of repeatability (Poorter et al. 2016 , Schnitzer and Carson 2016) and a lack of time to evaluate long-term effects (Hérault and Piponiot 2018). Forest simulators have proved useful to investigate eco-evolutionary processes through virtual experiments (Schmitt et al. 2019). I conducted a preliminary study on the development of an individual-based and spatially-explicit eco-evolutionary simulator to address the joint effects of topography and forest gap dynamics on the conditions for species coexistence and emergence. I specifically wanted to address the following questions:

1. What are the conditions for the stable coexistence of genotypes and species with topography and/or forest gap dynamics in the forest community?
2. What are the conditions for the successful establishment of genotypic adaptations to forest gap dynamics in the forest community?
3. What are the conditions for the reinforcement of species barriers or speciation of species connected through gene flow along topography?

I hope to develop these questions in a future contribution, but I could only explore the definition of a simplified eco-evolutionary simulator based on Schwilk and Kerr (2002) and Vincenzi and Piotti (2014), including individuals and their explicit spatial positions, which is still far from having the capacity to explore these specific questions. I built a one-dimensional simulator, for example an environmental gradient, and a two-dimensional simulator, for example a spatially explicit environmental matrix, with exactly the same processes. The environmental gradient (one-dimension) is defined by a length N and the environmental matrix (two-dimensions) is defined by a grid of size $N \times N$, with an individual growing on each cell. The environmental gradient (one-dimension) varies from the environmental minimum value $-E$ at an extreme to the maximum value E at the other extreme, and the environmental matrix (two-dimensions) varies in a grid defined by the product of the vectors $(-E, E)$. Each phenotype z_i of individual i is defined as the sum of its genotypic breeding value a_i and an environmental effect e_i, both drawn from a genetic and an environmental normal distribution:

$$
\begin{aligned}
z_i &= a_i + e_i \\
a_i &\sim N(\mu_G, \sigma_G^2) \\
e_i &\sim N(\mu_e, \sigma_E^2)
\end{aligned}
\tag{6}
$$

At the initialization step, i.e. the first generation, N or $N \times N$ individuals are randomly drawn from the previous distribution and recruited over the environmental space. At each time step, i.e., at each generation that does not overlap with others, N_s seedlings are produced in each cell. Seedlings inherit from two parents in the dispersal neighbourhood d. Genotypic breeding values a_s of seedlings are drawn from normal distributions centered on parental means and of half the variance of genetic variation (Vincenzi and Piotti 2014), and are used to compute seedling phenotypic value z_s:

$$
\begin{aligned}
z_s &= a_s + e_s \\
a_s &\sim N(mean(a_{P1}, a_{P2}), \frac{\sigma_G^2}{2}) \\
e_s &\sim N(\mu_e, \sigma_E^2)
\end{aligned}
\tag{7}
$$

Among the N_s seedlings one is recruited either with a determinist viability, e.g. keeping the seedling with the phenotypic value closer to the seedling environmental value, or with a probabilistic viability, e.g. with a random draw with probability equal to the inverse of the distance between seedling phenotypic value and environmental value. I implemented both simulators in a web interface using `C++` and `R` with the `Rcpp` (Eddelbuettel and François 2011) and `shiny` (Chang et al. 2019) packages. The code is available in Appendix 1 (Simulator S1 and Simulator S2) and the simulators are available online (one-dimension simulator: https://sylvainschmitt.shinyapps.io/simulator1D/, two-dimensions simulator: https://sylvainschmitt.shinyapps.io/simulator2D/). As a result of the ongoing work, both simulators have significant limitations or limiting assumptions, or even serious shortcomings, which are discussed below. But using many generations ($N_g = 58$) and default parameters in the two-dimensional simulator, I was able to produce two divergent "pure" populations with a hybrid population at their interface (Fig. 16).

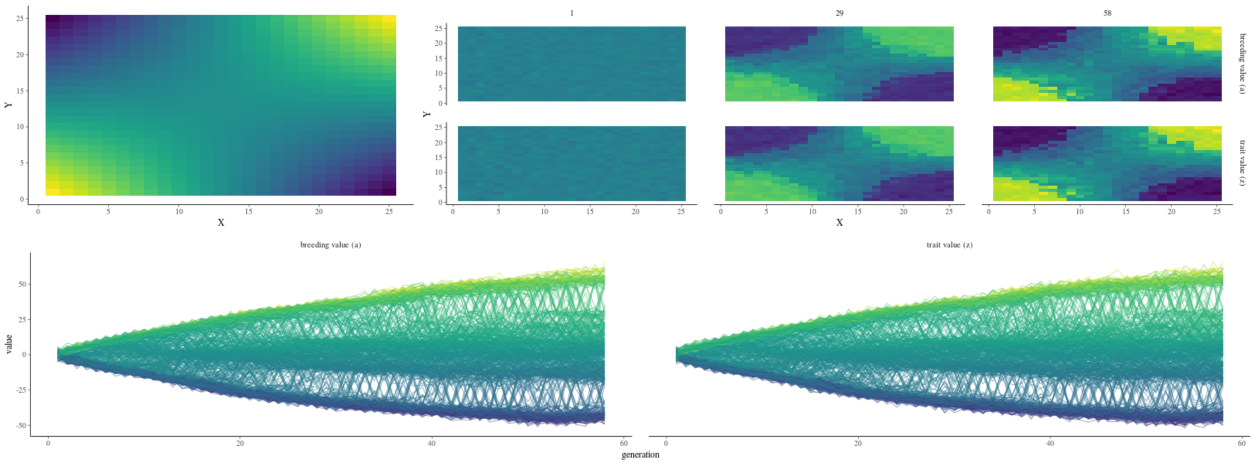

Figure 16: Results of the two-dimensional simulator with default settings over 58 generations. The upper left subplot shows the environmental matrix where the individuals develop, from -E in blue to E in yellow. The upper right subplot shows the breeding values a (upper row) and phenotypic values z (lower row) in the matrix for 3 different generations (the 1st in the left column, the 29th in the central column and the 58th in the right column), from -E in blue to E in yellow. The bottom subplot shows the breeding values a (left column) and phenotypic values z (right column) for each cell in the matrix (one line) with its associated environmental value, from -E in blue to E in yellow, over the 58 generations.

A serious shortcoming regarding the simulators is the dispersion. The shape of the dispersal kernel in one dimension is a line of length $2d+1$, which is correct, but it's a square of size $(2d+1) \times (2d+1)$ and not a discrete disk in two dimensions, which seems a strong bias. Moreover the seedling inherits from two parents in the dispersal neighbourhood d, whereas the seedling should inherit from a mother tree at a distance d_m from the seedling and from a father tree at a distance d_f from the mother tree. Limiting assumptions include (i) the use of normal distributions that I wish to replace by lognormal distributions to better fit the models developed in chapters 3 and 4, and (ii) the use of non-overlapping generations that I wish to replace by a timeline defined by treefall events and overlapping generations defined by an explicit definition of individual mortality through background and treefall mortality. Future directions include the development of proposed solutions for shortcomings and limiting assumptions and the definition of environmental gradients. I am planning to develop a topography generator with spatial autocorrelation matching the one observed in Paracou, or that can vary with a few parameters. In case of failure in the development of a topography generator, I am planning to discretize and simplify observed topographic gradients in Paracou plots. Last but not least, I plan to model the dynamics of forest gaps as an extrinsic factor, with each cell growing in neighbourhood crowding at each time step, and with spatio-temporal stochastic events leading to treefall, i.e. the death of individuals in the area of the treefall and the definition of the local neighbourhood crowding at low values. In doing so, I wish to address the joint effect of the topography and dynamics of forest gaps on the conditions of coexistence and emergence of species, and to explore their joint effect on the hyperdiversity of tropical forests.

The primordial role of individuals within species in tropical forest diversity

Despite the dominant role of species in community ecology, the results of my PhD thesis have never ceased to underline the primordial role of individuals within species in the diversity of tropical forests. Chapter 2 revealed the importance of individuals in response to variations in topography, with an essentially plastic response of functional traits and weak genotypic adaptations introduced in chapter 3. Chapter 4 revealed the importance of individuals in response to forest gap dynamics, with strong genotypic adaptations, including an adaptive performance response with individual growth. In addition, the partitioning of the variance of individual growth potential, without genotypic effect, between inter- and intra-species variation revealed only a weak role of species in individual growth trajectories in the species complexes *Symphonia* and *Eschweilera* clade *Parvifolia* (7 to 8%, Fig. 27). Indeed, Clark et al. (2011) and Read et al. (2016) have shown that considering species without the individuals that make them up can blur community processes, highlighting the need to consider intraspecies variation in order to develop a more robust theory of community ecology. A first step suggested by Read et al. (2016) and applied in chapters 3 and 4, is the use of hierarchical models associated with variance partitioning (Nakagawa and Schielzeth 2013).

Nevertheless, the importance of individuals within species in ecological communities is not a new idea. Forty years ago, Aarssen (1983) already stressed the need to take into account individual variability within species to define both the fundamental niche and the competitive ability. Our results on topography (chapters 1 to 3) relate indirectly to the fundamental niche, besides being measured in the realized niche; whereas our results on forest gap dynamics (chapters 1 and 4) relate to competitive ability. Interestingly, Aarssen (1983) suggested that competition was an important force in natural selection, echoing the results found in chapter 4. Callaway et al. (2012) suggested that phenotypic plasticity promotes the coexistence of species with the adjustment of species to their communities. We found that plasticity is an individual response to neighbourhood crowding, but that adaptation processes also play an important role in the adaptation of species to their neighbours. Clark et al. (2010) suggested intraspecific variation to be structured and not random, as revealed by leaf functional traits variation with ontogeny, light access, and topography (chapter 2), and adaptive growth response to forest gap dynamics (chapter 4). In addition, Clark (2010) suggested that the individual variation within species allows species to differ in their responses to the environment, even though species may not differ on average. Conversely, Chapter 2 showed that the response of individuals within species to topography among species for most functional traits, despite some divergent responses such as for leaf chlorophyll content. We argued that responses of individuals to topography that are consistent across species could favor neutral processes among species along the topography when species overlap (Le Bagousse-Pinguet et al. 2014), despite mean trait differences among species (chapter 2). The hypothesis following our observations differs thus from Clark (2010)'s hypothesis, but I think they are complementary and not contradictory, such as niche and neutral theories (Gravel et al. 2006, Hérault 2007). Some traits may favour neutrality among species with different mean values but consistent response of individual variation within species to environmental gradients; while other traits may favour divergence among species with similar mean values but different responses of individual variation within species to environmental gradients. Intraspecific variability may help individuals within species to be "sufficiently different or sufficiently similar" among species (Scheffer and Van Nes 2006). Anyway, chapters 2 and 4 both support the idea that intraspecific trait variability promotes species coexistence by allowing species to pass through both the abiotic filter, with topography (chapter 2), and the biotic filter, with forest gap dynamics (chapter 4).

Consequently, the results of my PhD thesis, combined with previous literature, strongly argue in favour of a better consideration of individual variation within species in order to understand coexistence of species and, ultimately, community assembly. Just as Salguero-Gómez et al. (2018) calls for the merging of trait-based and demographics approaches among species, I believe that the merging of population genomics and demography among individuals within species holds promise for a better understanding of species coexistence. Clark (2010) already emphasized the similarity between population genomics and demography:

> "Just as variation among individuals is required to maintain species by natural selection, providing a means for adaptive evolution in response to many factors in many dimensions, variation at the individual scale is also needed to explain why large numbers of intensely competing species coexist."

I do not question the usefulness of the species concept in ecology, as long as we recognize its limitations, because the species concept has helped and is helping to build community ecology (Mcgill et al. 2006), and including individual variation within species is not simple (Albert et al. 2011) and can be an enormous amount of work. But I sincerely think that we should develop a theory of community ecology starting with individuals, because interactions with environments happen after all at the individual level (Violle et al. 2012).

APPENDIX 1: DISCUSSION SUPPLEMENTARY MATERIALS

The following Supporting Information is available for the discussion:

Fig. 17. Principal component analyses of leaf functional traits for *Symphonia* and *Eschweilera* clade *Parvifolia* species.

Fig. 18. Growth trajectories of *Symphonia* and *Eschweilera* clade *Parvifolia* species.

Fig. 19. Site frequency spectra for *Symphonia* species.

Fig. 20. Phylogeny for *Symphonia* species.

Fig. 21. Variance partitioning of leaf functional traits in *Symphonia* species.

Fig. 22. Functioncal traits and individual growth potential for *Symphonia* species.

Fig. 23. Leaf thickness variation with precipitation for *Symphonia* species.

Fig. 24. Effect of sampling on the estimate of the species mean trait value within *Symphonia* species.

Fig. 25. Variance partitioning for neighbourhood crowding index and individual growth potential in *Eschweilera* clade *Parvifolia* species.

Fig. 26. Local basal area distribution prior to basal area loss in Paracou.

Simulator S1. `C++` code for the one-dimension eco-evolutionary simulator.

Simulator S2. `R` code for the two-dimensions eco-evolutionary simulator.

Fig. 27. Species variation in growth trajectories of *Symphonia* and *Eschweilera* clade *Parvifolia* species.

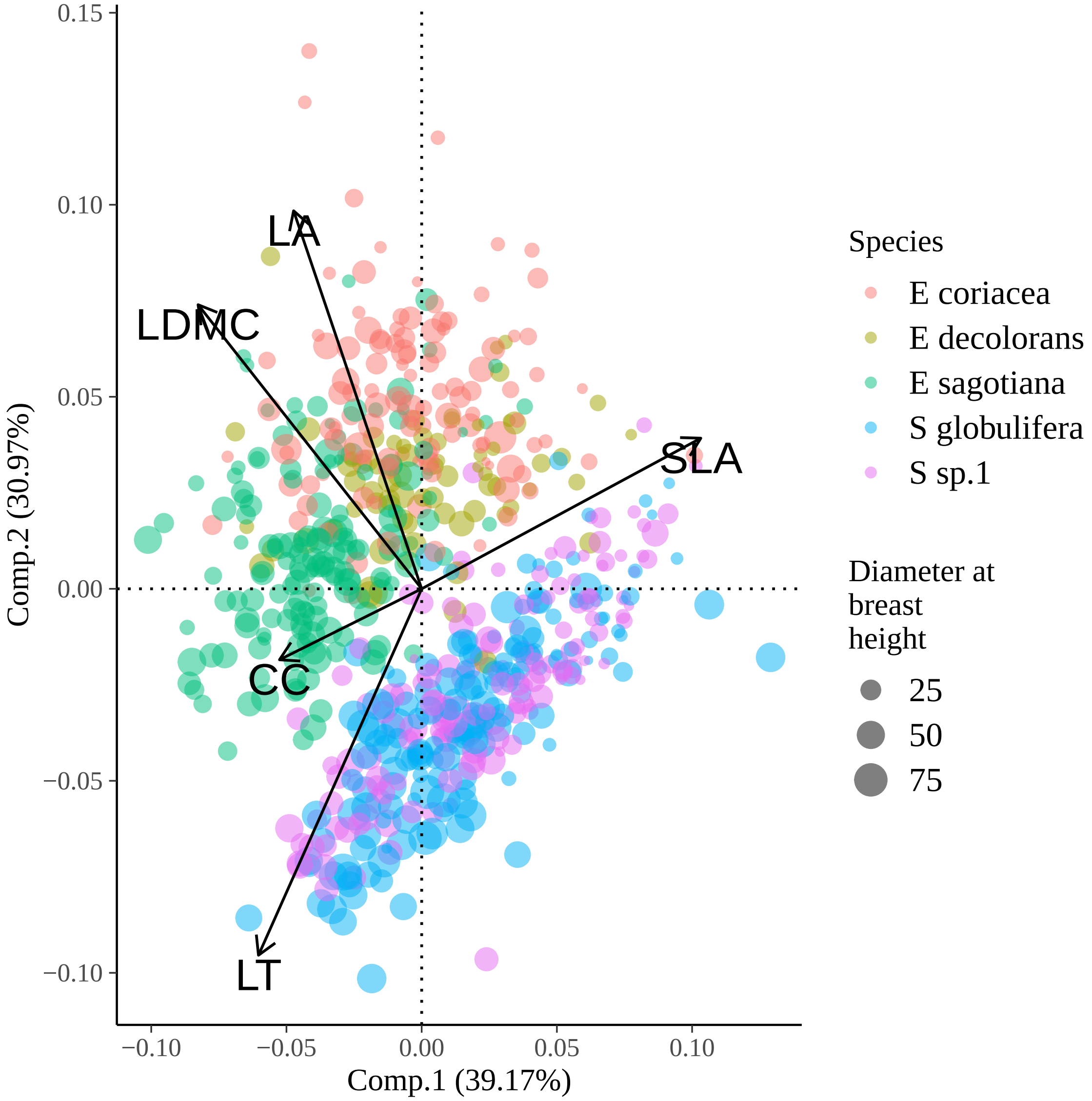

Figure 17: Principal component analyses of leaf functional traits for *Symphonia* and *Eschweilera* clade *Parvifolia* species. Dot colors indicate the species, whereas dot sizes indicate diameter at breast height.

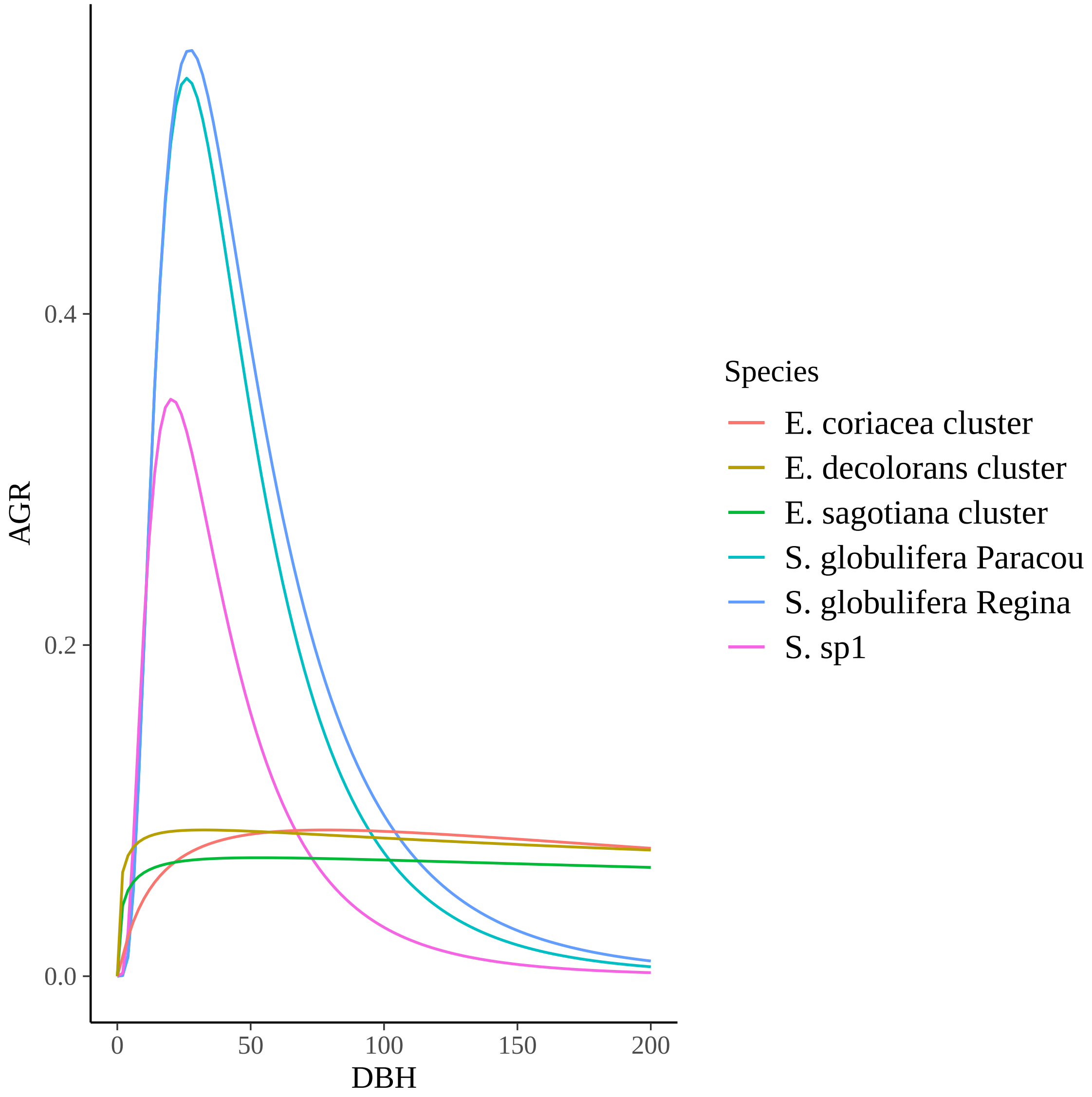

Figure 18: Growth trajectories of *Symphonia* and *Eschweilera* clade *Parvifolia* species.

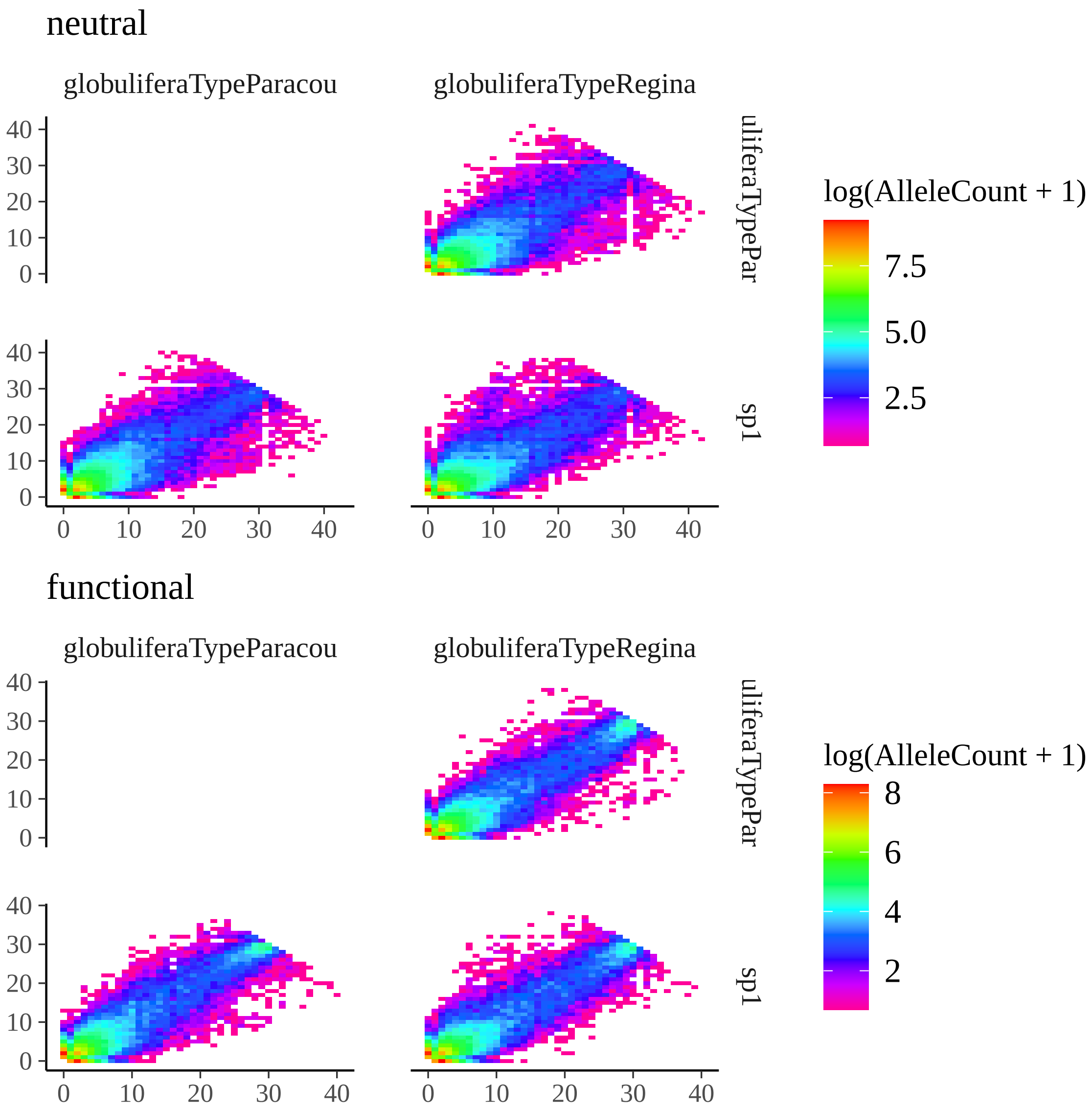

Figure 19: Pairwise site frequency spectra for *Symphonia* species. We used the genome-transcriptome alignments built for the design of probes sets to classify called SNPs into (i) anonymous SNPs, i.e. neutral (on scaffolds matching no transcripts), and (iii) genic SNPs, i.e. functional (within an exon).

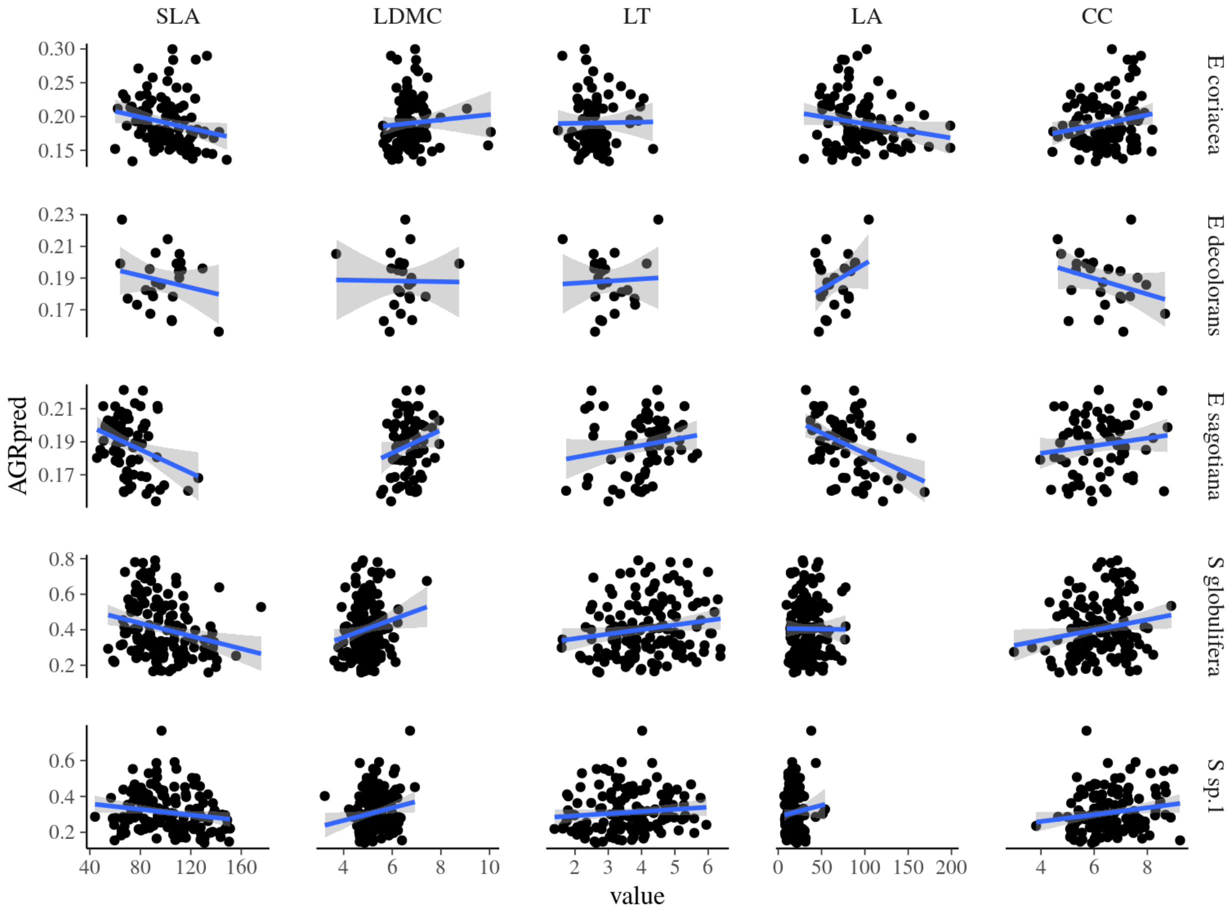

Figure 22: Functioncal traits and individual growth potential for *Symphonia globulifera* species. Individual growth predicted in 2015 against sampled trait value in 2015.

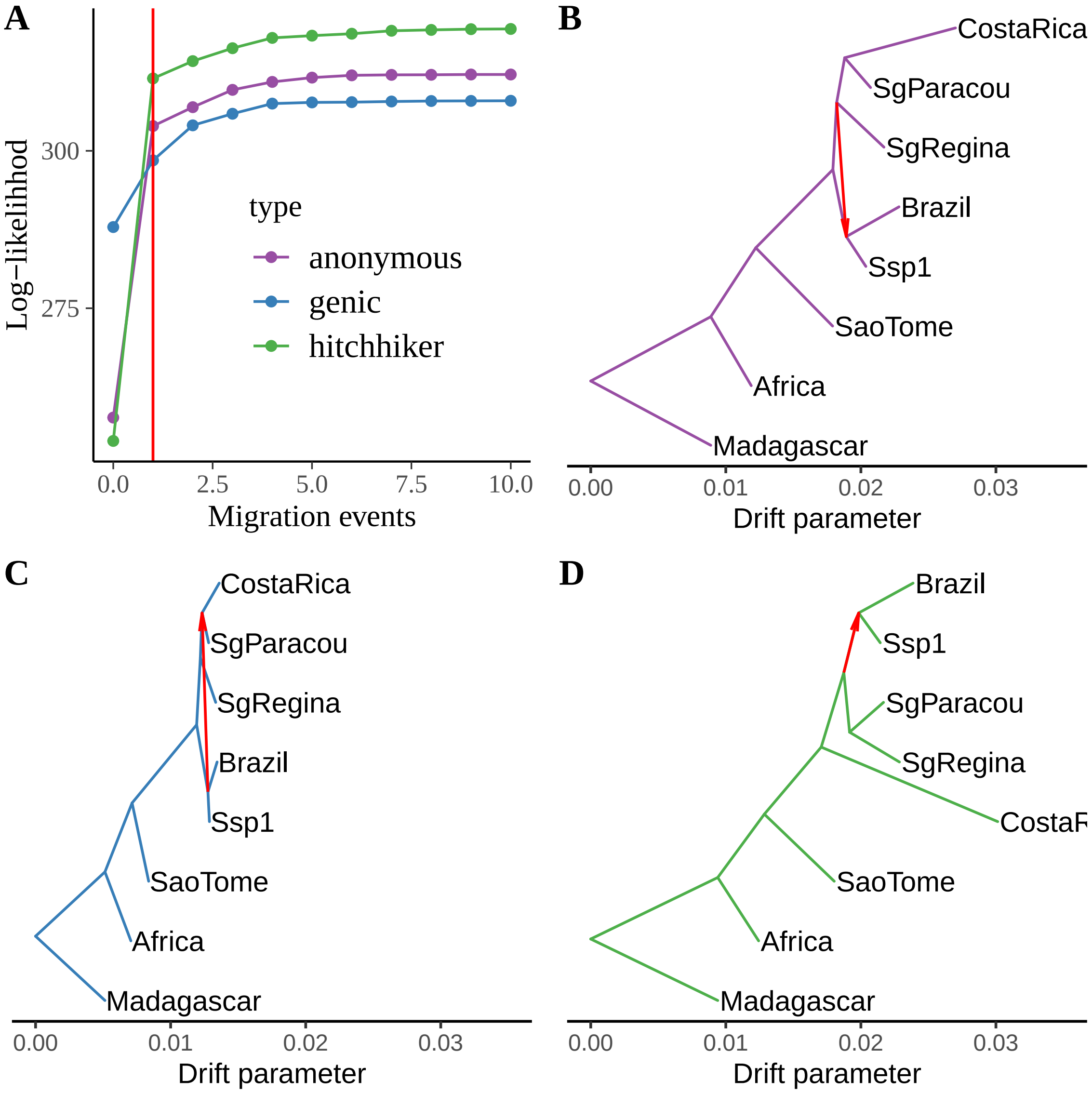

Figure 20: Phylogeny for *Symphonia* species. Drift-based phylogeny of *Symphonia* and *Pentadesma* populations with `treemix` (Pickrell and Pritchard 2012). Subfigure **A** present the log-likelihood of the phylogeny topology depending on the number of allowed migration events per SNP type, suggesting 1 migration event to better represent the phylogeny topology than none. Others subfigures represent the phylogeny for anonymous (**B**), genic (**C**) and putatively-hitchhiker (**D**) SNPs. The red arrow represents the most likely migration event. Population are named by their localities, including *Symphonia* species only or *Symphonia* and *Pentadesma* species in Africa. At the exception of the three Paracou populations: *S. sp1*, *S. globulifera type Paracou* and *S. globulifera type Regina* respectivelly named Ssp1, SgParacou and SgRegina.

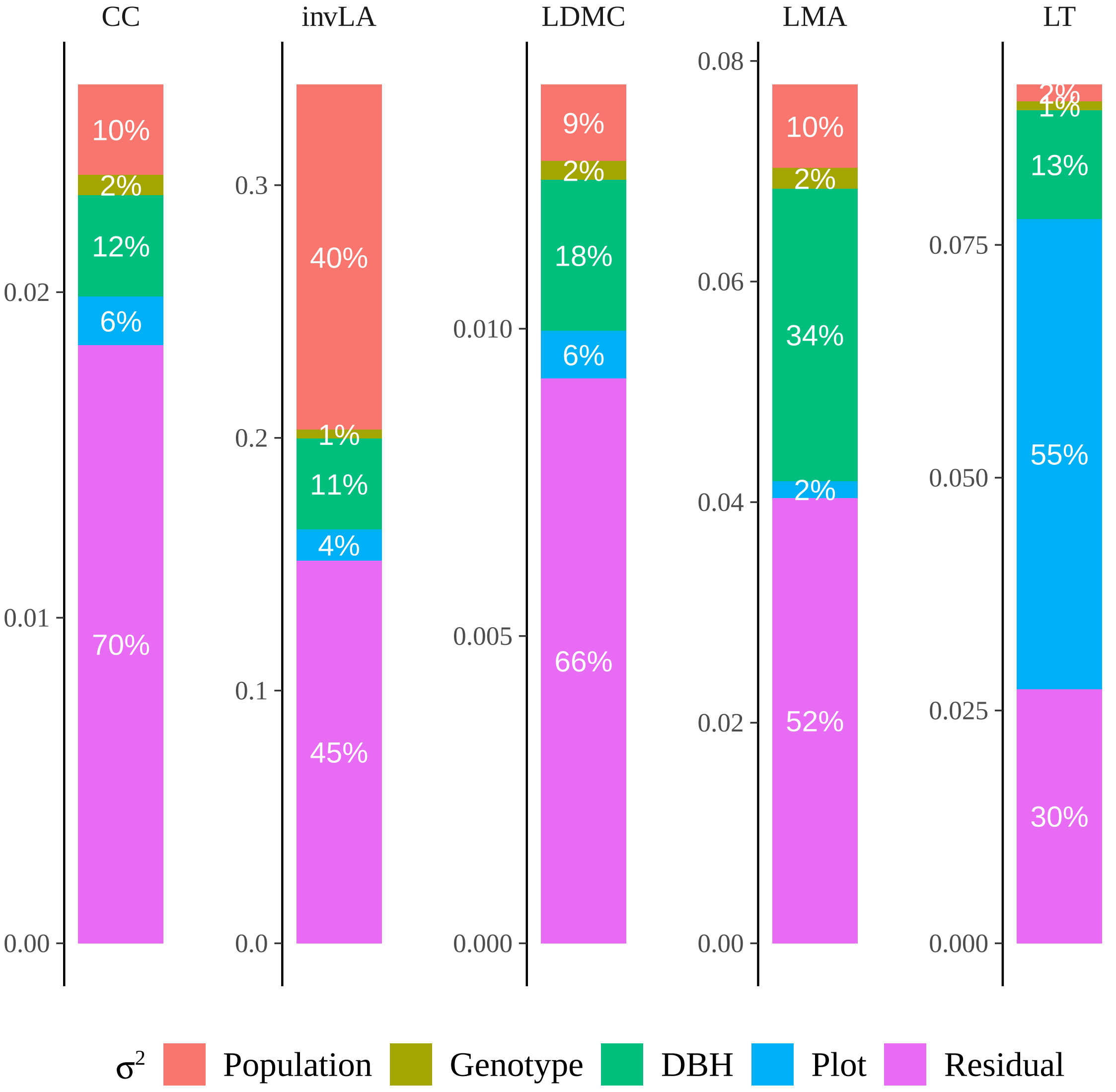

Figure 21: Variance partitioning of leaf functional traits in *Symphonia* species. . . .

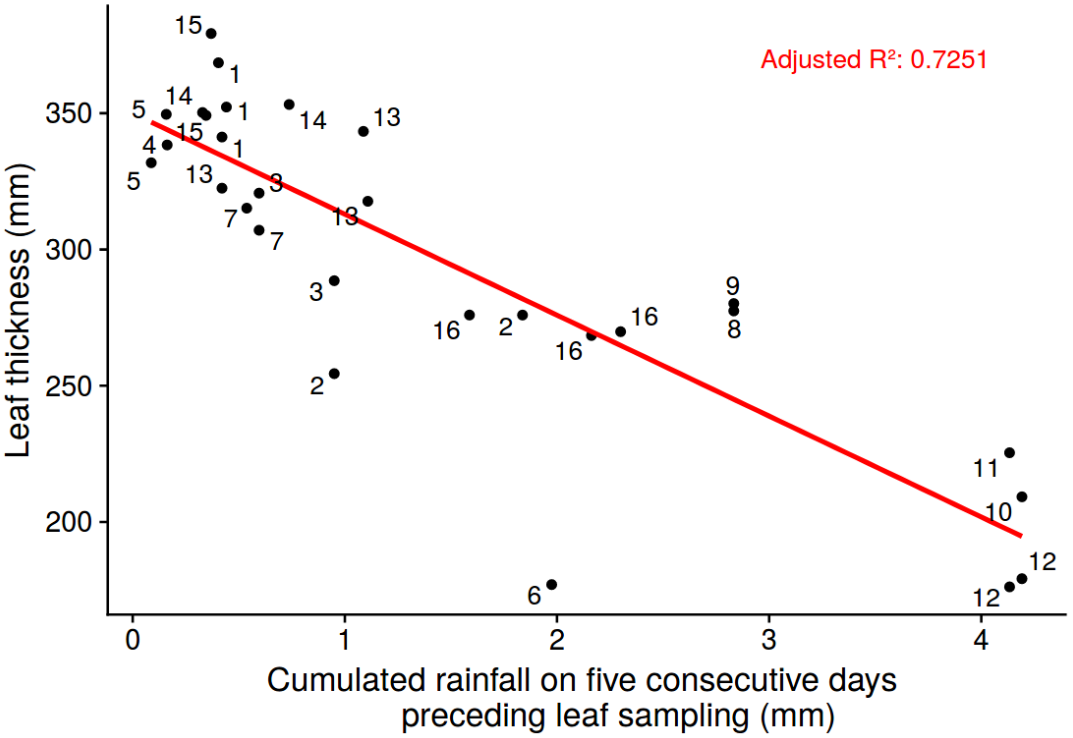

Figure 23: Leaf thickness variation with precipitation for *Symphonia globulifera* species. Leaf thickness in milimeters against cumulated rainfall on five consecutive days preceeding leaf sampling in milimeters.

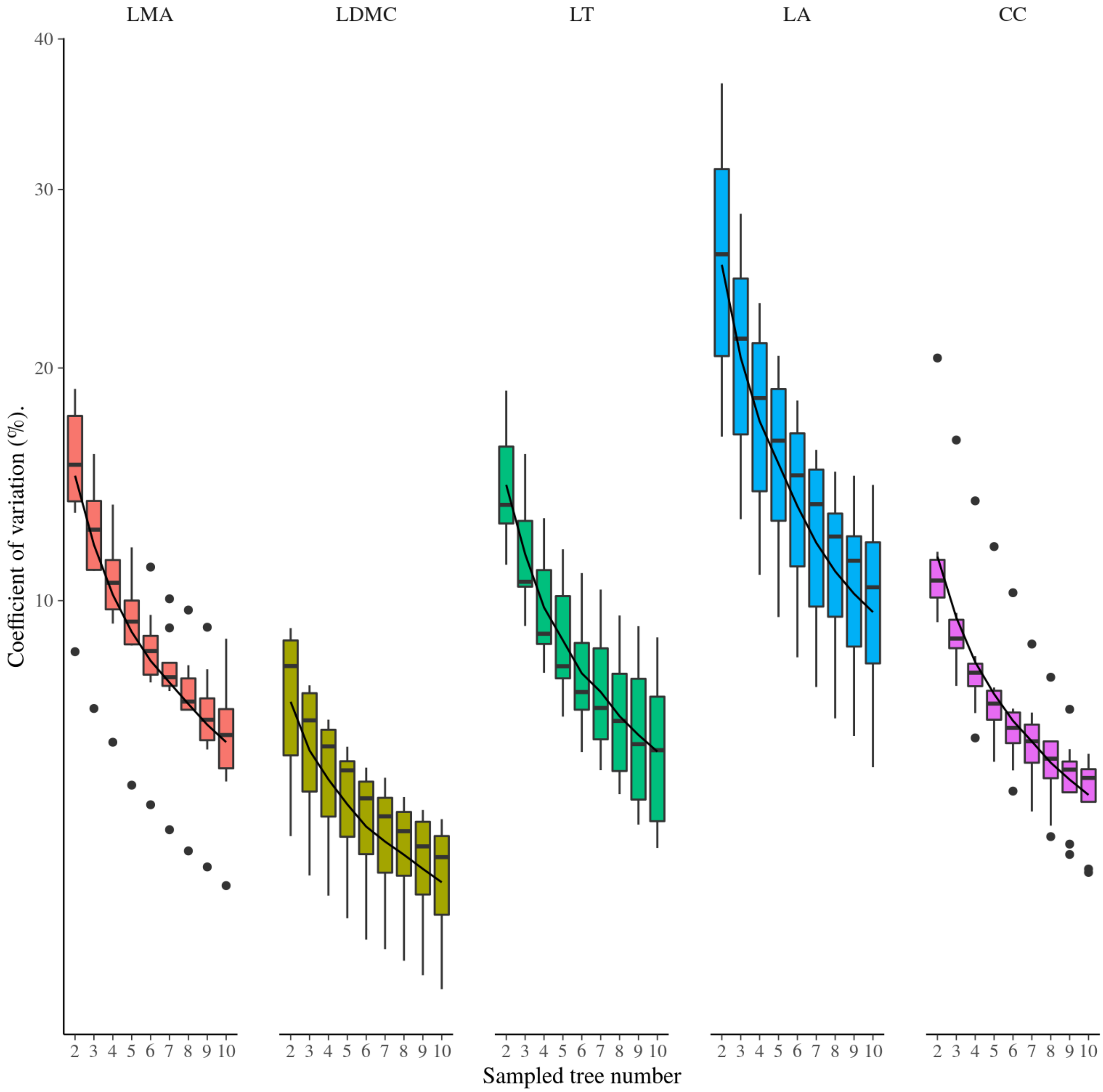

Figure 24: Effect of sampling on the estimate of the species mean trait value within *Symphonia globulifera* species. Coefficient of variation of mean estimation depending on the number of individuals sampled of DBH>30 cm.

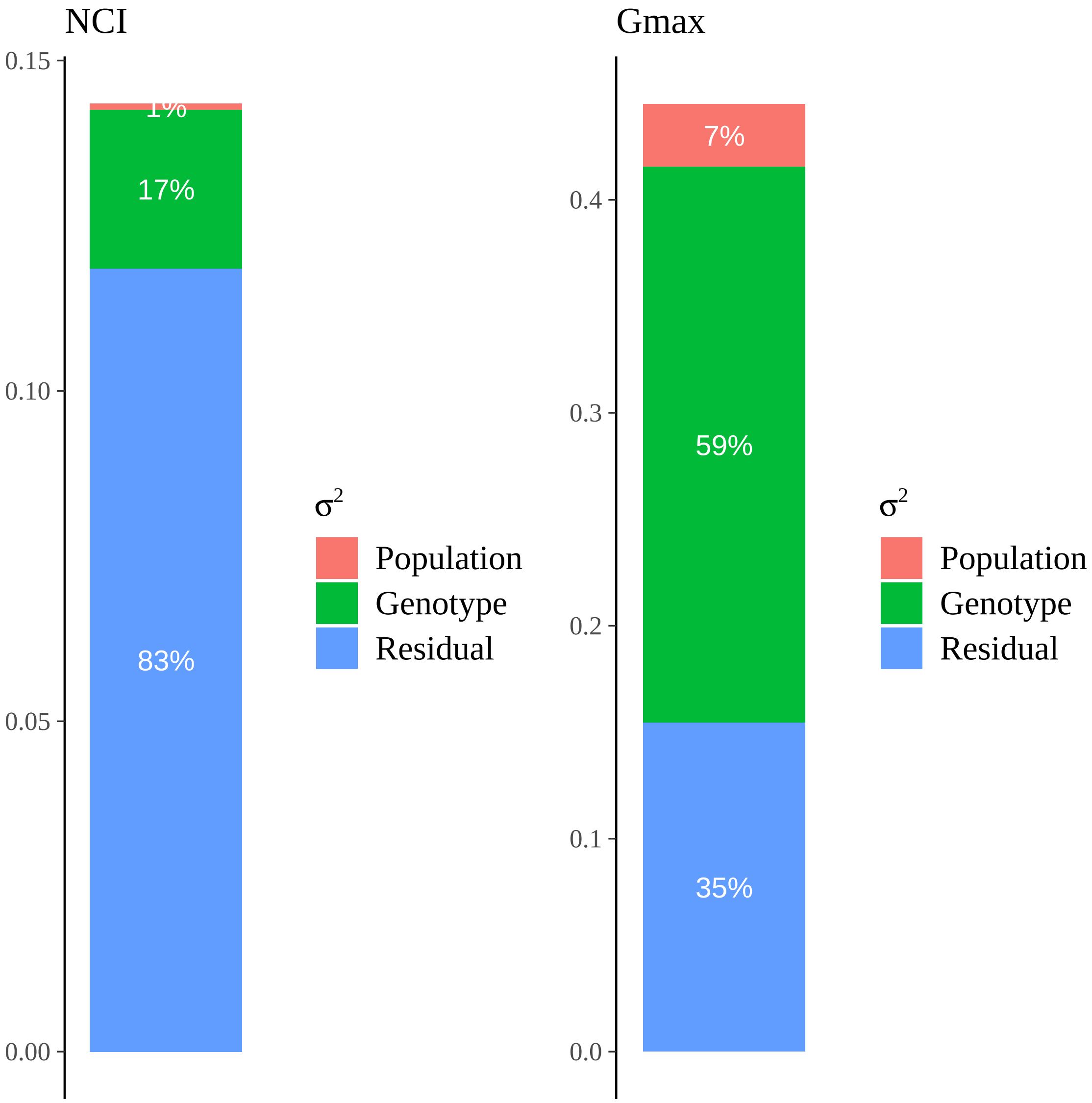

Figure 25: Variance partitioning for neighbourhood crowding index (NCI) and individual growth potential (Gmax) in *Eschweilera* clade *Parvifolia* species. Variance partitioning for neighbourhood crowding index (NCI), an indirect measurement of access to light, and individual maximum growth potential (Gmax). Variation of each variable has been partitioned into between-species (red), between-genotype (green), and residual (blue) variation.

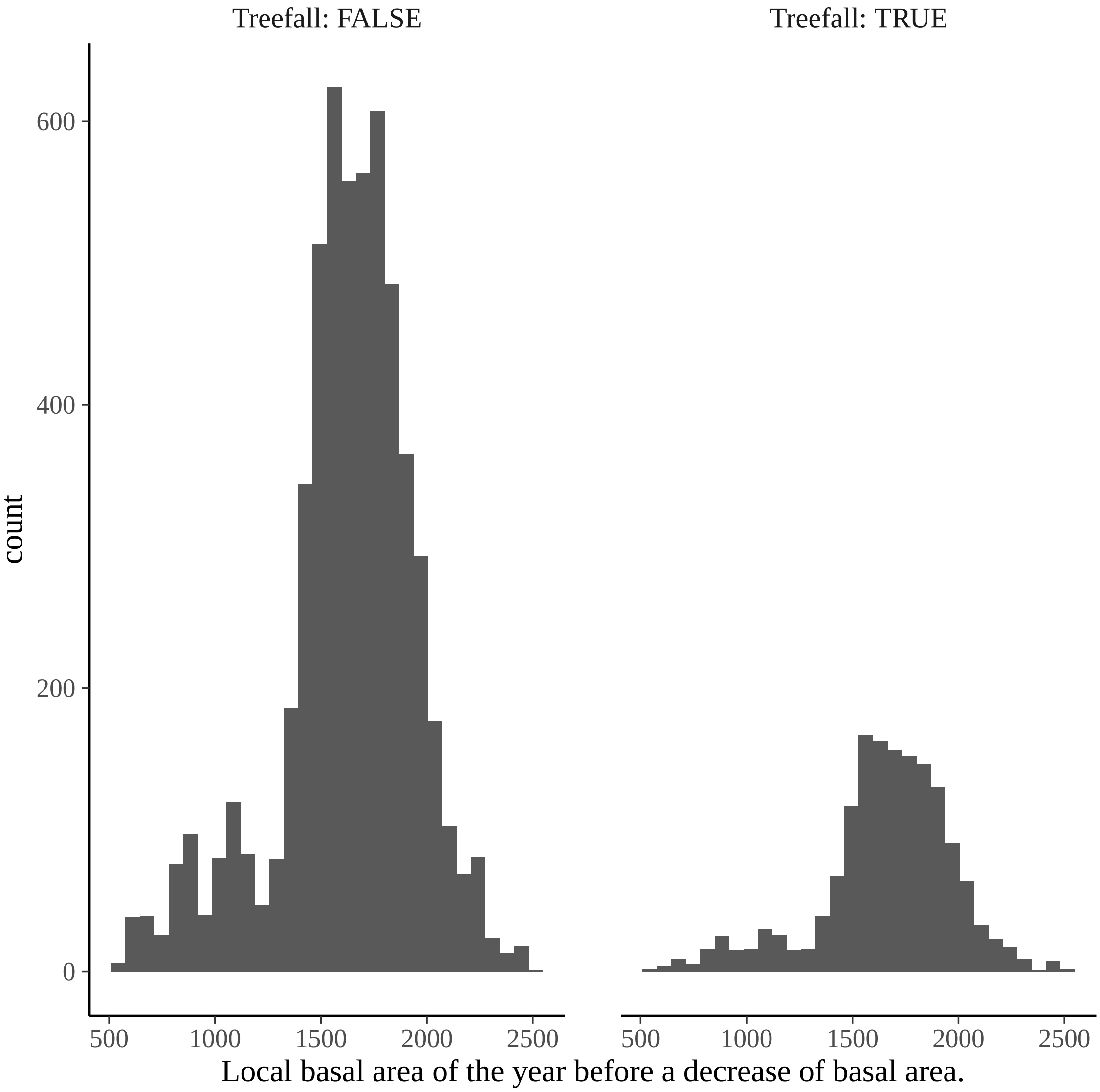

Figure 26: Local basal area distribution prior to basal area loss, i.e. the successional stage of the forest patch before a treefall occurs. Treefall are defined is a loss of basal area superior to 10.

Simulator S2: R code for the one-dimension eco-evolutionary simulator.

```
#include <Rcpp.h>
using namespace Rcpp;

// [[Rcpp::export]]
NumericVector build_gradient(
    double gradientlim,
    int length
){
  double step = gradientlim*2/(length-1) ;
  NumericVector gradient(length) ;
  gradient[0] = - gradientlim ;
  for (int i = 1; i < length; i++)
    gradient[i] = gradient[i-1] + step ;
  return gradient ;
}

// [[Rcpp::export]]
List simulator1D_cpp(
    int  Nind = 50,
    int Ngen = 50,
    double muG = 0,
    double sigmaG = 1,
    double muE = 0,
    double sigmaE = 1,
    double Elim = 10,
    int seedlings = 4,
    int dispersal = 1,
    bool viability_deterministic = true
) {
  NumericMatrix A(Ngen, Nind) ;
  NumericMatrix Z(Ngen, Nind) ;
  NumericVector E = build_gradient(Elim, Nind) ;
  NumericMatrix Aoffsprings(Nind, seedlings) ;
  NumericMatrix Zoffsprings(Nind, seedlings) ;
  NumericVector Ap(2*dispersal+1) ;
  NumericVector w(seedlings) ;
  IntegerVector seeds(seedlings) ;
  int imin , imax, winner ;
```

```
  double muS ;
  A.row(0) = rnorm(Nind, muG, sigmaG) ;
  Z.row(0) = rnorm(Nind, muE, sigmaE) ;
  for(int s = 0; s < seedlings; s++)
    seeds(s) = s ;
  for (int g = 1; g < Ngen; g++){
    for (int i = 0; i < Nind; i++){
      imin = 0 ;
      imax = Nind ;
      if(i-dispersal > 0){
        imin = i-dispersal ;
      }
      if(i+dispersal+1 < Nind){
        imax = i+dispersal+1 ;
      }
      NumericVector Ap(imax-imin) ;
      for(int p = 0; p < imax-imin; p++) Ap(p) = A(g-1,imin+p) ;
      for (int s = 0; s < seedlings; s++){
        Aoffsprings(i,s) = rnorm(1, mean(sample(Ap, 2)), sigmaG/2)[0] ;
        Zoffsprings(i,s) = Aoffsprings(i,s) + rnorm(1, muE, sigmaE)[0] ;
      }
      if(viability_deterministic){
        winner = which_min(sqrt(pow(Zoffsprings(i,_)-E(i), 2))) ;
      } else {
        w = 1/sqrt(pow(Zoffsprings(i,_)-E(i), 2)) ;
        winner = sample(seeds, 1, true, w)[0] ;
      }
      A(g,i) = Aoffsprings(i,winner) ;
      Z(g,i) =  Zoffsprings(i,winner) ;
    }
  }
  List sim = List::create(Named("A") = A,
                          Named("Z") = Z,
                          Named("E") = E) ;
  return sim;
}
```

Simulator S2: R code for the two-dimensions eco-evolutionary simulator.

```
simulator2D <- function(
    grid = 20, # size
    Ngen = 50,
    muG = 0, # genetics
    sigmaG = 1,
    muE = 0, # environment
    sigmaE = 1,
    Elim = 5,
    seedlings = 4, # reproduction
    dispersal = 1,
    viability_deterministic = T
){
    A <- array(dim = c(grid, grid, Ngen)) # objects
    Z <- array(dim = c(grid, grid, Ngen))
    A[,,1] <- array(rnorm(grid*grid, muG, sigmaG), dim = c(grid,grid))
    Z[,,1] <- A[,,1] + array(rnorm(grid*grid, muE, sigmaE),
                             dim = c(grid,grid))
    E <- seq(-Elim, Elim, length.out = grid) %*%
      t(seq(-Elim, Elim, length.out = grid))
    for(g in 2:Ngen){ # iterations
      Aoffsprings <- array(
        as.vector(
          sapply(1:grid, function(i)
            sapply(1:grid, function(j)
              sapply(1:seedlings, function(s)
                rnorm(1,
                      sample(A[max(1,i-dispersal):min(i+dispersal,grid),
                               max(1,j-dispersal):min(j+dispersal,grid),
                               g-1], 2),
                      sigmaG/2)
              )
            )
          )
        ), dim = c(grid, grid, seedlings))
        Zoffsprings <- Aoffsprings +
          array(rnorm(grid*grid*seedlings, muE, sigmaE),
                dim = c(grid,grid,seedlings))
        if(viability_deterministic){
```

```
      survivors <- array(apply(
       apply(Zoffsprings, 3,
          function(x) as.array(sqrt((x - E)^2),
                     dim = c(grid,grid))), 1, which.min),
       dim = c(grid,grid))
    } else {
     survivors <- array(
      apply(1/apply(Zoffsprings, 3,
             function(x) as.array(sqrt((x - E)^2),
                        dim = c(grid,grid))), 1,
         function(w)
          sample.int(seedlings, 1, replace = T, prob = w)),
      dim = c(grid,grid))
    }
    A[,,g] <- Aoffsprings[cbind(rep(1:grid, grid), rep(1:grid, each = grid),
                  as.vector(survivors))]
    Z[,,g] <- Zoffsprings[cbind(rep(1:grid, grid), rep(1:grid, each = grid),
                  as.vector(survivors))]

  }
  return(lapply(list("breeding value (a)" = A, "trait value (z)" = Z),
         function(M)
    reshape2::melt(M) %>%
     dplyr::rename(X = Var1, Y = Var2, generation = Var3)) %>%
    bind_rows(.id = "var") %>%
     left_join(reshape2::melt(E) %>%
           dplyr::rename(X = Var1, Y = Var2, environment = value),
          by = c("X", "Y")) %>%
     mutate(individual = paste0("X",X,"Y",Y)))
}
```

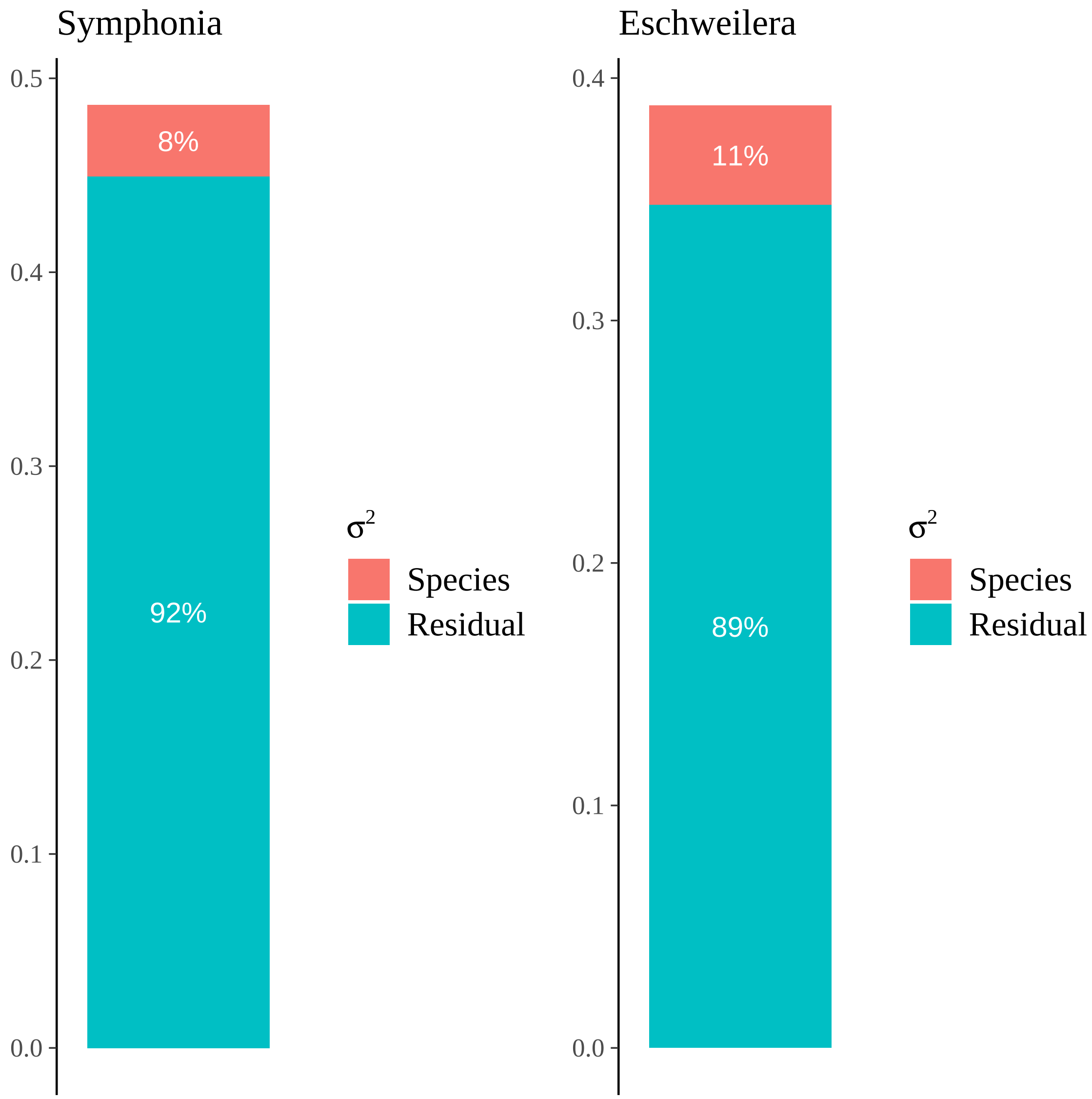

Figure 27: Species variation in growth trajectories of *Symphonia* and *Eschweilera* clade *Parvifolia* species.

APPENDIX 2: CHAPTER 1 SUPPLEMENTARY MATERIALS

Article title: **Topography shapes the local coexistence of tree species within species complexes of Neotropical forests**

Authors: Sylvain Schmitt, Niklas Tysklind, Géraldine Derroire, Myriam Heuertz, Bruno Hérault

The following Supporting Information is available for this article:

Fig. 28. Correlation of abiotic topographic variables and neighbor crowding indexes.

Tab. 6. Model tested for species complex distribution.

Fig. 29. Habitat suitability of single taxa model for every model form.

Tab. 7. Model parameters for each complex with scaled descriptors.

Tab. 8. Model parameters for each complex with scaled descriptors.

Model S1. Stan code for the inference of species complex presencer.

Model S2. Stan code for the inference of species joint-presence.

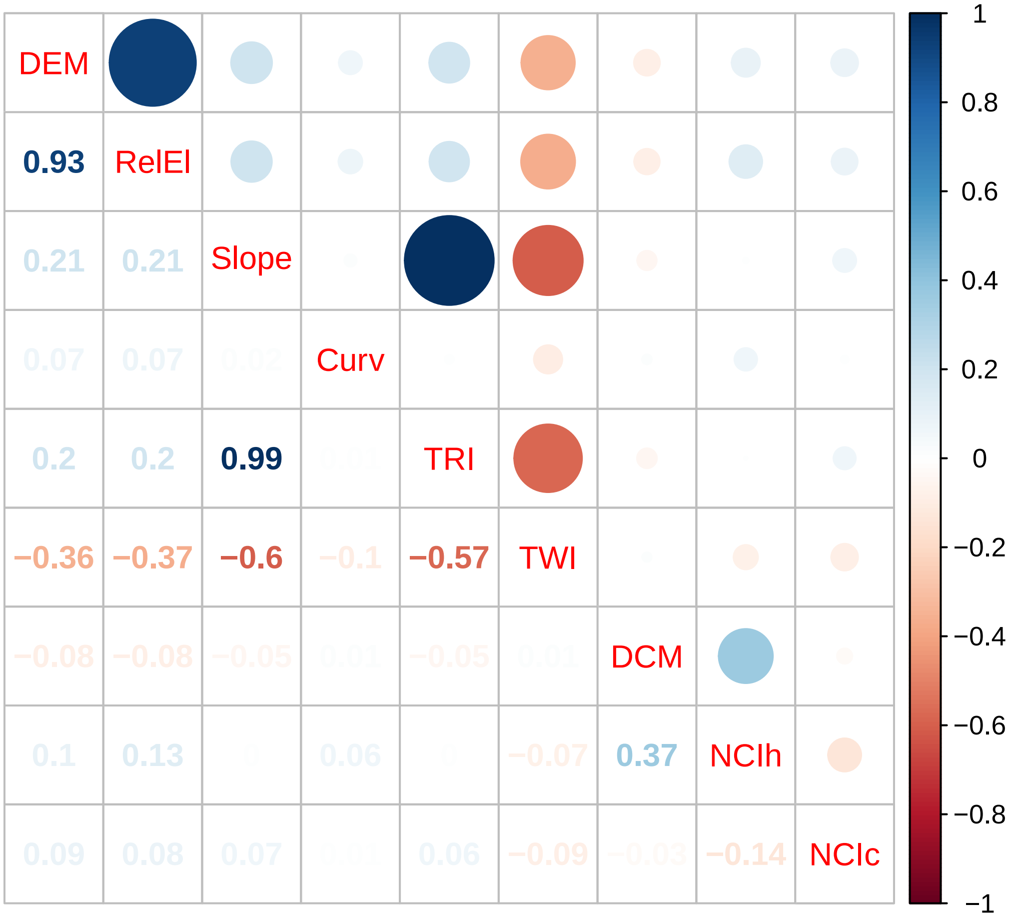

Figure 28: Correlation of abiotic topographic variables and neighbor crowding indexes (NCI). All variables, relative elevation (RelEl), slope, curvature (Curv), aspect, topographic ruggedness index (TRI), and topographic wetness index (TWI) are derived from the digital elevation model (DEM) obtained through LiDAR campaign in 2015, the digital canopy model (DCM) has been obtained in the same campaign, and neighbor crowding index (NCI) of heterospecific (NCIh) or conspecific (NCIc) are derived from Paracou census campaign of 2015.

Table 6: Model tested for species complex distribution.

Name	Formula
B_0	$Presence \sim \mathcal{B}ernoulli(logit^{-1}(\alpha_0))$
B_α	$Presence \sim \mathcal{B}ernoulli(logit^{-1}(\alpha_0 + \alpha * Environment))$
B_{α,α_2}	$Presence \sim \mathcal{B}ernoulli(logit^{-1}(\alpha_0 + \alpha * Environment + \alpha_2 * Environment^2))$
$B_{\alpha,\beta}$	$Presence \sim \mathcal{B}ernoulli(logit^{-1}(\alpha_0 + \alpha * Environment + Environment^\beta))$
$B_{\alpha,\beta}2$	$Presence \sim \mathcal{B}ernoulli(logit^{-1}(\alpha_0 + \alpha * (Environment + Environment^\beta)))$
$B_{\alpha,\beta}3$	$Presence \sim \mathcal{B}ernoulli(logit^{-1}(\alpha_0 + Environment^\alpha + Environment^\beta))$

Table 7: Model parameters for each complex with scaled descriptors.

complex	α	β_{NCI}	β_{TWI}	γ_{NCI}	γ_{TWI}
Iryanthera	-3.338	-1.414	1.054	0.547	-0.237
Licania	-1.488	-0.716	0.056	-0.017	-0.208
Parvifolia	-1.403	-0.840	0.207	-0.254	-0.193
Symphonia	-2.423	-1.296	-0.110	-0.255	0.106
Talisia	-2.006	-1.699	-0.340	-1.263	0.017

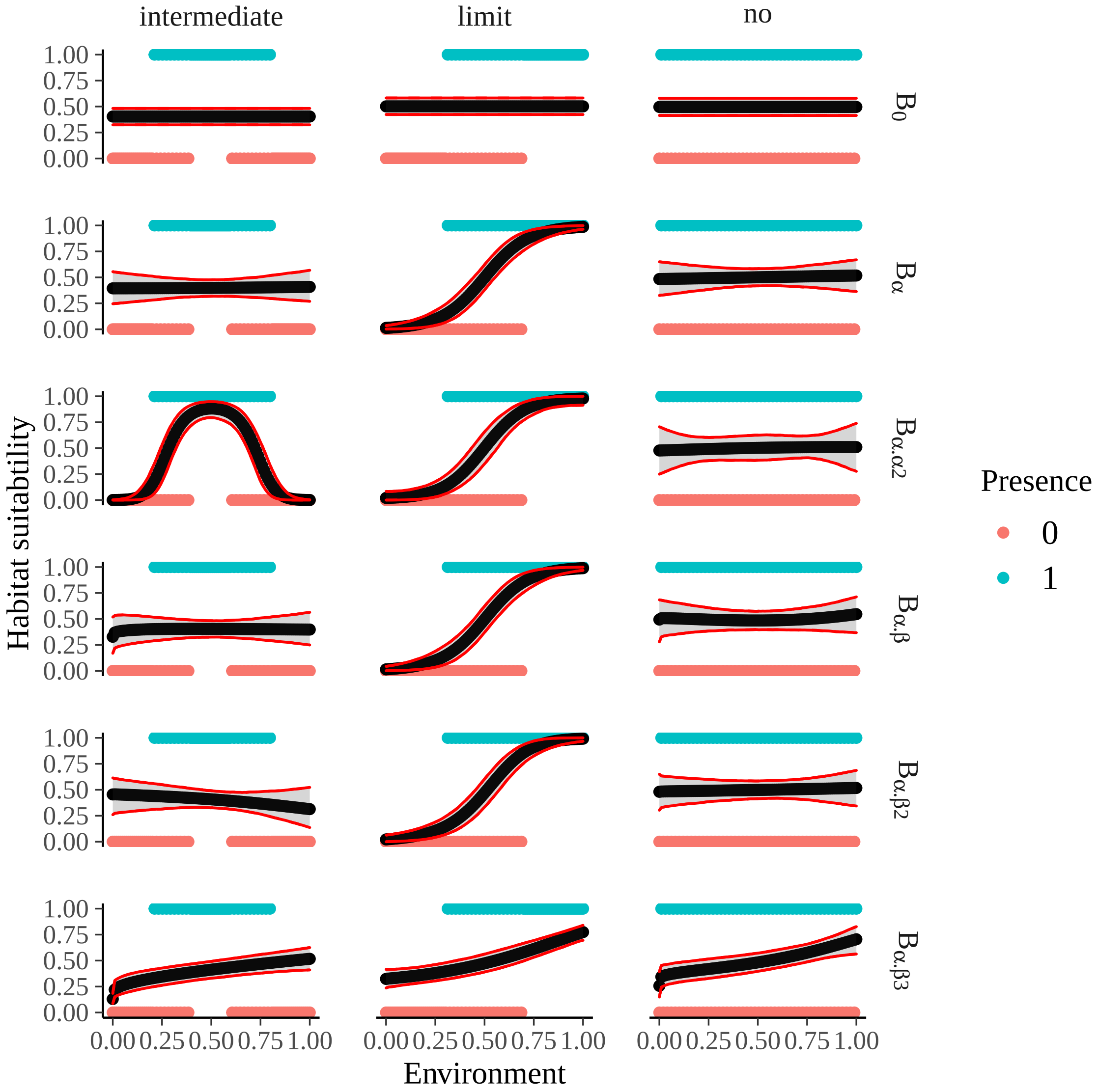

Figure 29: Habitat suitability of single taxa model for every model form (see Supplementary Material Tab. 6) and three theoretical species distribution cases. Three species distribution cases have been simulated: (i) the environmental variable has no effect, (ii) the niche optimum is an intermediate value of the environmental variable range, and (iii) the niche optimum is a limit of the environmental variable range. Blue and red dots represent simulated presences and absences respectively, whereas the black line represents the fitted corresponding model with its credibility interval in grey. The model B,2 shows the best behavior with the three distribution cases.

Table 8: Model parameters for each complex with scaled descriptors.

SpeciesLong	α	β_{NCI}	β_{TWI}	γ_{NCI}	γ_{TWI}
E coriacea	0.954	0.278	1.186	-0.236	-0.142
E decolorans	-0.041	0.244	0.051	0.574	-0.723
E grandiflora_form2	-0.455	-0.520	0.028	-0.557	-0.109
E pedicellata	-0.631	-0.576	-0.033	-0.520	0.145
E sagotiana	1.411	1.444	-1.875	1.299	0.430
E wachenheimii	-1.135	-0.846	0.709	-0.510	0.264
I hostmannii	0.133	-0.228	0.285	-0.538	0.396
I sagotiana	-0.125	0.225	-0.231	0.512	-0.377
L alba	3.459	0.643	-0.048	-2.108	0.362
L canescens	-0.036	0.296	-1.087	0.622	0.462
L laxiflora	-0.234	-0.274	0.086	-0.258	-0.665
L membranacea	-0.164	0.142	1.286	0.487	-0.250
L micrantha	-0.626	-0.003	0.362	0.570	-0.056
L ovalifolia	-0.839	-0.134	0.313	0.512	0.021
L parvifructa	-0.553	-0.651	-0.023	-0.787	-0.362
L sprucei	-0.966	-0.024	-0.910	0.950	0.472
S globulifera	-0.551	-0.754	0.905	-0.937	0.299
S sp.1	0.546	0.716	-0.850	0.986	-0.324
T hexaphylla	0.062	0.213	-0.564	0.417	0.204
T praealta	0.056	-0.101	0.074	-0.230	0.101
T simaboides	-0.155	-0.185	0.477	-0.120	-0.267

Model S1: Stan code for the inference of species complex presence

```
functions {
  real scale(vector x) {
    return sqrt(sum(x .* x)/(num_elements(x) - 1)) ;
  }
}
data {
  int<lower=1> N ;                // # of individuals
  int<lower=1> K ;                // # of environmental descriptors
  int<lower=0, upper=1> Y[N] ;    // individuals presence or absence (0-1)
  matrix[N,K] X ;                 // environmental descriptors
  int<lower=1> N_pred ;
  matrix[N_pred,K] X_pred ;
}
transformed data {
  matrix[N,K] X_std ;
  matrix[N_pred,K] X_pred_std ;
  for(k in 1:K) {
    X_std[,k] = X[,k] / scale(X[,k]) ;
    X_pred_std[,k] = X_pred[,k] / scale(X[,k]) ;
  }
}
parameters {
  real alpha ;       // intercept
  vector[K] beta ;   // sigmoidal slope
  vector[K] gamma ;  // quadratic form
}
model {
  alpha ~ normal(0, 1) ;
  beta ~ normal(0, 1) ;
  gamma ~ normal(0, 1) ;
  Y ~ bernoulli_logit(alpha + X_std * beta + (X_std .* X_std) * gamma) ;
}
generated quantities {
  vector[N_pred] Y_pred ;
  Y_pred = inv_logit(alpha + X_pred_std * beta + (X_pred_std .* X_pred_std) * gamma) ;
}
```

Model S2: Stan code for the inference of species joint-presence

```
functions {
  real dirichlet_multinomial_lpmf(int[] y, vector alpha) {
    real alpha_plus = sum(alpha);
    return lgamma(alpha_plus) + sum(lgamma(alpha + to_vector(y)))
                - lgamma(alpha_plus+sum(y)) - sum(lgamma(alpha));
  }
  real scale(vector x) {
    return sqrt(sum(x .* x)/(num_elements(x) - 1)) ;
  }
}
data {
  int<lower = 1> N  ;       // # of individuals
  int<lower = 1> S  ;       // # of species
  int<lower = 1> K  ;       // # of environmental descriptors
  int<lower = 0, upper=1> Y[N, S]  ; // individuals presence or absence for each species
  matrix[N,K] X ;           // environmental descriptors
  int<lower=0> N_pred ;
  matrix[N_pred,K] X_pred ;
}
transformed data {
  matrix[N,K] X_std ;
  matrix[N_pred,K] X_pred_std ;
  for(k in 1:K) {
    X_std[,k] = X[,k] / scale(X[,k]) ;
    X_pred_std[,k] = X_pred[,k] / scale(X[,k]) ;
  }
}
parameters {
  vector[S] alpha ; // intercept
  matrix[S,K] beta ; // sigmoidal slope
  matrix[S,K] gamma ; // quadratic form
}
model {
  alpha ~ normal(0,1) ;
  for(k in 1:K){
    beta[,k] ~ normal(0,1) ;
    gamma[,k] ~ normal(0,1) ;
  }
```

```
  for (n in 1:N)
    Y[n] ~ dirichlet_multinomial(softmax(alpha + beta*to_vector(X_std[n,])
                                  + gamma*to_vector(X_std[n,] .* X_std[n,])))  ;
                                  // likelihood
}
generated quantities {
  matrix[N_pred,S] Y_pred ;
  for(n in 1:N_pred)
    Y_pred[n,] = to_row_vector(softmax(alpha + beta*to_vector(X_pred_std[n,])
                              + gamma*to_vector(X_pred_std[n,] .* X_pred_std[n,]))) ;
}
```

APPENDIX 3: CHAPTER 2 SUPPLEMENTARY MATERIALS

Article title: **Topography consistently drives intra- and inter-specific leaf trait variation within tree species complexes in a Neotropical forest**

Authors: Sylvain Schmitt, Bruno Hérault, Émilie Ducouret, Anne Baranger, Niklas Tysklind, Myriam Heuertz, Éric Marcon, Saint Omer Cazal, Géraldine Derroire

The following Supporting Information is available for this article:

Fig. 30. Principal Component Analysis of abiotic topographic variables.

Fig. 31. Diameter at breast height and Dawkins index correlation.

Fig. 32. Diameter at breast height distribution between sampled indivduals and other *Symphonia* and *Eschweilera* individuals of Paracou.

Tab. 9. Log-likelihood for diameter model depending on model form (linear vs Michaelis-Menten).

Fig. 33. Effect of tree diameter on leaf functional trait variation.

Fig. 34. Species niche breadth along the topographic wetness index for all species from Paracou.

Fig. 35. Random effects of plots on leaf functional trait variation.

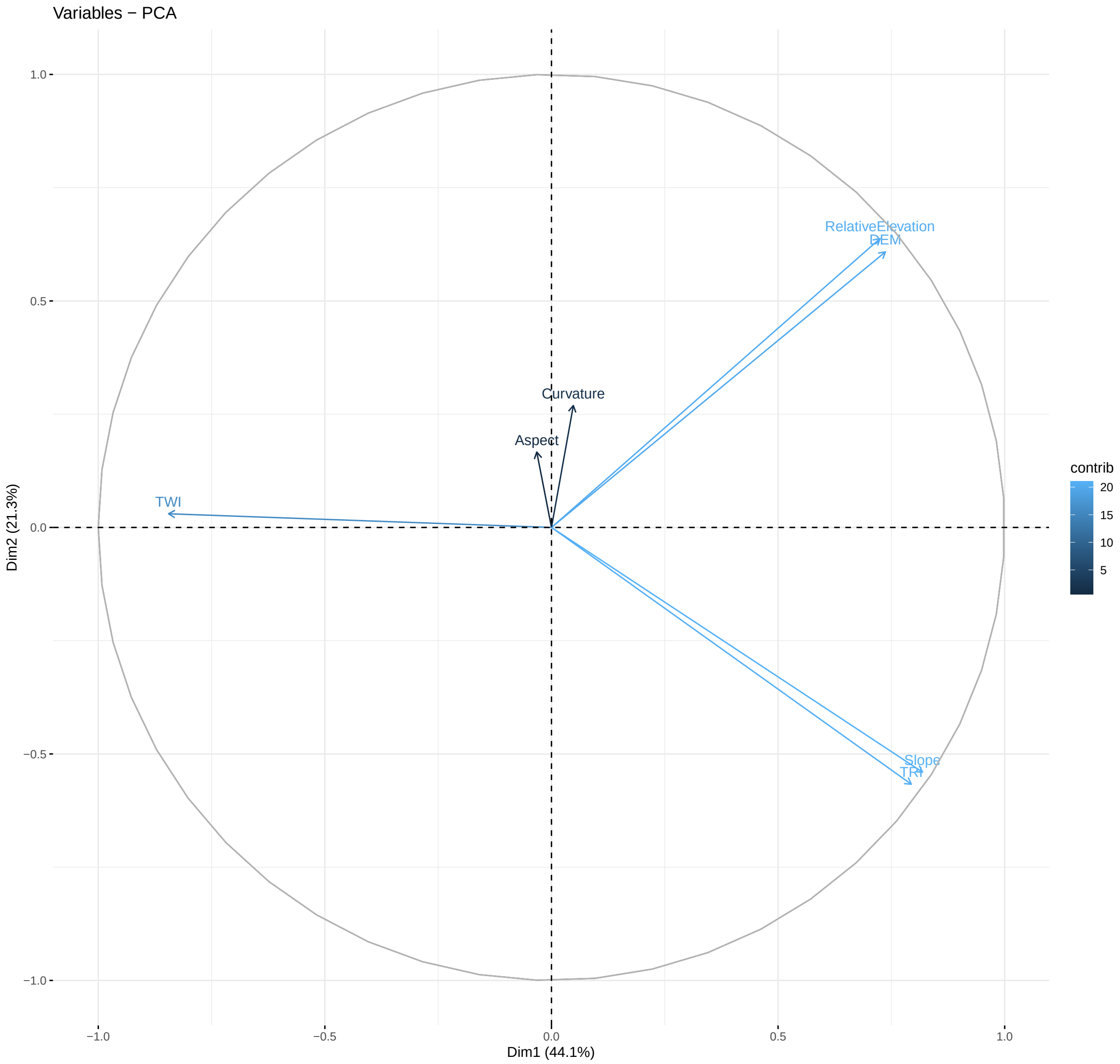

Figure 30: Principal Component Analysis (PCA) of abiotic topographic variables. All variables, slope, curvature, aspect, topgraphic rudgeness index (TRI), and topgraphic wetness index (TWI) are derived from the digital evlevation model (DEM) obtaine through LiDAR campaign in 2015.

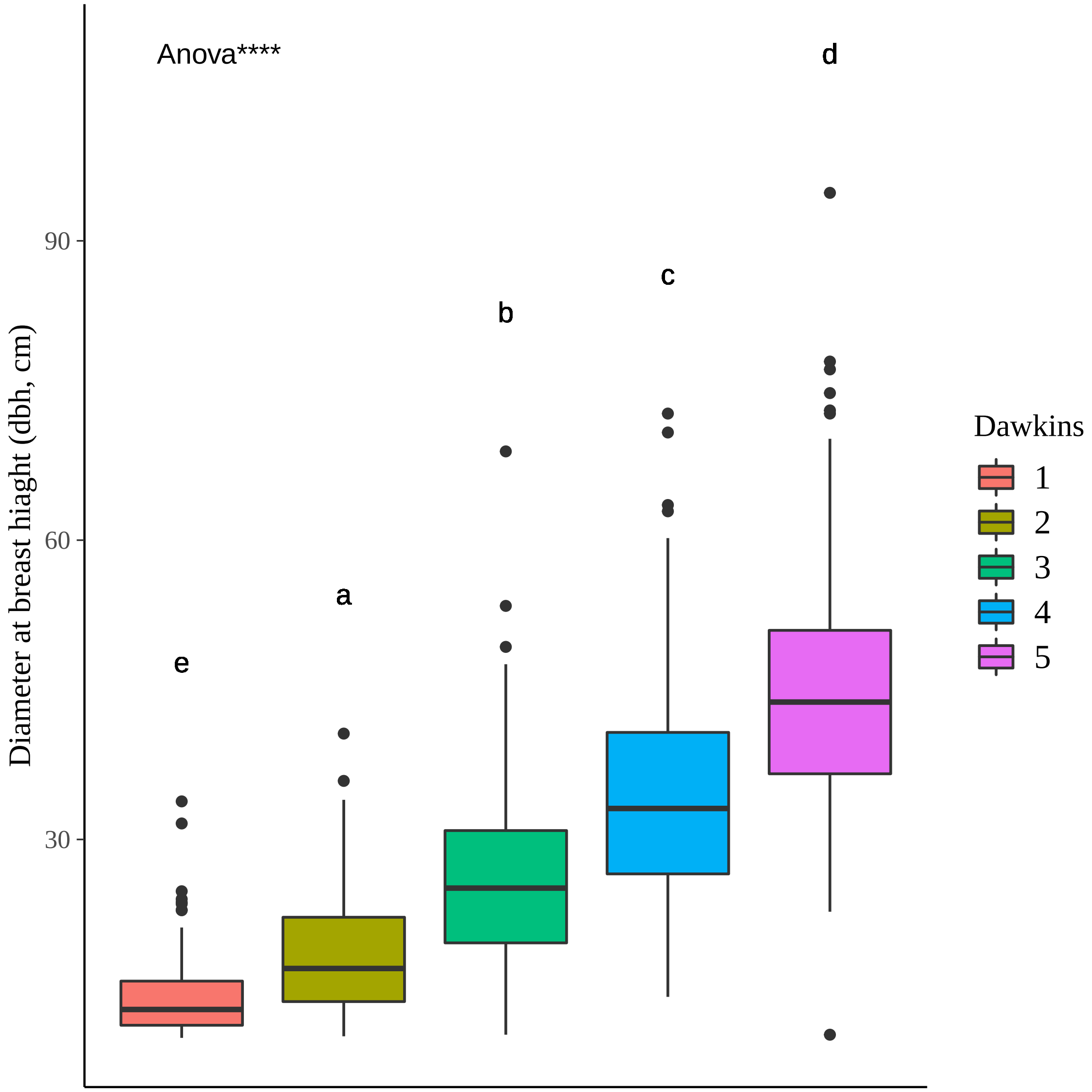

Figure 31: Diameter at breast height (DBH) and Dawkins index correlation. Box colors indicates the Dawkins index. DBH and Dawkins index correlation has been investigated by Anova. **** indicates a $p - value < 0.0001$. Letters indicate post-hoc groups investigated by Tukey Honest Significant Differences.

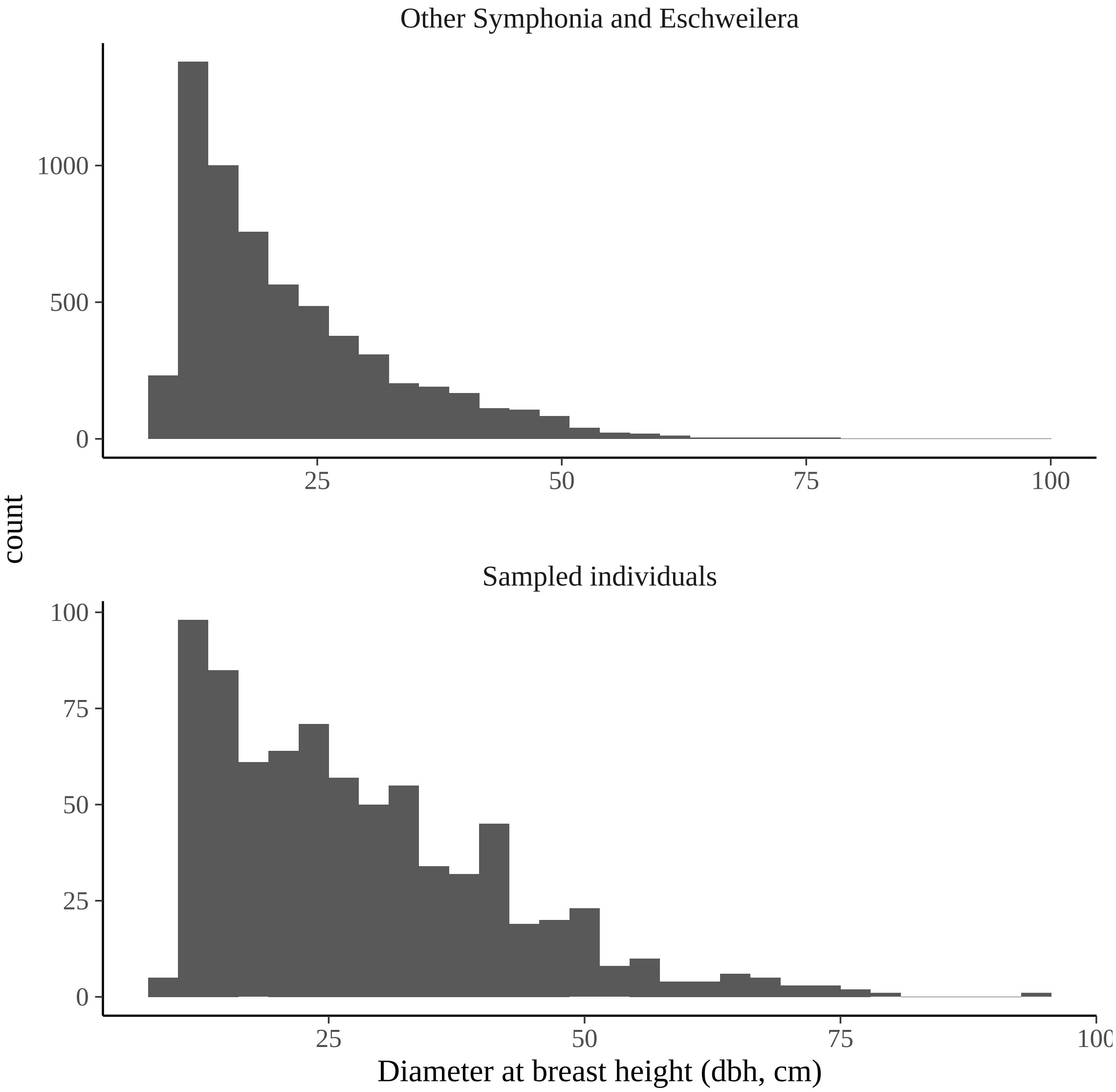

Figure 32: Diameter at breast height (DBH) distribution between sampled indivduals and other *Symphonia* and *Eschweilera* individuals of Paracou.

Table 9: Log-likelihood for diameter model depending on model form (linear vs Michaelis-Menten).

Genus	Trait	Linear	Michaelis Menten	Difference
Eschweilera	LMA	-85.212	-78.300	-6.911
Eschweilera	$LDMC$	-42.237	-44.454	2.217
Eschweilera	LT	-14.265	-8.660	-5.605
Eschweilera	$\frac{1}{LA}$	411.503	414.119	-2.615
Eschweilera	CC	-190.383	-192.942	2.559
Symphonia	LMA	-103.963	-97.755	-6.208
Symphonia	$LDMC$	48.134	56.714	-8.580
Symphonia	LT	-159.831	-159.919	0.088
Symphonia	$\frac{1}{LA}$	-91.641	-86.634	-5.006
Symphonia	CC	-185.400	-176.199	-9.200

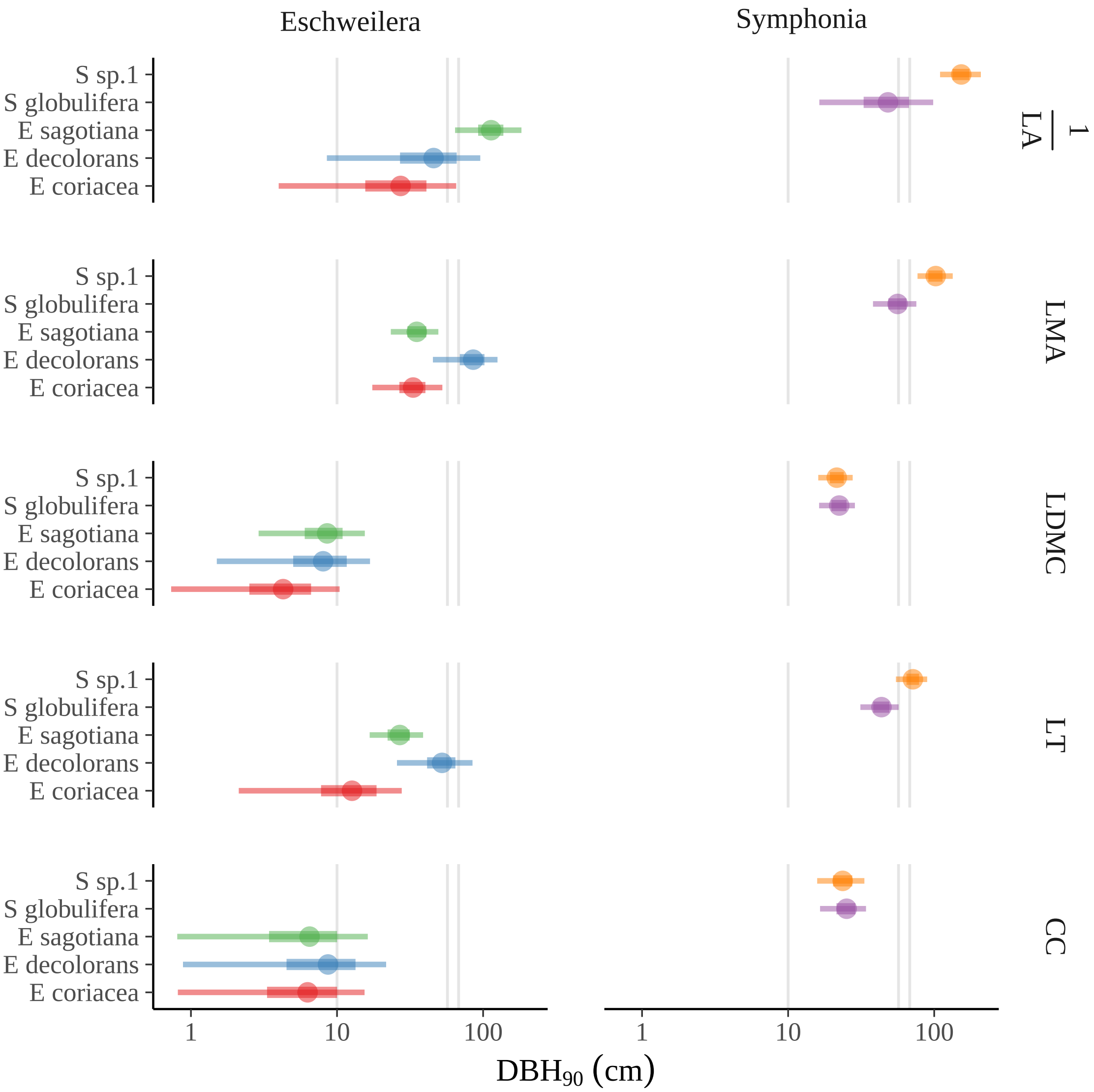

Figure 33: Effect of tree diameter on leaf functional trait variation. The posterior distribution of species diameter at breast height for which a given trait reaches 90% of its maximum value (DBH_{90}) was estimated for every trait for all species in both complexes using Bayesian inference. Circles represent the mean estimate, thick lines the 50% confidence interval and thin lines the 95% confidence interval, and color the corresponding species. Vertical lines indicate from left to right: (i) tree recruitment diameter and (ii) and (iii) 95th percentile of diameter for *Eschweilera* and *Symphonia*, respectively.

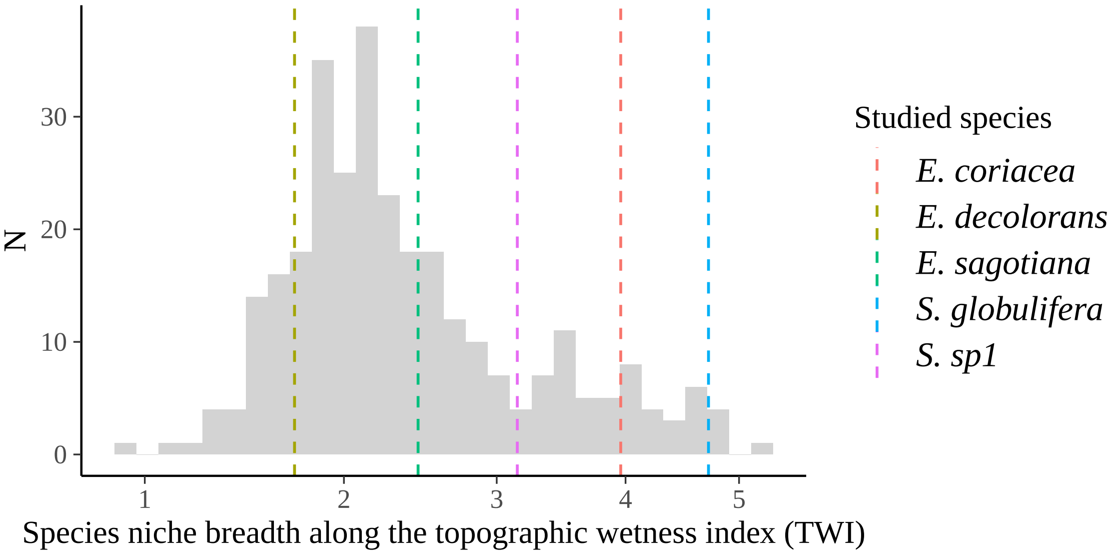

Figure 34: Species niche breadth along the topographic wetness index (TWI) for all species from Paracou. Niche breadth has been calculated as the difference between the 95th quantile and the 5th quantile of TWI for all species from Paracou with at least 20 individuals. Dashed vertical lines represent niche breadth value for species from this study indicated by line color. E. coriacea and the two Symphonia species have bigger niche breadth than most Paracou species but E. sagotiana and E. coriacea have niche breadth similar to the majority of Paracou species.

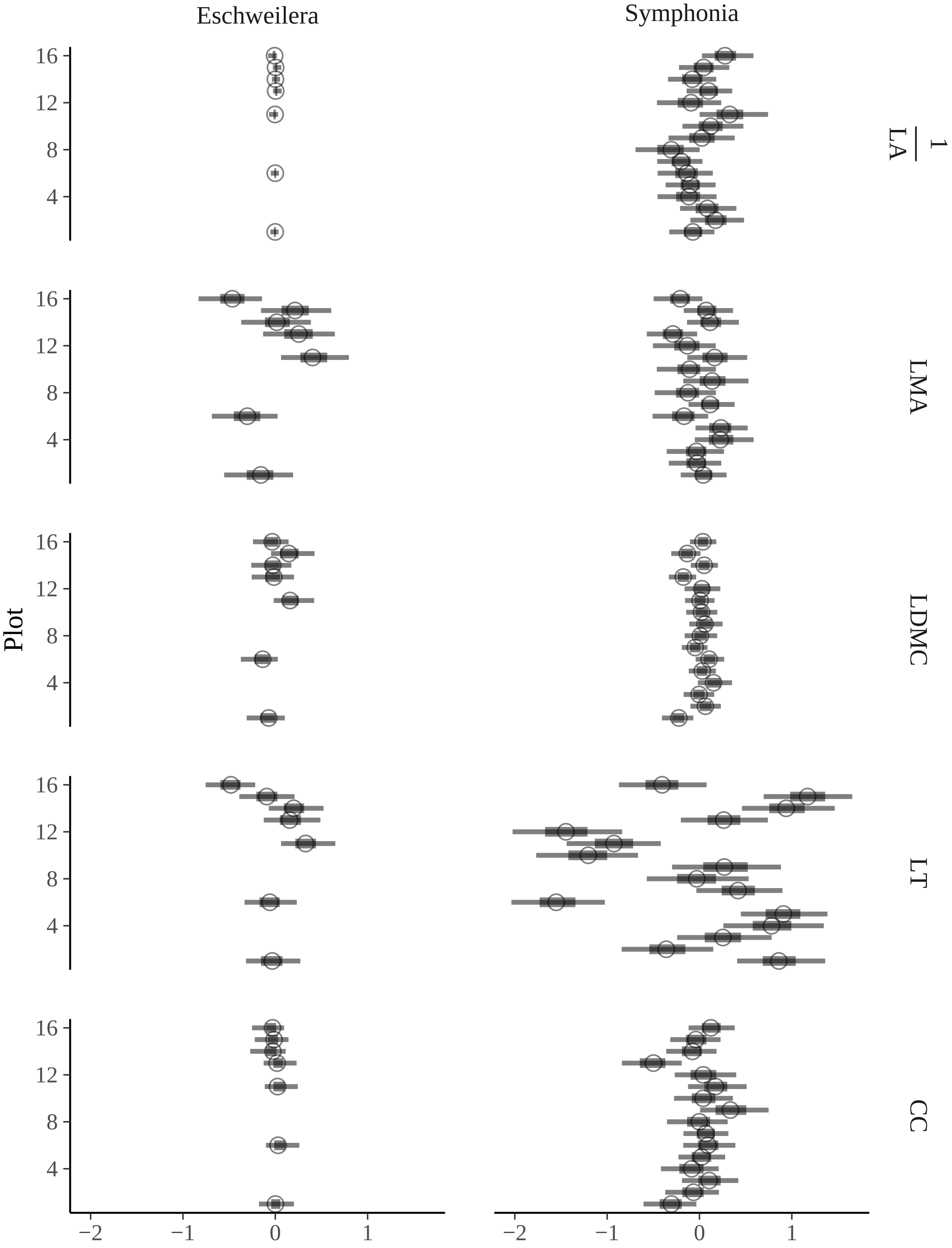

Figure 35: Random effects of plots on leaf functional trait variation. The posterior distribution of plot effect was estimated for every trait for all plots in both complexes using Bayesian inference. Circles represent the mean estimate, thick lines the 50% confidence interval and thin lines the 95% confidence interval, and color the corresponding species.

APPENDIX 4: CHAPTER 3 SUPPLEMENTARY MATERIALS

Article title: **Topography drives microgeographic adaptations among closely-related species of two tropical tree species complexes**

Authors: Sylvain Schmitt, Niklas Tysklind, Bruno Hérault, Myriam Heuertz

The following Supporting Information is available for this article:

Method S1. Design of the probes set for *Symphonia*.

Method S2. Design of the probes set for *Eschweilera*.

Model S1. Stan code for the animal model

Tab. 10. *Eschweilera* botanical species and genetic clusters

Fig. 36. Target selection for the capture experiment of *Symphonia*

Fig. 37. Target selection for the capture experiment of *Eschweilera*

Fig. 38. SNP abundance per library for *Eschweilera*

Fig. 39. Library abundance per SNP for *Eschweilera*

Fig. 40. Outgroup detection for *Eschweilera*

Fig. 41. Cross-validation for *Symphonia* population structure

Fig. 42. *Symphonia* population structure using admixture

Fig. 43. *Symphonia* population structure using hybrid index

Fig. 44. Outlier SNPs among *Symphonia* species

Method S1: Design of the probes set for *Symphonia*.

For *Symphonia globulifera*, the genomic and transcriptomic resources used for the design were comprised of a published low-coverage draft genome from Africa (Olsson et al. 2017), an unpublished draft genome from French Guiana [Scotti et al., in prep], an unpublished transcriptome from 20 juveniles from French Guiana [Tysklind et al., in prep], and reduced-representation genomic sequence reads of individuals from French Guiana [Torroba-Balmori et al., unpublished]. We aligned genomic reads on the two genome drafts with `bwa` (Li and Durbin 2009). We kept scaffolds from the two genome drafts with a length superior to 1 kbp and at least one matching alignment with a read with a single match on the genome, and merged the two filtered genome drafts with `quickmerge` (Chakraborty et al. 2016). We aligned transcripts on the new filtered genome draft with `BLAT` (Kent 2002) and selected 533 scaffolds without transcript-match, *i.e.* anonymous scaffolds. We masked repetitive regions with `RepeatMasker` (Smit et al. 2015) and selected 533 1-kbp anonymous loci within the 533 previous scaffolds.

Similarly, we filtered transcripts from the 20 juveniles of *Symphonia globulifera* from French Guiana [Tysklind et al., in prep] based on SNP quality, type and frequency. We further detected open reading frames (ORFs) using `transdecoder` (Haas et al. 2013), and selected transcripts with non-overlapping ORFs including a start codon. We kept ORFs with an alignment on scaffolds from the aforementioned genome draft for *Symphonia* using `BLAT` (Kent 2002), and masked repetitive regions with `RepeatMasker` (Smit et al. 2015). We selected 1,150 genic loci of 500-bp to 1-kbp, from 100 bp before the start to a maximum of 900 bp after the end of the ORFs, resulting in 1-Mbp genomic loci that included a coding region.

Method S2: Design of the probes set for *Eschweilera*.

For *Eschweilera*, the genomic and transcriptomic resources used for the design were comprised of transcriptomes from *Eschweilera sagotiana* and *Eschweilera coriacea* (Vargas et al. 2019), and unpublished reduced representation genomic reads (M. Heuertz pers. com.). We mapped reciprocally *E. coriacea* and *E. sagotiana* transcriptomes using `BLAT` (Kent 2002), and in reciprocal best matches, we kept a single transcript to avoid paralogs and have robust targets among species. We further detected open reading frames (ORFs) using `transdecoder` (Haas et al. 2013), and selected transcripts with non-overlapping ORFs including a start codon. We selected 1,530 transcriptomic loci of 500-bp to 1-kbp, from 100 bp before the start to a maximum of 900 bp after the end of the ORFs, resulting in 0.83-Mbp of transcriptomic loci. To build anonymous targets, we built a *de novo* assembly of ddRAD-seq genomic data using `ipyrad` (Eaton and Overcast 2020), mapped consensus sequences on transcripts using `BLAT` (Kent 2002), and kept consensus sequences with no match on transcripts. We masked repetitive regions with `RepeatMasker` (Smit et al. 2015) and selected 2.2k anonymous loci resulting in a length 0.52-Mbp.

Model S1: Stan code for the bayesian inference of the animal model.

```
data {
  int<lower=0>  N ; // # of individuals
  int<lower=0>  P ; // # of populations
  real y[N] ; // phenotype
  int<lower=1, upper=P> population[N] ; // populations
  cov_matrix[N] K ; // kinship covariance matrix
}
transformed data{
  matrix[N, N] A = cholesky_decompose(K) ; // cholesky-decomposed kinship
  real Vy = variance(log(y)) ;
}
parameters {
  vector<lower=0>[P] mu ; // intercept
  vector[N] epsilon ; // genotypic noise
  real<lower=0, upper=sqrt(Vy)> sigma ; // genetic variance
}
transformed parameters {
  real<lower=0> Vp = variance(log(mu[population])) ; // population variance
  real Vr = square(sigma) ;
  real Vg = Vy - Vp - Vr ;
  vector[N] alog = sqrt(Vg)*A*epsilon ;
}
model {
  y ~ lognormal(log(mu[population]) + alog, sigma) ;
  epsilon ~ std_normal() ;
  mu ~ lognormal(0, 1) ;
  sigma ~ normal(0, 1) ;
}
```

Table 10: Confusion matrix (percentage) between genetic cluster and botanical identification for *Eschweilera* clade *Parvifolia*.

Species	E. coriacea cluster	E. decolorans cluster	E. sagotiana cluster
E. coriacea	65	8	13
E. decolorans	15	77	7
E. sagotiana	20	16	80

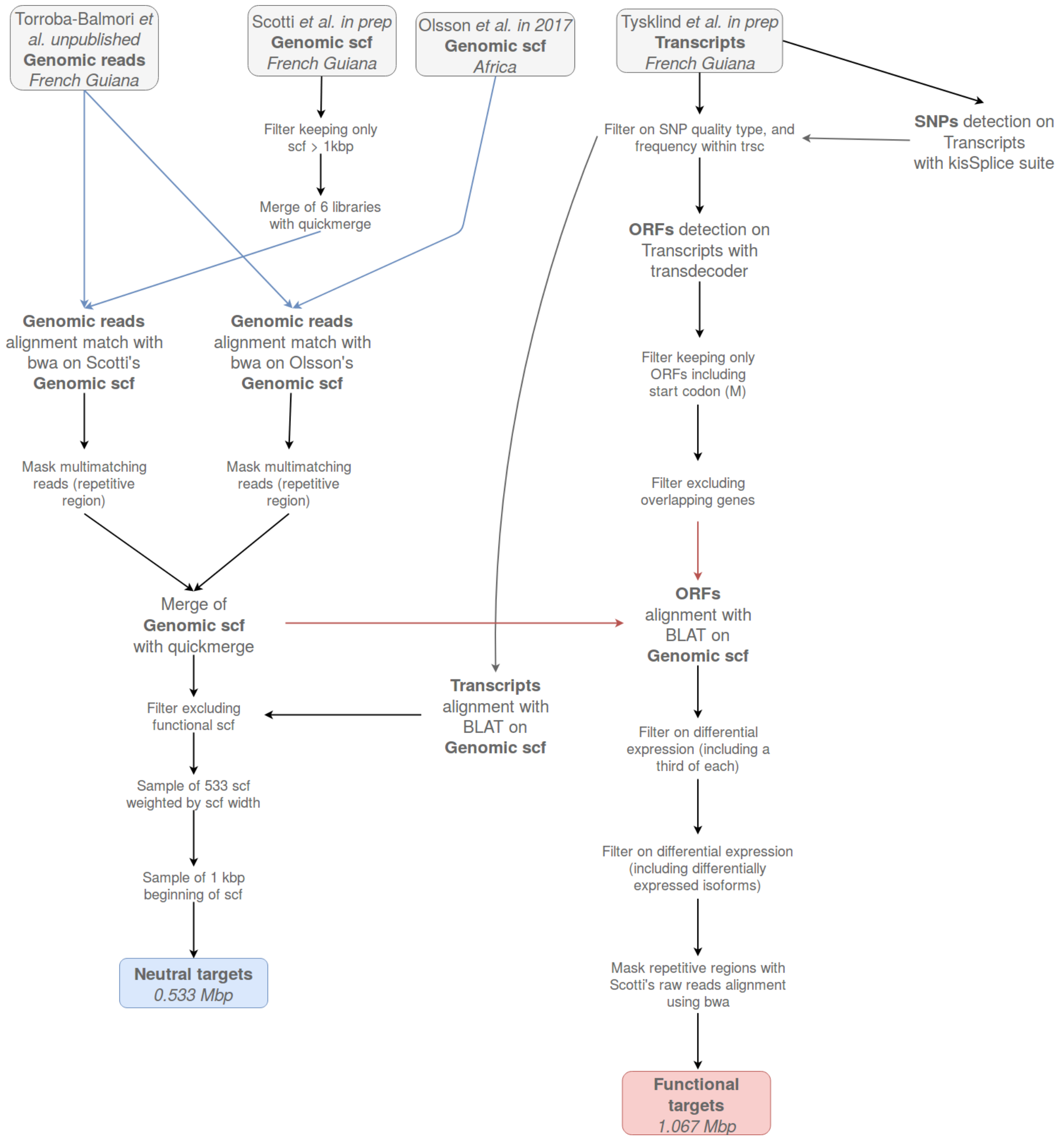

Figure 36: Scheme of target selection for the capture experiment of *Symphonia globulifera* as described in the manuscript.

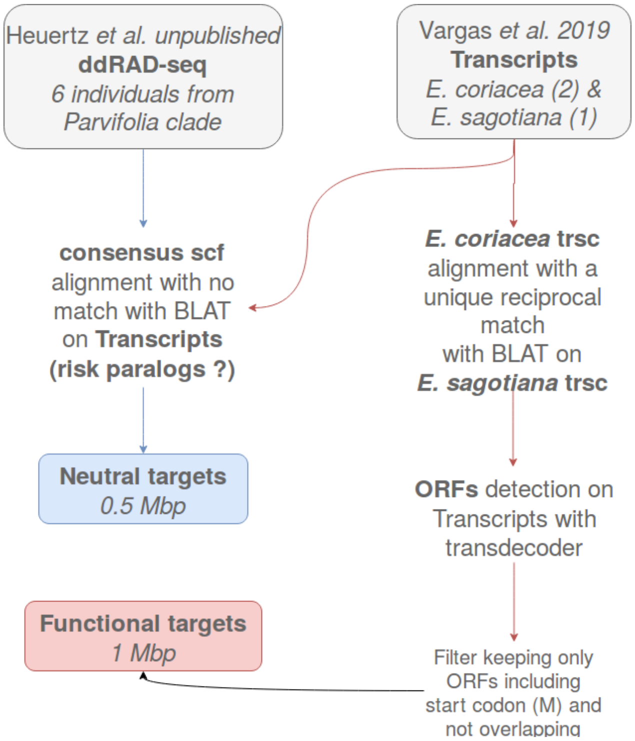

Figure 37: Scheme of target selection for the capture experiment of *Eschweilera* clade *Parvifolia* as described in the manuscript.

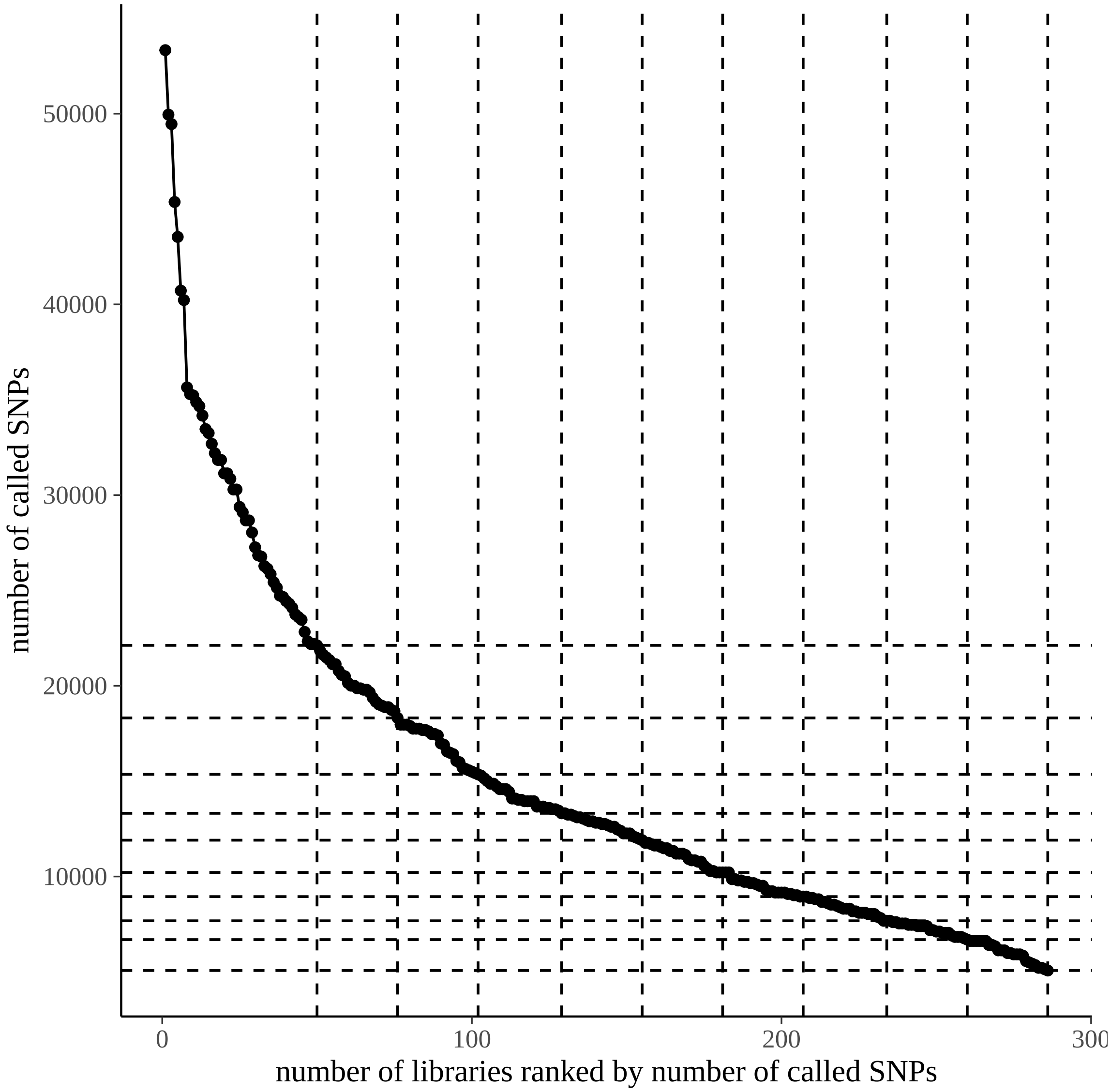

Figure 38: SNP abundance per library rank for raw data of *Eschweilera* clade *Parvifolia*. Dashed lines represent tested filters.

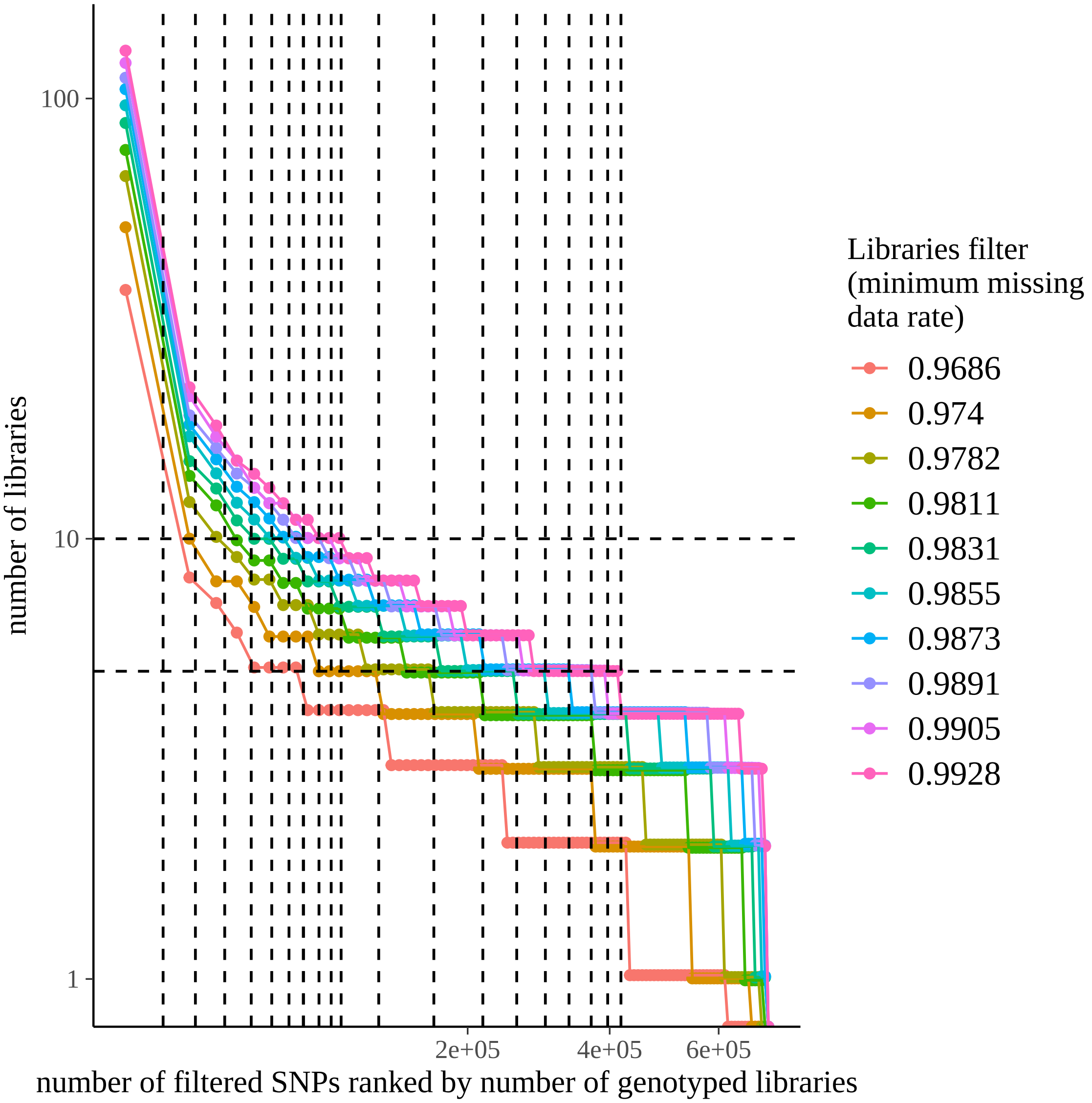

Figure 39: Library abundance per SNP rank for library-filtered data of *Eschweilera* clade *Parvifolia*. Dashed lines represent tested filters.

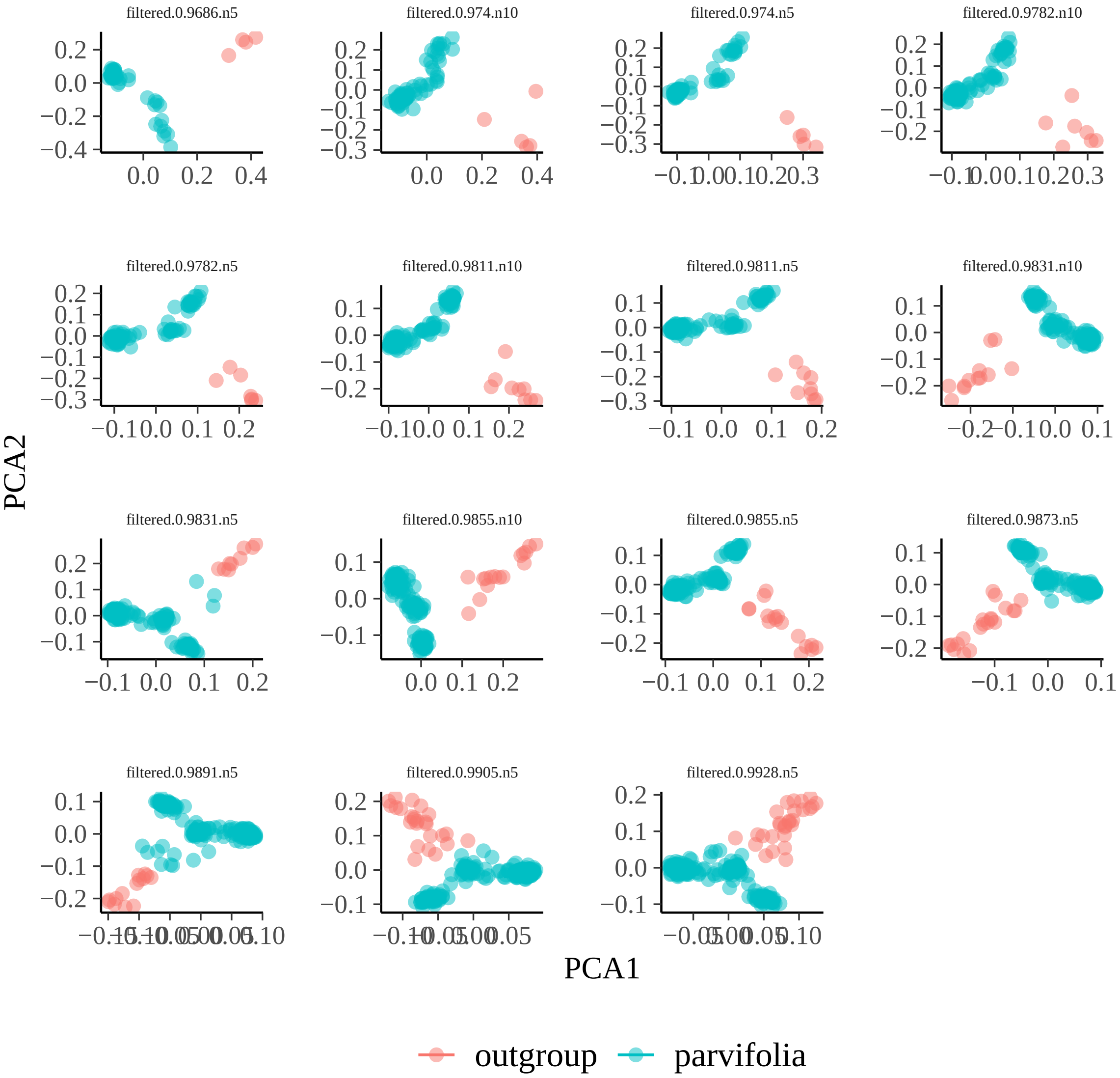

Figure 40: Outgroup detection with *Eschweilera* individual clustering in the genomic principal component analysis (gPCA) in two groups using K-means for every filter.

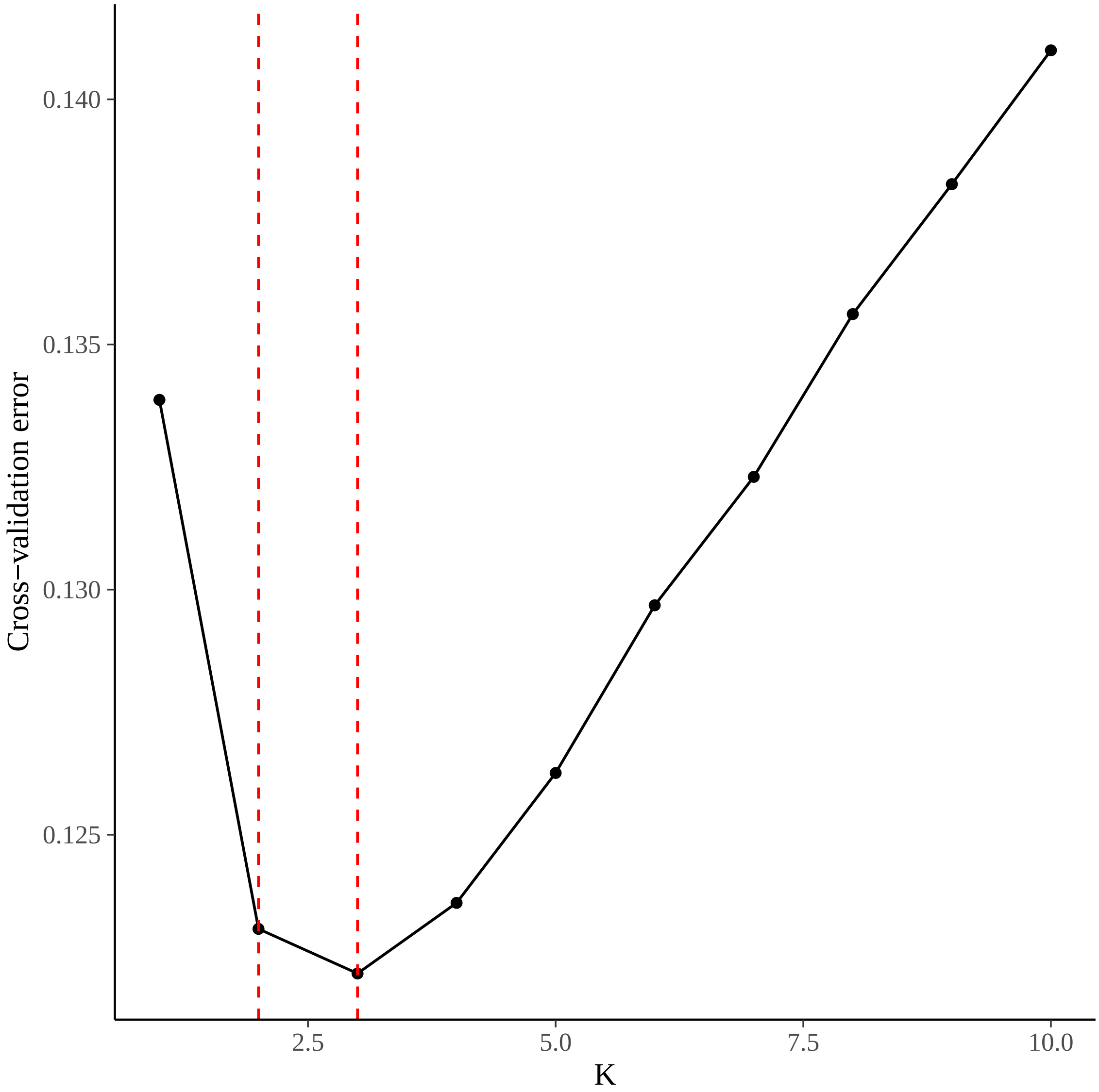

Figure 41: Cross-validation for the clustering of *Symphonia* individuals using admixture. Y axis indicates cross-validation mean error, suggesting that K = 2 or K = 3 gene pools represent the best solution for genetic structure in *Symphonia* in Paracou.

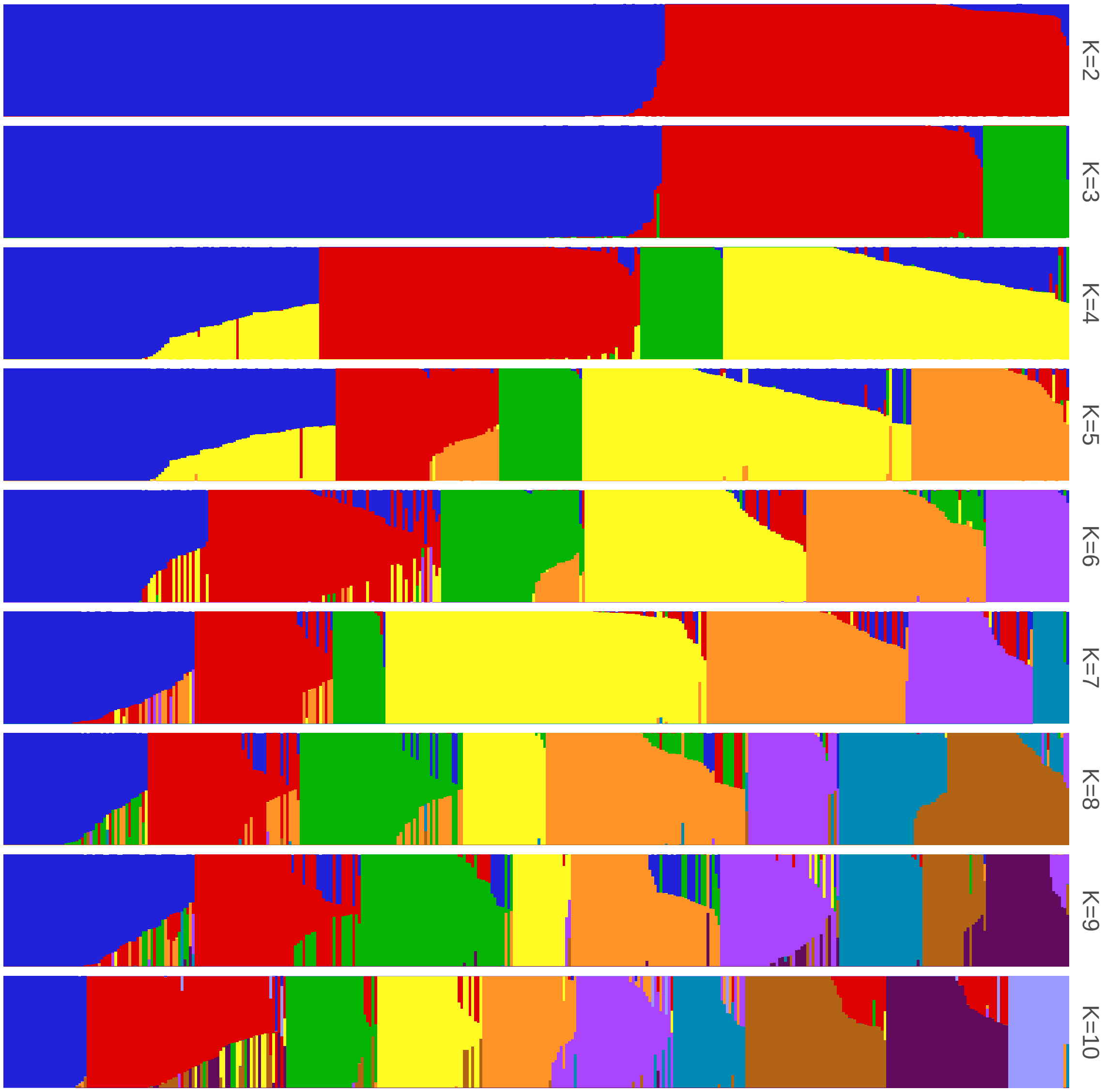

Figure 42: Population structure of *Symphonia* individuals from K=2 to K=10 using admixture.

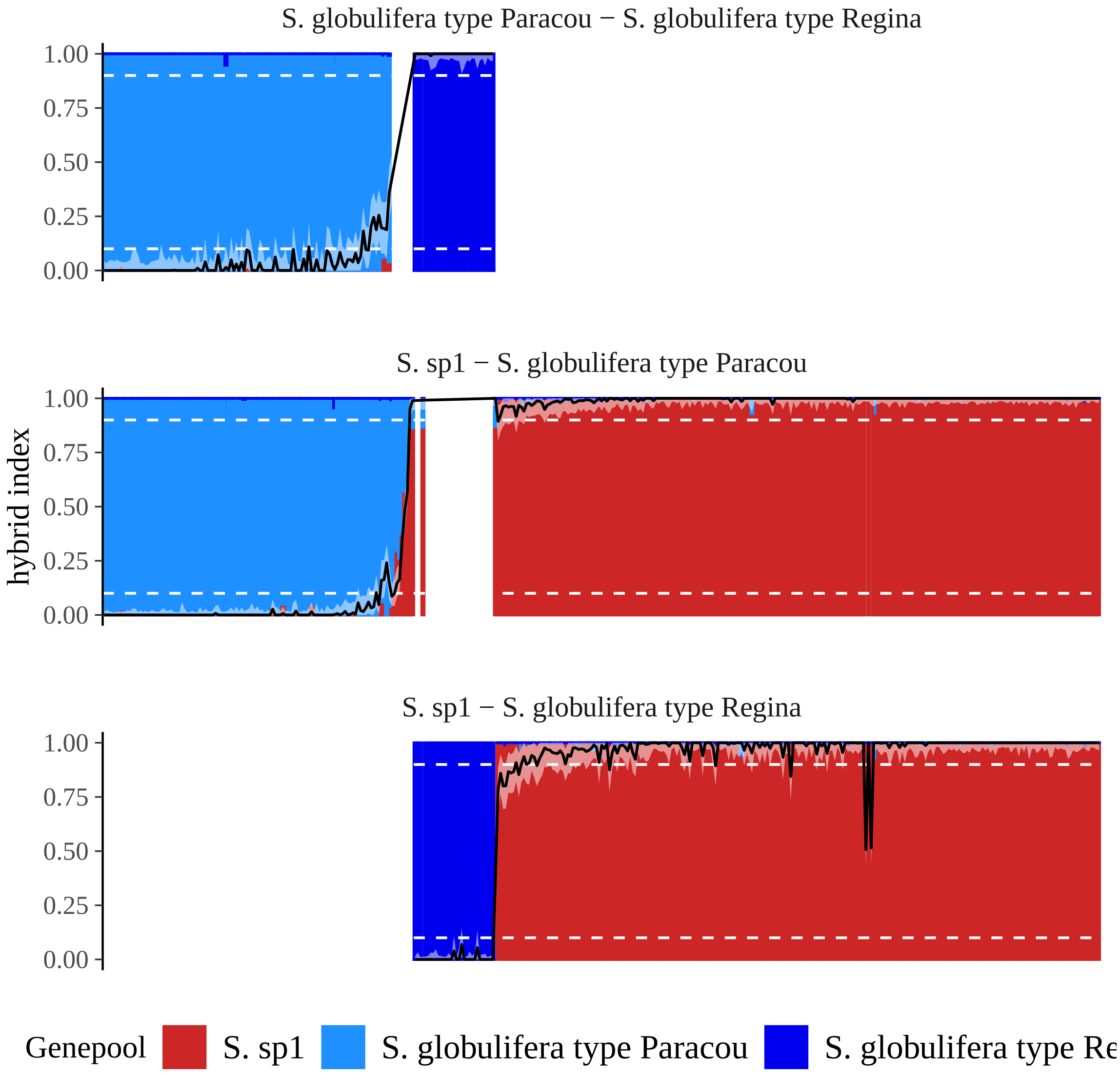

Figure 43: Genotypinc constitution of *Symphonia* using hybrid index. Admixture coefficients (black line) are given with 90% confidence interval (light shade). Admixture coefficients of 10 and 90% are indicated by white stippled lines.

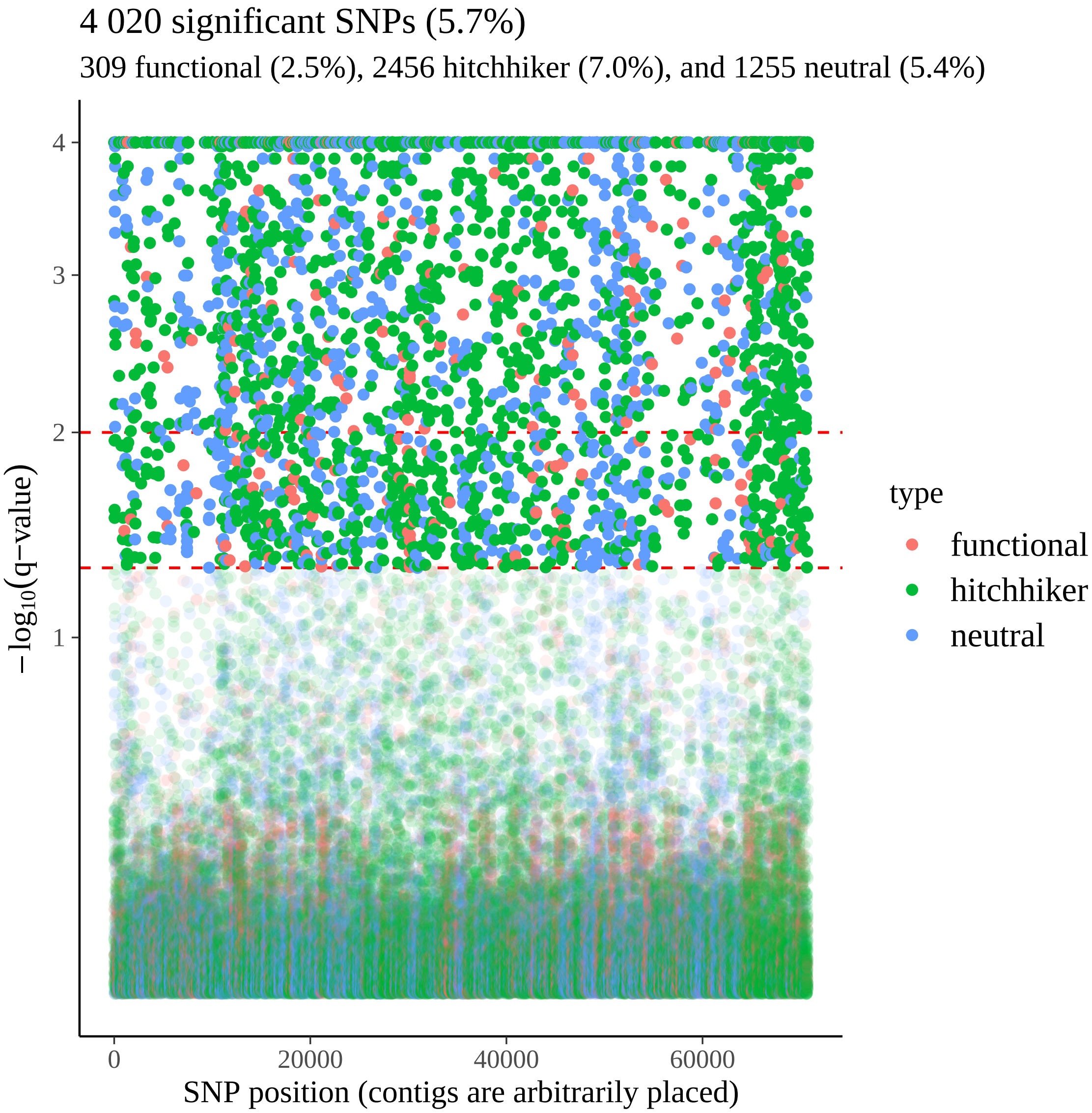

Figure 44: High-differentiation outlier SNPs for *Symphonia* individuals detected with bayescan. We used the genome-transcriptome alignments built for the design of probes sets (Method S1) to classify called SNPs into (i) anonymous SNPs (on scaffolds matching no transcripts), (ii) putatively-hitchhiker SNPs (close to a transcript or within an intron), and (iii) genic SNPs (within an exon).

APPENDIX 5: CHAPTER 4 SUPPLEMENTARY MATERIALS

Article title: **Forest gap dynamics: an underexplored factor that drives divergent adaptive growth strategies within tropical tree species**

Authors: Sylvain Schmitt, Niklas Tysklind, Myriam Heuertz, Bruno Hérault

The following Supporting Information is available for this article:

SI Materials and Methods.

SI Materials and Methods.

Part of the analyses are common with and described in Schmitt et al. (in prep).

Study site

The study was conducted in the Paracou field station, in the coastal forests of French Guiana, South America. The site is characterized by an average of 3,041 mm annual rainfall and a mean air temperature of 25.71 °C (Aguilos et al. 2018). Old tropical forest with an exceptional richness (i.e. over 750 woody species) grows across the succession of small hills of this area, which rise to 10–40 m a.s.l. (Gourlet-Fleury et al. 2004). The site comprises 16 permanent plots (fifteen 6.25 ha plus one 25 ha) which have been censused (DBH>10) every 1-2 years for more than 35 years. Nine of the plots were logged and subjected to human-induced disturbance in 1986 (details on the experiment in Hérault and Piponiot 2018).

Plant material

Four hundred and two individuals of *Symphonia globulifera* (Clusiaceae) were sampled in 2017 during the dry season (from September to December) in Paracou. *Symphonia globulifera* L.f (Clusiaceae) was previously recognized as composed of two morphotypes in French Guiana (Sabatier et al. 1997, Molino and Sabatier 2001, Baraloto et al. 2007). *S. globulifera sensu stricto* and *Symphonia sp.1* occur in sympatry but in differentiated habitats, with *S. globulifera* preferentially growing in valley bottoms with an acquisitive functional strategy and *S. sp1* preferentially exploiting a variety of drier habitats with a conservative functional strategy (Allié et al. 2015, Schmitt et al., in prep; Schmitt et al. 2020). *Symphonia* have been highlighted as a species complex with low (phylo-)genetic species resolution and high levels of plastid DNA sharing among sister species (Baraloto et al. 2012a, Gonzalez et al. 2009, Torroba-Balmori et al. 2017, Caron et al. 2019). In addition, outgroups for genetic analysis in *Symphonia* were comprised of 13 individuals of *Symphonia globulifera* from Africa (Sao Tome, Gabon, Cameroun, Congo, Benin, Liberia, Ivory Coast, and Ghana), seven *Symphonia globulifera* from South America (Brazil, Costa Rica and Panama), two *Symphonia nectarifera* Jum. & H. Perrier from Madagascar, two *Symphonia urophylla* (Decne. ex Planch. & Triana) Benth. & Hook.f. ex Vesque from Madagascar, five *Pentadesma butyracea* Sabine from Benin and Cameroon and one *Pentadesma grandifolia* Baker f. from Cameroon. Leaves were collected from the 432 individuals (402 + 30 outgroups) and dessicated using silica gel.

Sequence capture

Design of probes set

The genomic and transcriptomic resources used for the design were comprised of a published low-coverage draft genome from Africa (Olsson et al. 2017), an unpublished draft genome from French Guiana [Scotti et al., in prep], an unpublished transcriptome from 20 juveniles from French Guiana [Tysklind et al., in prep], and reduced-representation genomic sequence reads of individuals from French Guiana [Torroba-Balmori et al., unpublished]. We aligned genomic reads on the two genome drafts with `bwa` (Li and Durbin 2009). We kept scaffolds from the two genome drafts with a length superior to 1 kbp and at least one matching alignment with a read with a single match on the genome, and merged the two filtered genome drafts with `quickmerge` (Chakraborty et al. 2016). We aligned transcripts on the new filtered genome draft with `BLAT` (Kent 2002) and selected 533 scaffolds without transcript-match, *i.e.* anonymous scaffolds. We masked repetitive regions with `RepeatMasker` (Smit et al. 2015) and selected 533 1-kbp anonymous loci within the 533 previous scaffolds.

Similarly, we filtered transcripts from the 20 juveniles of *Symphonia globulifera* from French Guiana [Tysklind et al., in prep] based on SNP quality, type and frequency. We further detected open reading frames (ORFs) using `transdecoder` (Haas et al. 2013), and selected transcripts with non-overlapping ORFs including a start codon. We kept ORFs with an alignment on scaffolds from the aforementioned genome draft for *Symphonia* using `BLAT` (Kent 2002), and masked repetitive regions with `RepeatMasker` (Smit et al. 2015). We selected 1,150 genic loci of 500-bp to 1-kbp, from 100 bp before the start to a maximum of 900 bp after the end of the ORFs, resulting in 1-Mbp genomic loci that included a coding region.

Genomic libraries and sequence capture

Genomic DNA was extracted from 5 mg of dried leaf tissue with a CTAB protocol (Doyle and Doyle 1987). DNA extracts were digested with ‘Ultra II FS Enzyme Mix’ (new England Biolabs Inc, MA, USA) for a target size of 150 bp, and libraries built with the ‘NEBNext Ultra II FS DNA Library Prep kit for Illumina’(New England Biolabs Inc, MA, USA). We amplified and tagged libraries using 5 μL of adaptor-ligated DNA, 8.3 μL of ‘NEBNext Ultra II Q5 Master Mix’ (new England Biolabs Inc, MA, USA), 2x 1.6 μL of Index Primer i5 and i7 from ‘NEBNext Multiplex Oligos for Illumina (Dual Index Primers Set 1 and Set 2)’ (new England Biolabs Inc, MA, USA). Initial denaturation (98°C for 30 s) was followed by 8 cycles (98°C for 10 s and 65°C for 1 min 30 s) and a final extension (65°C for 5 min). We pooled libraries in four equimolar multiplexes for each genus. We obtained a custom made set of 20,000 80-mer probes for each genus using myBaits Custom 1-20K (Arbor Biosciences, MI, USA) and conducted the capture experiments using the corresponding myBaits V4 protocol with a hybridization time of 80 hours. We pooled the four multiplexes and sequenced them in two lanes of an Illumina HiSeq 4000 instrument obtaining 2x150bp pair-end reads for each genus.

SNP calling and filtering

We assessed the quality off raw reads using `multiqc` (Ewels et al. 2016) and trimmed them with `trimmomatic` (Bolger et al. 2014). We kept only pair-end reads without adaptors and a phred score above 15 in a sliding window of 4. Seventy percent of trimmed reads mapped off-targets using `bwa` (Li and Durbin 2009). We thus mapped trimmed reads on the hybrid reference built for the sequence capture experiment using `bwa` (Li and Durbin 2009), `picard` (Broad Institute 2018), `samtools` (Li et al. 2009) and `bedtools` (Quinlan and Hall 2010). We called variants for each individual using `HaplotypeCaller`, aggregated variants using `GenomicsDBImport` and jointly-genotyped individuals using `GenotypeGVCFs` all in `GATK4` software (Auwera et al. 2013). We filtered biallelic SNPs with a quality above 30, a quality by depth above 2, a Fisher strand bias below 60 and strand odds ratio above 3 using `GATK4` (Auwera et al. 2013). Finally, we filtered individuals and SNPs for missing data with a maximum of 95% and 15% of missing data per individual and SNP, respectively, using `plink2` (Chen et al. 2019). We obtained 454,262 biallelic SNPs over 385 individuals without outgroups, that we used for population genetic analyses. Since low-frequency alleles and linkage disequilibrium will bias the number of fixed loci and increase the number of false-positives in genomic scans for outliers (Foll and Gaggiotti 2008), we built a second dataset for quantitative genomics and genomic scans, filtering variants with a minor allele frequency above 5% (18 individuals) and with linkage disequilibrium $r^2 < 0.99$. We further removed admixed individuals (see population genetic analyses for criteria) and retained 70,737 biallelic SNPs over 372 individuals.

Analyses

Genetic species delimitation We investigated population genetic structure using `admixture` (Alexander and Lange 2011), using 10 repetitions of K genetic groups varying from 1 to 10 and assessed the number of gene pools with cross validation. We defined individuals with a membership to gene pools below 90% as admixed and the remaining individuals as genetically pure. We further investigated admixture with the `introgress` R package (Gompert and Alex Buerkle 2010), using genetically pure individuals as parental populations and all individuals as the hybrid population. We validated gene pool delimitation by comparison with botanical identifications using a confusion matrix, and we conducted a second blind-identification of every collected individual in November 2019.

Neighbour crowding effect on neutral and adaptive genetic variation We did environmental association analyses (Rellstab et al. 2015) in each complex using general linear mixed models developed for genome wide association studies (GWAS). We used mean neighbourhood crowding index (NCI; Uriarte et al. 2004a) over the last 30 years, an indirect measurement of access to light and forest gap dynamics, as the response variable and genetic structure (gene pools representing species) and relatedness (kinship matrix) as explanatory variables, as it is common practice (Rellstab et al. 2015). This analysis assumed that the neighbour crowding conditions where individuals have grown above 10-cm DBH are strongly correlated to the individual heritable phenotypes (e.g. Eckert et al. 2010). The mean neighborhood crowding index NCI_i from tree individual i was calculated as follow:

$$NCI_i = \overline{\sum_{j|\delta_{i,j}<20m} DBH_{j,t}^2.e^{-\frac{1}{4}\delta_{i,j}}}$$

with $DBH_{j,t}$ the diameter of the neighbouring tree j in year t and $\delta_{i,j}$ its distance to the individual tree i. NCI_i is computed for all neighbours at a distance $\delta_{i,j}$ inferior to the maximum neighbouring distance of 20 meters. The power of neighbours $DBH_{j,t}$ effect was set to 2 to represent a surface. The decrease of neighbours diameter effect with distance was set to -0.25 to represent trees at 20 meters of the focal trees having 1% of the effect of the same tree at 0 meters. NCI_i is computed as the mean of yearly $NCI_{i,t}$ over the last 30 years denoted by the overline.

We used genetic species and individual kinship in an animal model (Wilson et al. 2010) to estimate genetic variance associated with neighbour crowding index. We used a lognormal likelihood given that distributions of environmental variables were positive and skewed. We inferred individual kinship using KING (Manichaikul et al. 2010), as the method is robust to population structure. We set negative kinship values to null as they were confounding with population structure, and we further ensured that the matrix was positive-definite using the `nearPD` function from the R package `Matrix`. The environment $y_{s,i}$ where individual i in species s grows was inferred with a lognormal distribution with the following formula:

$$y_{s,i} \sim logN(log(\mu_s.a_i), \sigma_1^2)$$
$$a_i \sim MVlogN_N(log(1), \sigma_2^2.K)$$

where μ_s is the mean environment of species s, a_i is the breeding value of the individual i and σ_1^2 is the shape parameter of the lognormal. Individual breeding values a_i are defined following a multivariate lognormal law $\mathcal{MV}\updownarrow\wr\}\mathcal{N}$ of co-shape matrix defined as the product of the kinship matrix K with estimated individual genotypic variation σ_2^2. To estimate variances on a normal scale, we log-transformed species fixed effect, genetic additive values, and we calculated conditional and marginal R^2 (Nakagawa and Schielzeth 2013). A Bayesian method was used to infer parameters using `stan` language [Carpenter et al. (2017) and `rstan` package (Stan Development Team 2018) in the R environment (R Core Team 2020) using the No-U-Turn Sampler alogirthm (NUTS, Hoffman and Gelman 2014), which performs better for estimating genetic parameters and breeding values (Nishio and Arakawa 2019).

Neutral and adaptive genetic variation effect on individual growth

We investigated effects of ecological and evolutionary processes on individual growth, using genetic species and kinship. The individual growth of individual i in population p between individual recruitment y_0 and 2017, correspond to the difference of DBH between the two years, and is defined with a hierarchical model in a lognormal distribution as follow:

$$DBH_{y=2017,p,i} - DBH_{y=y0,p,i} \sim logN(log[\sum_{y=y0}^{y=2017} AGR(DBH_{y,p,i})], \sigma_1^2)$$

where the difference of DBH $DBH_{y=2017,p,i} - DBH_{y=y_0,p,i}$ is defined with a lognormal distribution located on the logarithm of the sum of annual growth rates AGR during the period $y_0 - 2017$ and of shape σ_1. The annual growth rates AGR for individual i in population p at year y with a diameter of $DBH_{y,p,i}$ is defined following a Gompertz model (Gompertz 1825) already identified as the best model for growth-trajectories in Paracou (Hérault et al. 2011):

$$AGR(DBH_{y,p,i}) = Gmax_i.exp(-\frac{1}{2}[\frac{log(\frac{DBH_{y,p,i}}{Doptp})}{Ksp}]^2)$$

where $Gmax_i$ is the maximum growth potential (maximal AGR during individual life) for individual i, $Dopt_p$ is the population optimal diameter at which the individual reach its maximum growth potential, and Ks_p is the population kurtosis defining the width of the bell-shaped growth-trajectory (see figure 1 in Hérault et al. 2011). To ease model inference population optimal diameter $Dopt_p$ and kurtosis Ks_p were defined as random population effect centered on a global $Dopt$ and Ks with corresponding variances $\sigma^2_{P,Dopt}$ and $\sigma^2_{P,Ks}$. Individual i maximum growth potential $Gmax_i$ was defined in a nested Animal model with a lognormal distribution:

$$Gmax_i \sim logN(log(Gmax_p.a_i), \sigma_{R,Gmax})$$
$$a_i \sim MVlogN(log(1), \sigma_{G,Gmax}.K)$$

where $Gmax_p$ is the mean $Gmax$ of population p, a_i is the breeding value of individual i, and $\sigma_{R,Gmax}$ is the shape of the lognormal distribution. Individual breeding values a_i are defined following a multivariate lognormal law $MVlogN$ with a co-shape matrix defined as the product of the kinship matrix K and the genotypic variation $\sigma_{G,Gmax}$. To estimate variances on a normal-scale, we log-transformed population fixed effect, genetic additive values, and calculated conditional and marginal R^2 (Nakagawa and Schielzeth 2013). We used Bayesian inference with No-U-Turn Sampler (NUTS, Hoffman and Gelman 2014) using `stan` language (Carpenter et al. 2017).

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