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L'évolution des biomes chez la sous-famille
des Cercidoideae (Fabaceae/Leguminosae)

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Ce mémoire intitulé

L'évolution des biomes chez la sous-famille
des Cercidoideae (Fabaceae/Leguminosae)

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Résumé

Certaines lignées de plantes tendent à rester dans le même biome au cours du temps (conservatisme de biome), tandis que d'autres semblent s'adapter plus facilement à de nouveaux biomes (changements de biome). Les ~396 espèces (14 genres) de la sous-famille des Cercidoideae se retrouvent dans plusieurs biomes à travers le monde, en particulier dans les régions tropicales de l'Amérique du Sud, de l'Asie et de l'Afrique. Ces espèces diffèrent aussi au niveau de leur port, pouvant être des arbres, arbustes, lianes ou herbacées. Après avoir établi une liste révisée d'espèces de la sous-famille, incluant tous les synonymes connus et leurs noms acceptés, des données d'occurrence ont été téléchargées depuis le Global Biodiversity Information Facility (GBIF) et d'autres bases de données d'herbiers. Après avoir nettoyé les données d'occurrences, des cartes de répartition des espèces ont été produites. Ces cartes ont été comparées avec des cartes publiées de biomes tropicaux afin d'attribuer chaque espèce à un biome et à un continent. Les biomes de forêt tropicale humide (179 espèces), de savane (117 espèces), succulent (65 espèces) et tempéré (7 espèces et sous-espèces) ont été identifiés comme importants pour décrire la répartition globale des Cercidoideae, avec plusieurs espèces se trouvant dans plus d'un biome. Après avoir reconstruit une phylogénie calibrée dans le temps, nous avons effectué des estimations de caractères ancestraux afin d'évaluer le nombre et la direction des changements de biome, de port et de continent. Les analyses suggèrent que plusieurs changements de biomes ont eu lieu dans l'histoire évolutive de la sous-famille, les changements du biome succulent à la forêt tropicale humide et de la forêt tropicale humide à la savane étant les plus communs, tandis qu'il n'y avait aucun changement depuis la savane. Sept changements de port ont eu lieu, dont trois qui sont associés à des changements de biome (un est caractéristique du genre *Tylosema* (Schweinf.) Torre & Hillc., un du genre *Lysiphyllum* (Benth.) de Wit et un de l'espèce *Phanera retusa* Benth.). Les analyses montrent aussi que les changements de biomes tendent à avoir lieu au sein d'un même continent et que les dispersions vers de nouveaux continents tendent à se produire au sein d'un même biome. Par contraste avec d'autres sous-familles de légumineuses plus conservées au niveau des biomes, les changements fréquents observés au sein des Cercidoideae suggèrent une capacité d'adaptation à des environnements significativement différents à travers le temps.

Mots clés : biogéographie; changements de biomes; conservatisme phylogénétique de biomes;

Fabaceae; légumineuses; biomes tropicaux; estimation de caractères ancestraux

Abstract

Some plant lineages remain within the same biome over time (biome conservatism), whereas others seem to adapt more easily to new biomes (biome shifts). The ~396 species (14 genera) in subfamily Cercidoideae of Leguminosae (Fabaceae) are found in many biomes around the world, particularly in the tropical regions of South America, Asia and Africa, and display a variety of habits/growth forms (small trees, shrubs, lianas and herbs). After establishing an updated expert-verified species list, including all known synonyms and their accepted names, we downloaded and cleaned occurrence records from the Global Biodiversity Information Facility (GBIF) and other herbarium databases to produce species distribution maps. These maps were compared with existing biome maps to attribute species to biomes and continents. Rainforest (179 species), savanna (117 species), succulent (65 species) and temperate (7 species and subspecies) biomes were found to be important in describing the global distribution of Cercidoideae, with many species occurring in multiple biomes. After reconstructing a time-calibrated phylogeny, we performed ancestral state reconstructions to evaluate the number and direction of shifts in biome, habit and continents. Analyses suggest multiple biome shifts throughout the phylogeny, shifts from succulent to rainforest and from rainforest to savanna being the most common, while no shifts were observed from the savanna. Seven shifts in habit occurred, of which at least three were associated with biome shifts (one subtends the genus *Tylosema* (Schweinf.) Torre & Hillc., one subtends the genus *Lysiphyllum* (Benth.) de Wit and one occurs in *Phanera retusa* Benth.). Analyses also show that biome shifts tend to occur within the same continent and that dispersals to new continents tend to occur within the same biome. In contrast to other more biome-conserved legume subfamilies, the frequent shifts observed in Cercidoideae suggest ability for adaptation to significantly different environments through time.

Keywords: biogeography; biome shifts; phylogenetic biome conservatism; Fabaceae; legumes; tropical biomes; ancestral character reconstruction

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Liste de sigles et abréviations

LPWG : Legume Phylogeny Working Group

WCVP : World Checklist of Vascular Plants

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Chapitre 1: Introduction générale

1.1 Mise en contexte et constitution du mémoire

Dans son chapitre sur la distribution géographique dans l'Origine des espèces, Darwin écrit que "le naturaliste voyageant du nord au sud, par exemple, ne manque jamais d'être frappé de la manière dont des groupes successifs d'êtres spécifiquement distincts, bien qu'en étroite relation les uns avec les autres, se remplacent mutuellement" (Darwin c1909). Bien que des études s'intéressent depuis longtemps à comprendre si les espèces proches parentes vivent aussi dans les mêmes milieux (Harper et al. 1961), d'expliquer pourquoi les organismes sont répartis comme ils le sont à travers les continents et comment ces patrons de répartition ont évolué à travers le temps demeurent des questions intrigantes. Des études plus récentes démontrent une tendance des espèces apparentées à être plus similaires en termes d'écologie qu'elles le sont à des espèces plus éloignées (Losos 2008; Burns and Strauss 2011), mais on constate aussi que certaines lignées de plantes semblent avoir changé d'habitat plus fréquemment que d'autres au cours de leur évolution (Ogburn and Edwards 2015; Cardillo et al. 2017). On peut se demander alors quels facteurs peuvent expliquer la capacité de ces lignées à s'établir plus facilement dans de nouveaux environnements. L'étude de l'histoire naturelle de ces lignées et de l'évolution de traits fonctionnels peut aider à expliquer ce type de changements.

L'objectif de ce projet est d'étudier les changements de biomes dans un groupe d'espèces de légumineuses, la sous-famille des Cercidoideae, se trouvant sur presque tous les continents et dans une variété de biomes distincts, en déterminant a) les biomes auxquelles appartiennent les plus de 300 espèces de Cercidoideae b) le nombre et les types de changements de biomes au cours de l'évolution de ce groupe et c) de considérer l'évolution d'un trait fonctionnel en particulier, le port des espèces (arborescent, arbustif ou lianescent), en lien avec les changements de biomes identifiés.

Ce chapitre a pour premier objectif d'introduire les concepts de biome, d'évolution de biome et de conservatismisme de biome. Ensuite nous présenterons le groupe d'étude, les Cercidoideae, et plus généralement le contexte évolutif des légumineuses. Finalement, nous présenterons les objectifs et hypothèses de cette étude.

1.2 Biomes: évolution et conservatisme

Dans un contexte de changements globaux, avec toutes leurs conséquences sur les écosystèmes et sur la biodiversité, il devient essentiel d'identifier les patrons de végétation à l'échelle mondiale et de comprendre les facteurs à l'origine de leur formation et de leur évolution. Les biomes sont alors un concept important, utile pour les études écologiques et biogéographiques puisqu'ils permettent de définir des communautés biotiques et de les caractériser par leur physionomie et aspects fonctionnels, plutôt qu'uniquement par leur composition en espèces. En particulier, la compréhension des biomes au niveau fonctionnel (phénologie et physiologie végétale) est nécessaire pour mieux modéliser les interactions entre les changements climatiques et le cycle global du carbone, puisque celui-ci aide à comprendre les variations spatio-temporelles dans la production primaire globale (Xia et al. 2015). De plus, des régions écologiques définies et délimitées permettent la mise en place de plans de conservation plus efficaces (Olson et al. 2001).

La façon de définir un biome évolue et varie avec les auteurs. Par exemple, des biomes peuvent être délimités uniquement sur la base du climat (Mucina 2019), peuvent être définis par la physionomie végétale (combinaisons de formes de croissance) (Mucina 2019), ou même sur la base du VPI ("vegetation productivity index"), du NDVI ("normalized difference vegetation index") et de la hauteur de la végétation, entre autres (Higgins et al. 2016). De façon générale et dans un contexte d'étude phytogéographique, on peut définir les biomes comme étant des unités géographiques occupées par des communautés végétales dont la structure, les caractéristiques physiologiques et les aspects fonctionnels sont similaires (Moncrieff et al. 2016; Mucina 2019; Ringelberg et al. 2020). Ces traits fonctionnels peuvent alors refléter l'adaptation de ces organismes aux conditions de leur biome. La délimitation des biomes prend généralement en compte les facteurs environnementaux et climatiques aussi (Mucina 2019).

Des études effectuées sur diverses lignées de plantes à répartitions globales indiquent une tendance des lignées de plantes à rester dans les mêmes biomes à travers le temps. Plusieurs études indiquent aussi que les espèces apparentées tendent à être plus similaires entre elles en termes d'écologie qu'elles le sont à des espèces plus éloignées (Crisp et al. 2009; Pyron et al. 2015). Cette tendance de conservatisme de biome chez les plantes a été démontrée, entre autres, dans le genre brésilien

Cryptanthus Otto & A. Dietr. (Bromeliaceae) (Cruz et al. 2017), dans le groupe pantropical *Caesalpinia* (Fabaceae) (Gagnon et al. 2019) et dans plusieurs autres clades tropicaux (Wiens and Donoghue 2004), dont des groupes néotropicaux d'eucalypts, de graminées et de légumineuses (Crisp et al. 2009). Cependant dans d'autres études, on observe que certaines lignées d'angiospermes auraient déjà subi plusieurs changements de biomes (ou de niches), notamment chez la famille des Montiaceae (Ogburn and Edwards 2015), des Proteaceae (Cardillo et al. 2017), des Anacardiaceae (Weeks et al. 2014) et chez le clade *Pterocarpus* des Fabaceae (Schley et al. 2022).

Plusieurs auteurs définissent le conservatisme de biome comme étant la capacité des espèces à conserver des traits écologiques et distributions ancestraux (Wiens and Graham 2005; Crisp et al. 2009). Les raisons pour lesquelles, dans un environnement changeant, certaines espèces vont migrer tandis que d'autres vont s'adapter au nouveau milieu demeurent incertaines, mais plusieurs hypothèses existent. Par exemple, il a été suggéré que la probabilité pour une lignée de changer de biome pourrait être fonction de l'âge des biomes et de l'exposition des lignées à de nouveaux environnements à travers le temps, ce qui implique que des changements de biomes pourraient être favorisés pour des biomes adjacents et/ou largement interconnectés (Edwards and Donoghue 2013; Donoghue and Edwards 2014). Des études suggèrent aussi que certains traits morphologiques préexistants chez des espèces peuvent faciliter leur établissement dans de nouveaux biomes (Edwards and Donoghue 2013; Donoghue and Edwards 2014). Par exemple, il existe plusieurs adaptations connues aux environnements soumis à des feux, comme l'écorce liégeuse épaisse et la capacité de repousser à partir de rhizomes (Pennington et al. 2009; Simon et al. 2009) et au gel, comme le port ligneux, les feuilles décidues et les vaisseaux conducteurs de petits diamètres (Zanne et al. 2014). Puisque certains biomes s'étendent sur plusieurs continents, il est à noter qu'il est possible qu'un groupe change de répartition ou de continent (dans une colonisation transocéanique, par exemple), sans changer de biome (Crisp et al. 2009). D'ailleurs, une théorie qu'il soit "plus facile de se déplacer que de s'adapter" est souvent citée dans le contexte du conservatisme de biome (Donoghue 2008; Edwards and Donoghue 2013; Donoghue and Edwards 2014; Pyron et al. 2015; Gagnon et al. 2019; Ringelberg et al. 2020). Le conservatisme de biome et le changement de biome jouent certainement un rôle majeur dans la distribution de la biodiversité à l'échelle globale et dans la composition en espèces des biomes (Crisp et al. 2009;

Donoghue and Edwards 2014), mais leur importance chez les lignées de plantes à fleur doit être évalué.

1.3 Évolution et biogéographie des légumineuses

La famille des Fabaceae ou Leguminosae présente une répartition cosmopolite: on retrouve des espèces dans presque tous types d'écosystèmes terrestres, où elles peuvent avoir des morphologies très distincts, de grands arbres de forêts tropicales humides à de petites herbacées de prairies tempérées, en passant par des arbustes de savanes tropicales et des lianes (Koenen et al. 2019). Les Fabaceae sont aussi la troisième plus grande famille de plantes à fleurs (angiospermes) en termes de nombre d'espèces, après les orchidées (Orchidaceae) et les asteracées (Compositae ou Asteraceae) et incluent un grand nombre d'espèces de grande importance en agriculture, telles que les haricots, le soja, l'arachide, les lentilles et le trèfle. On caractérise aussi la majorité des espèces de légumineuses par leur capacité de fixer l'azote (N) grâce à une symbiose avec des bactéries dans les nodules des racines (Sprent 1994).

De nombreuses études se sont déjà intéressées à la biogéographie des légumineuses (Davis et al. 2002; Lavin et al. 2004; Schrire et al. 2005; Gagnon et al. 2019; Ringelberg et al. 2020; Schley et al. 2022). En étudiant les patrons de répartition globale des groupes monophylétiques de légumineuses et en considérant les conditions écologiques telles que l'humidité (humide à sec), la température (tropical à tempéré) et les perturbations (ex., soumis ou non à des feux), Schrire et al. (2005) ont identifié et défini quatre principaux biomes importants pour cette famille: le biome succulent (« succulent biome »), le biome savane (« grass biome »), le biome tempéré et le biome forêt tropicale humide. Le biome succulent est défini comme étant un biome de forêt tropicale sèche, de fourré et bushland, semi-aride, non tolérant au feu, riche en plantes grasses et pauvre en graminées. Le biome des savanes est défini comme étant un biome de forêt tropicale sèche saisonnière, boisé et savane, tolérant au feu, pauvre en plantes grasses et riche en graminées. Le biome de la forêt tropicale humide est majoritairement restreint aux tropiques équatoriales et est caractérisé par un climat chaud et humide avec de fortes précipitations (absence de saison sèche). Le biome tempéré inclut des régions chaudes et froides des hémisphères Nord et Sud et est celui des quatre biomes qui couvre la plus grande surface. Tel que défini par Schrire et al. (2005), ce biome comprend à la fois des régions humides et des régions sèches, incluant des régions de

savanes tempérées (comme les prairies), mais qui sont tous des régions de hautes latitudes. D'autres biomes ont aussi été considérés comme étant importants pour les légumineuses, tel le Caatinga brésilien, le Cerrado brésilien, le Chaco en Amérique du Sud (tous inclus dans le biome succulent) (Pennington et al. 2009; Gagnon et al. 2019; Ringelberg et al. 2020; Cardoso et al. 2021) ainsi que les lomas péruviens et certains habitats côtiers comme les mangroves (Gagnon et al., 2019).

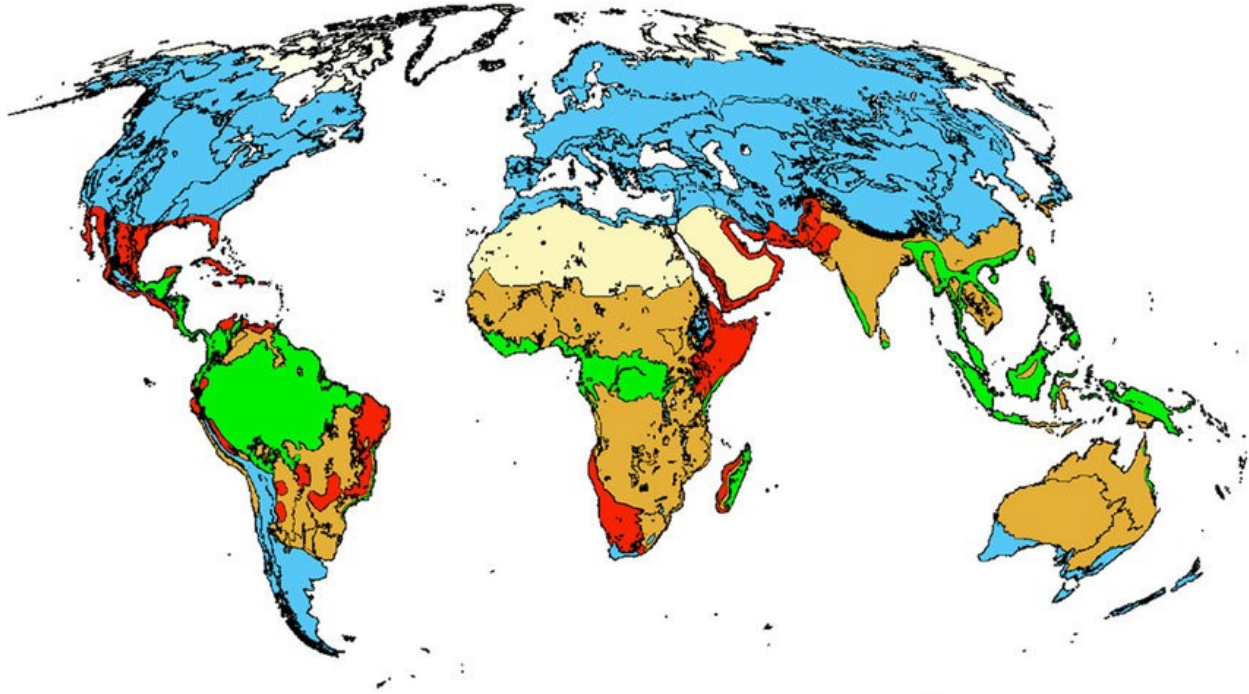


Fig. 1.1- Les quatre biomes définis par Schrire et al. (2005) décrivant la répartition des légumineuses dans le monde: le biome succulent (rouge), le biome savane (brun), le biome forêt tropicale humide (vert) et le biome tempéré (bleu).

L'origine des légumineuses date probablement du début du Tertiaire, autour de la mer de Téthys et est suivi peu après d'une rapide diversification à travers le monde (Lavin et al. 2004; Schrire et al. 2005). Bien qu'on ait pensé que certaines lignées des légumineuses auraient divergé plus tôt que d'autres, les analyses les plus récentes suggèrent que les six lignées majeures (i.e., les six sous-familles, LPWG 2017) auraient divergé de façon presque simultanée (ordre non significatif) (Koenen et al. 2020a, 2020b). Les analyses récentes montrent que le groupe-couronne ("crown node") des légumineuses date du Maastrichtien ou du début du Paléocène (Koenen et al. 2019). La fin du Miocène a été une période de diversification importante des plantes, incluant les

légumineuses, dû au refroidissement planétaire et à l'augmentation conséquente de la saisonnalité (Hughes et al. 2015).

1.4 La sous-famille des Cercidoideae (Fabaceae)

Au sein de la famille des Fabaceae, six clades (correspondant tous au rang de sous-famille) sont reconnus, dont la sous-famille des Cercidoideae (LPWG, 2017). Cette dernière comprend 14 genres (*World Checklist of Vascular Plant*; Sinou et al. 2020) et environ 396 espèces (WCVP). Les 14 genres reconnus par le *World Checklist of Vascular Plants* sont les suivants: *Adenolobus* (Harv. ex Benth.) Torre & Hillc., *Barklya* F.Muell., *Bauhinia* Plum. ex L., *Brenierea* Humbert, *Cercis* L., *Cheniella* R.Clark & Mackinder, *Gigasiphon* Drake, *Griffonia* Baill., *Lysiphyllum* (Benth.) de Wit, *Phanera* Lour., *Piliostigma* Hochst., *Schnella* Raddi, *Tournaya* A.Schmitz et *Tylosema* (Schweinf.) Torre & Hillc. Les espèces de Cercidoideae sont caractérisées par des feuilles unifoliées ou bifoliées, des fleurs souvent papillonées et peuvent avoir un port arborescent, buissonnant ou lianescent, avec plusieurs espèces présentant des vrilles et/ou des épines (LPWG, 2017). Quelques autres traits qui distinguent les Cercidoideae des autres sous-familles des légumineuses sont leurs graines avec une hile apicale en forme de croissant, sans aile ou arille et leur pollen rarement en tétrades (LPWG, 2017).

La sous-famille des Cercidoideae a été considérée comme étant une des premières lignées de légumineuses à diverger (Lavin et al. 2004; Bruneau et al. 2008), mais l'étude la plus récente soutient plutôt une relation de groupe-frère entre les Cercidoideae et les Detarioideae, ce clade formant le groupe-frère du reste des légumineuses (Duparquetioideae, Dialioideae, Caesalpinioideae et Papilionoideae) (Koenen et al. 2020a), mais avec peu de support pour cette relation et des divergences très rapides entre les six sous-familles. Une duplication entière de génome caractérise l'ensemble des Cercidoideae, en excluant les espèces du genre *Cercis* (Cannon et al. 2015). Des études montrent une concentration d'événements de duplication entière de génome autour de l'extinction de masse du Crétacée-Permien et suggèrent que les lignées polyploïdes pourraient être avantagées par rapport aux lignées diploïdes par un plus grand potentiel de diversification (Koenen et al. 2019).

Les Cercidoideae (tout comme les Fabaceae en générale) présentent une répartition large, les plus de 300 espèces de Cercidoideae étant réparties à travers plusieurs biomes différents (Cannon et al. 2015) et présentant des ports distincts (arborescents, lianescents, arbustifs). Des corrélations à grande échelle ont été suggérées entre le climat et certains traits fonctionnels tels que la hauteur des plantes, la masse des graines, la densité du bois, la superficie des feuilles et les concentrations foliaires en phosphore et azote (Echeverría-Londoño et al. 2018), ainsi que les traits liés à la tolérance au gel chez les angiospermes (Zanne et al. 2014). Plusieurs études indiquent que le port des espèces a joué un rôle dans l'évolution de certaines lignées de plantes. Par exemple, une étude par Couvreur et al. (2015) sur la diversité spécifique et la diversification des palmiers dans les forêts tropicales suggère qu'un changement d'un port non grimpant vers un port grimpant aurait joué un rôle important dans la diversification des palmiers. Dans le groupe des Caesalpinia, Gagnon et al. (2019) ont montré que les changements de biomes sont peu fréquents mais liés à des changements de port. Le port grimpant a évolué plusieurs fois de façon indépendante à travers les angiospermes et se trouve dans plus de 130 familles (Gentry 1992), ce qui suggère que ce soit un trait d'importance écologique. Bien que des études récentes démontrent une corrélation entre le port, le biome et la distribution géographique au niveau continental dans certaines lignées de plantes (Couvreur et al. 2015; Gagnon et al. 2019), la dynamique évolutive entre ces trois facteurs demeure sous-étudiée. Puisque les clades de Cercidoideae présentent une variété de ports, dans une variété de biomes et sur tous les continents, l'étude de ces traits fonctionnels et de leur rôle dans la facilitation des transitions entre biomes contribue à la compréhension générale de l'adaptation des plantes aux changements environnementaux. L'étude de l'évolution des Cercidoideae et de ses biomes associés pourrait servir d'exemple, applicable à d'autres lignées et régions géographiques d'intérêt écologique.

1.5 Description du projet

Pour mieux comprendre la dynamique évolutive des espèces dans le temps et l'espace, et les facteurs historiques et écologiques qui régissent ces patrons de répartition, nous étudierons la sous-famille des Cercidoideae. Cela implique d'abord d'établir la répartition mondiale des espèces actuelles de Cercidoideae, afin de déterminer à quel(s) biome(s) appartient chaque espèce, puis d'établir une phylogénie de la sous-famille, calibrée dans le temps à l'aide de fossiles. Nous étudierons alors le changement de biome et le conservatisme de biome au sein de la sous-famille

des Cercidoideae par des méthodes d'estimation de biomes ancestraux. Nous tenterons d'évaluer la fréquence de ces deux phénomènes, au cours de l'évolution des lignées en tenant compte du port des espèces, afin de mieux comprendre les facteurs à l'origine de la répartition des Cercidoideae dans l'espace et le temps. En effet, les espèces de Cercidoideae étant largement distribuées dans le monde, l'étude de cette sous-famille implique l'analyse de patrons de végétation à grande échelle et prend en compte plusieurs biomes différents (Schrire et al. 2005). De plus, l'étude phylogénétique des biomes concernés peut permettre d'identifier des facteurs potentiels à l'origine des changements de biomes et de la capacité de certaines lignées à mieux s'adapter que d'autres et à dépasser les frontières de leurs biomes (Donoghue and Edwards 2014). En plus des biomes, nous tiendrons compte aussi des continents sur lesquels les espèces de Cercidoideae se trouvent. Puisque les biomes considérés sont répartis sur plusieurs continents et que les changements de biomes peuvent impliquer ou non des changements de continents, il est pertinent de mieux comprendre l'histoire biogéographique et d'identifier les continents ancestraux des Cercidoideae. En effet, la répartition des espèces à travers plusieurs continents implique probablement que des événements de dispersions de longues distances ont eu lieu au cours de l'évolution des Cercidoideae.

1.6 Objectifs du projet et hypothèses

Dans le cadre de cette étude, nous abordons trois grands objectifs qui visent à mieux comprendre la dynamique d'évolution des plantes dans l'espace et le temps.

Afin d'établir dans quels biomes et sur quels continents se trouvent les espèces de Cercidoideae, nous avons premièrement établi la répartition géographique globale de la sous-famille en réalisant des cartes d'occurrences d'espèces. En comparant ces cartes avec des cartes de biomes issues d'autres études, il a été possible de décrire la répartition des Cercidoideae en fonction des biomes considérés et d'attribuer chaque espèce à un ou plusieurs biomes. Ces attributions, basées sur des données d'occurrences provenant de spécimens d'herbiers digitalisés et vérifiés en consultant les descriptions d'habitat provenant de flores et autres monographies, constituent des données nécessaires pour faire les analyses d'estimation de biomes ancestraux. L'étude de ces données d'occurrences en lien avec les cartes de biomes permet aussi de contribuer à la description des

aires de répartition des espèces de Cercidoideae et les types d'habitats dans lesquels elles se trouvent.

Le deuxième objectif est d'étudier les changements de biomes et le conservatisme de biomes dans un contexte phylogénétique. Nous voulons savoir s'il y a eu changement de biomes ou conservatisme de biome à travers l'évolution des Cercidoideae. En établissant la fréquence des changements de biomes, il sera possible d'identifier des paires de biomes entre lesquelles les transitions sont plus fréquentes, ou au contraire, des biomes qui regroupent des lignées qui changent très peu de biomes (Donoghue and Edwards 2014), et nous tiendrons compte de la direction de ces changements.

Plusieurs auteurs proposent que la probabilité qu'une lignée change de biome soit plus élevée pour les lignées qui se trouvent dans des biomes adjacents ou largement connectés (Donoghue and Edwards 2014; Pyron et al. 2015). De plus, les biomes adjacents ont souvent des climats plus similaires. On peut donc penser que s'il y a des changements de biomes pour Cercidoideae, ils vont plus fréquemment avoir lieu entre 1) les biomes de forêt tropicale humide et savanes, qui partagent plusieurs frontières à la fois en Amérique du Sud, en Asie et en Afrique, et 2) entre les biomes succulent et savane, qui sont à proximité et souvent interconnectés en Afrique et en Amérique du Sud, et qui ont en plus des climats similaires. Les biomes succulent et forêt tropicale humide sont peu connectés en Afrique, mais partagent des frontières en Amérique Central. On suppose donc que ce type de changement sera moins fréquent mais s'il existe, il aura lieu seulement au niveau de ces régions de l'Amérique Central. D'autre part, bien que le biome tempéré soit très vaste, il est beaucoup moins connecté aux autres biomes (en particulier dans l'Hémisphère Nord). On peut donc penser que le biome tempéré va être très peu impliqué dans les changements de biomes.

Il est possible que certains traits fonctionnels, tels que le port des espèces aient facilité la transition entre biomes (Couvreur et al. 2015; Ogburn and Edwards 2015; Gagnon et al. 2019). Il est donc pertinent de prendre en compte le port des espèces de Cercidoideae (arborescent, lianescent ou arbustif) dans l'étude des biomes, et de se demander si celui-ci aurait pu jouer un rôle dans la facilitation de certaines transitions vers de nouveaux biomes. Des études montrent que certains

groupes de plantes lianescentes (e.g. Bignoniaceae, Lohmann et al., 2013) ont des répartitions géographiques plus larges (dans plusieurs biomes) comparativement à des groupes non lianescents et suggèrent que cela pourrait indiquer que les espèces lianescentes sont moins soumises à du conservatisme de niche (Hughes et al. 2013; Lohmann et al. 2013) . On peut donc penser que les lignées de Cercidoideae comprenant des espèces lianescentes ont plus fréquemment changé de biome que les groupes à espèces arborescentes.

Chapitre 2- Article: Biome Evolution in Subfamily Cercidoideae (Fabaceae/Leguminosae)

Biome Evolution in Subfamily Cercidoideae (Fabaceae/Leguminosae)

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2.1 Introduction

Phylogenetic studies have shown both that more closely related species tend to be more ecologically similar (Burns and Strauss 2011) and that there is a tendency for plant lineages to remain within the same biome over time (biome conservatism) (Wiens and Donoghue 2004; Pennington et al. 2009; Crisp et al. 2009). Phylogenetic biome or niche conservatism can be defined as “the extent to which species retain ancestral ecological traits and environmental distributions” (Crisp et al. 2009). Biome or niche conservatism have been documented, for example, in many Neotropical clades within the eucalypts, grasses and legumes (Crisp et al. 2009), in succulent biome clades (Pennington et al. 2009; Gagnon et al. 2019; Ringelberg et al. 2020) and in more endemic clades such as the Brazilian genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae) (Cruz et al. 2017). However, there is also evidence from the study of other plant families that in some lineages frequent biome shifts have occurred over time (Simon et al. 2009; Weeks et al. 2014; Cardillo et al. 2017; Schley et al. 2022), as has been suggested in the legume family (Schrire et al. 2005). The prevalence of biome conservatism vs. shifts has been studied in several plant lineages, in particular widely distributed pantropical clades make ideal candidates for studying these phenomena as they provide a framework for studying the dynamics of biome shifts across multiple different biomes. The species-rich and morphologically diverse family Leguminosae (Fabaceae) includes several pantropical clades in which phylogenetic relationships are now better resolved. Most recently, biome evolution has been studied in the *Caesalpinia* group (subfamily Caesalpinioideae; Gagnon et al., 2019) and the *Pterocarpus* clade (subfamily Papilionoideae; Schley et al. 2022), two pantropical clades which include species that occur in both dry and wet biomes but in which biome shifts vary in frequency and direction. While the *Caesalpinia* group

displayed strong phylogenetic succulent biome conservatism since at least the Miocene, many biome shifts were shown to have occurred in the Pterocarpus clade from the late Miocene to the Pliocene, most frequently from moist forests into grasslands in Africa and from dry forest into rainforest in the Neotropics.

Four major biomes were described by Schrire et al. (2005) as being important in studying global distribution patterns in legumes: a temperate biome, which includes warm and cold regions of the northern and southern hemisphere, and three tropical biomes that include a rainforest biome, savanna biome and succulent biome. The rainforest biome is characterized by a warm and humid climate with heavy rainfall (year-round precipitation/no dry season). The savanna biome (or grass biome) is a seasonally dry, grass-rich and fire-tolerant biome with a distribution range that includes all continents. The succulent biome is also seasonally dry, but grass-poor and rich in succulent species that have specialized water-storing tissues (Ringelberg et al. 2020), is not fire-tolerant and is absent from Asia and Australia/Oceania. The succulent biome (which includes the seasonally dry tropical forest or SDTF; Pennington et al., 2009; DRYFLOR, 2016) has been somewhat neglected in past studies (in comparison to the rainforest biome) but has now become a conservation priority due to high species endemism and large threatened areas (DRYFLOR et al. 2016). A quantitative map of the succulent biome has recently been produced (Ringelberg et al., 2020). There are many more ways to define or delineate biomes, including definitions based solely on climate, however, these four biomes are most relevant to the evolution of legumes and have been considered in several biogeographical studies of other legume clades (Estrella et al. 2017; Gagnon et al. 2019; Ringelberg et al. 2020; Schley et al. 2022).

Many studies focusing on plant evolution have shown tendencies in the types or directions of observed biome shifts. Frequent shifts have been identified between rainforest and dry open forest biomes in some plant lineages, in particular, during the Miocene in the Neotropics where changes in climate resulted in the expansion of rainforests and contraction of dry forests, and since the Miocene in Africa where increased aridity led to the expansion of grasslands (Estrella et al. 2017; Antonelli et al. 2018; Couvreur et al. 2020; Schley et al. 2022). Different factors have been suggested to influence the likelihood of plants to shift biomes, including the age of biomes and exposure of lineages to new environments over time, meaning that shifts may occur more

frequently between adjacent and/or more interconnected biomes, and certain morphological traits may also be pre-existent in species and facilitate transitions to new biomes (Edwards & Donoghue, 2013; Donoghue & Edwards, 2014). However, to better understand what drives lineages to conserve or switch from their ancestral biomes, and better explain species distribution patterns across continents, phylogenetic biome conservatism and evolution need to be further investigated in other widespread pantropical clades.

The legume subfamily Cercidoideae (Leguminosae/Fabaceae) includes 14 genera (Sinou et al., 2020) and approximately 396 species (WCVP) (distributed across many different biomes (and all four biomes described in Schrire et al. 2005), with a large number of species found in the tropical regions of South America, Asia and Africa (Schrire et al., 2005; LPWG, 2017). Species can have an arborescent, shrubby, lianescent or herbaceous habit, mostly unarmed but sometimes with tendrils or spines, and are characterized by unifoliate or bifoliate leaves (LPWG, 2017). As Cercidoideae species occur in a variety of biomes on almost all continents and have distinct habits, this is an ideal group for investigating the prevalence of biome conservatism vs. shifts and the direction of shifts. The phylogenetic analyses of Sinou et al. (2020) based on plastid and duplicated copies of the nuclear LegCyc locus suggested that multiple biome shifts and continental disjunctions have occurred in Cercidoideae, however, these patterns have not been fully examined and further investigation is necessary to better understand whether and how shifts in biome and biogeography are related.

Several studies have suggested that species habit has played a role in the evolution of certain plant lineages. For example, the Couvreur et al. (2015) study on species richness and diversification history of palms in tropical rainforest suggested that shifts from a non-climbing habit to a climbing habit have played an important role in the diversification of palms. In the Caesalpinia Group, Gagnon et al. (2019) showed that biome shifts were infrequent but closely associated with shifts in growth form. The climbing habit in plants has evolved independently numerous times throughout angiosperms and is found in over 130 families (Gentry, 1992), suggesting that lianescence is an ecologically important trait. Additionally, while many lianas are considered to be light-demanding, rapid-growing under high-light conditions and exhibit higher plasticity than less light-demanding species (Yuan et al. 2016), shade-tolerant lianescent species exist as well.

This phenotypic flexibility and rapid growth could make lianas more competitive in the dense tropical forest and other variable environments in which they are often found (Yuan et al. 2016), making the lianescent habit advantageous in adapting to new biomes. In particular, it has been suggested that light-demanding lianas grow faster than light-demanding trees and Cai et al. (2007), focusing on three Asian liana species of the genera *Phanera* and *Cheniella* and two Asian tree species of the genus *Bauhinia* (Cercidoideae), indicated that this is the result of higher specific leaf area, leaf mass ratio and leaf area ratio (Cai et al. 2007). However, it remains unclear to what extent habit shifts have co-occurred with biome shifts in Cercidoideae, and whether differences in growth form can lead to phenotypic advantages that would facilitate changes in biomes.

The main objective of this paper is to study biome shifts in a phylogenetic context, determining the extent to which there have been biome shifts or biome conservatism throughout the evolution of Cercidoideae lineages and identifying pairs of biomes between which we see more frequent shifts than others. We will also consider the direction of biome shifts as well as their associations with patterns of habit evolution and biogeographical history. We generated a time-calibrated phylogeny to reconstruct ancestral biomes, habit and continents, using Bayesian analyses and stochastic character mapping, and test the hypotheses that a) Cercidoideae lineages exhibit multiple biome shifts throughout their evolution, b) that these shifts occur most often between the succulent and savanna biome and between the rainforest and savanna biomes, which are the most geographically close and are often interconnected, and c) that lianescent lineages have shifted biomes more frequently than non-lianescent lineages, given their potential advantage of their phenotypic flexibility and rapid growth in new or variable environments. Understanding these phenomena can help explain not only the global distribution patterns that we observe in extant species but understanding if species can switch biomes or not can also provide insight into the survival and potential invasiveness or vulnerability of species under climate change.

2.2 Methods

Species occurrence data

We checked the names and taxonomy of all species of Cercidoideae included in the *World Checklist of Vascular Plants* (WCVP, <https://wcvp.science.kew.org/>) (species list developed and published by the Legume Phylogeny Working Group (LPWG), June 2021). Our species list

includes all known synonyms and their accepted names and was verified by members of our laboratory and other members of the Legume Phylogeny Working Group. The verified checklist is available on the Catalogue of Life ChecklistBank (<https://data.catalogueoflife.org/dataset/2304/about>) and on the Legume Data Portal (<https://www.legumedata.org/taxonomy/cercidoideae/>).

Occurrence records were downloaded from the *Global Biodiversity Information Facility* (GBIF, 2020) (<https://www.gbif.org/>), *Latin American Seasonally Dry Tropical Forest Floristic Network* (DryFlor, <http://www.dryflor.info/>), *Southwestern Environmental Information Network* (SEINet, <https://swbiodiversity.org/>) and *speciesLink* (<http://www.splink.org.br/>) for 14 genera in Cercidoideae: *Adenolobus* (Harv. ex Benth.) Torre & Hillc. (GBIF doi: 10.15468/dl.3fv3ph), *Barklya* F.Muell. (GBIF doi: 10.15468/dl.s483xj), *Bauhinia* Plum. ex L. (GBIF doi: 10.15468/dl.epcb8p), *Brenierea* Humbert (GBIF doi: 10.15468/dl.tvjv2m), *Cercis* L. (GBIF doi: 10.15468/dl.6xnttt), *Cheniella* R.Clark & Mackinder (GBIF doi: 10.15468/dl.z229hg), *Gigasiphon* Drake (GBIF doi: 10.15468/dl.e2nfd9), *Griffonia* Baill. (GBIF doi: 10.15468/dl.k4enf3), *Lysiphyllum* (Benth.) de Wit (GBIF doi: 10.15468/dl.22qy3f), *Phanera* Lour. (GBIF doi: 10.15468/dl.as44t9), *Piliostigma* Hochst. (GBIF doi: 10.15468/dl.3s2hq5), *Schnella* Raddi (GBIF doi: 10.15468/dl.mxdh5m), *Tournaya* A.Schmitz (GBIF doi: 10.15468/dl.mezxk8) and *Tylosema* (Schweinf.) Torre & Hillc (GBIF doi: 10.15468/dl.teh76e). Records from different sources were merged to have a single dataset per genus. These records were then subject to an extensive data cleaning process in order to match each occurrence to their accepted name according to our species list as well as to remove doubtful occurrences. This included removing occurrence records that were not associated with preserved specimens (mostly observations), that had missing or imprecise coordinates (degree-level only or with a latitude or longitude of exactly zero) or coordinates that are those of country (or regional) centroids or botanical gardens. Records identified as being cultivated or introduced were also removed and the “notes” and “locality” columns that exist in the datasets were also searched for keywords such as “botanical garden”, “garden”, “ornamental” or “cultivated”. Species-level maps were produced to check individual occurrence records for outliers such as occurrences located in oceans (using the ‘identify’ function in R to check individual occurrences). The occurrence datasets were cleaned

using R (R Core Team 2021) and the cleaning process was based on R scripts from Gagnon et al. (2019) and Ringelberg et al. (2020).

After removing duplicate records (i.e. occurrences with the same coordinates), we obtained a total of 27,314 occurrence records for 340 species and subspecies in Cercidoideae. Occurrence maps were produced in R for each species using the ggplot2 (Wickham 2016) and maps (Becker and Wilks 2021) R packages (Annexe I, Annexe II).

Biome maps

Occurrence maps were compared with existing biome maps to automatically determine to which biome each occurrence point (geographic coordinates) belongs and this information was considered when manually attributing individual species to biomes (see next section for methods). Three georeferenced biome maps were considered: a map of the rainforest biome (Corlett and Primack 2011), a map of the succulent biome (Ringelberg et al. 2020) and a map of the grass biome (Figure I in Lehmann et al. 2019). We were not able to find a recent map of the savanna biome covering all continents on which it exists. Lehmann et al.'s map of the globally distributed grass biome includes many areas that we consider to be part of the tropical savanna biome and in which Cercidoideae species are found. However, this map also includes other grass biomes such as the temperate grasslands of North America and Northern China, which we do not consider to be part of the savanna biome. Therefore, we used Lehmann et al.'s grass biome map and considered Cercidoideae species found within it to be tropical savanna species, except for the 14 species and subspecies in the genus *Cercis* which are considered to be temperate (POWO, 2022) and were assigned to the temperate biome (even though our map shows that some *Cercis* occurrences are found within Lehmann et al.'s grass biome (Annexe I-Carte 5)).

As our objective was to determine the number of occurrences in each biome, we had to modify these three maps for our purposes. Because the succulent map is continuous, whereby each grid cell represents the fraction of models that predict the occurrence of stem succulents, whereas the rainforest and grass maps are binary, we converted the succulent map to binary using a threshold of 33%, which was the threshold used by Ringelberg et al. (2019) to convert their map to binary. In addition, because the succulent biome map is at a higher resolution (0.25 deg) than the rainforest

and grass maps (0.1 deg), the latter two were converted to the 0.25 deg resolution using the `disaggregate` function in the raster R package (Hijmans and van Etten 2012).

While all three biome maps had some areas of overlap with each other, the areas of overlap between the rainforest and succulent biome maps were smaller and more localized whereas the grass biome map overlapped greatly with both of these regions. Three significant areas of overlap between the rainforest and succulent biome maps were identified: an area along the Atlantic coast of Brazil most likely belonging to the rainforest biome (Roesch et al. 2009); a small region in south-eastern Madagascar belonging to the rainforest biome (Aebli 2015; Babineau and Bruneau 2017); and a small region close to the southern border of Mexico most likely corresponding to the rainforest biome (Urbazaev et al. 2018). Additionally, Cercidoideae species that occur within these small areas of overlap were most often reported as rainforest species, according to literature. We therefore removed these areas of overlap from a modified succulent biome map and considered them to belong to the rainforest biome. Areas of overlap between the grass and succulent biome maps were particularly large, because the succulent biome was not differentiated from grass biomes in Lehmann et al.'s (2019) map. We therefore removed these areas of overlap from the grass biome map. Large areas of overlap also exist between the rainforest and grass biome maps, particularly in the Guineo-Congolian region as well in the Amazonian Rainforest. It was more challenging to determine whether these areas should be described as part of the rainforest or savanna biomes, in part due the effects of recent anthropic factors such as deforestation and because these could be transition zones or "savanna-rainforest mosaics" (Aleman et al. 2020). The study by Aleman et al (2019) also indicated that coexistence of rainforest and savanna in tropical Africa is limited and that African forests and savannas have distinct floristic composition. While the collection dates of the occurrence records span that last 100 years approximately, many of these areas of overlap, including those belonging to the Guineo-Congolian region and the Amazonian Rainforest, have been subject to recent anthropic pressures, and the resulting disturbed environment tends to be a drier environment resembling the tropical savanna (Aleman et al., 2020). For this reason, we decided to consider these areas of overlap as part of the rainforest biome and removed them from Lehmann et al.'s map. We therefore used three biome maps (Fig. 2.1): the succulent biome map (Ringelberg et al., 2020) without areas of overlap with the rainforest biome map (Corlett & Primack, 2011), the grass biome map (Lehmann et al. 2019) without areas of

overlap with the succulent and rainforest maps, and the rainforest map from Corlett & Primack, (2011) without modifications.

We did not use maps to assign species to the temperate biome as we did not find a suitable map. The five species in the genus *Cercis* included in our phylogeny were attributed to the temperate biome based on information found in literature and based on occurrence data. (The nine other species and subspecies of *Cercis* that were not included in the phylogeny are likely temperate species as well.) No other Cercidoideae species occur in the temperate biome. It's worth noting that Lehmann et al.'s grass biome map does include regions that are part of the temperate biome, such as areas of North America where *Cercis* species occur. However, while these areas may be considered as part of the grass biome, they are distinct from the dry tropical savanna biome and succulent biome that we consider in this study.

Map of the rainforest, succulent and grass biomes

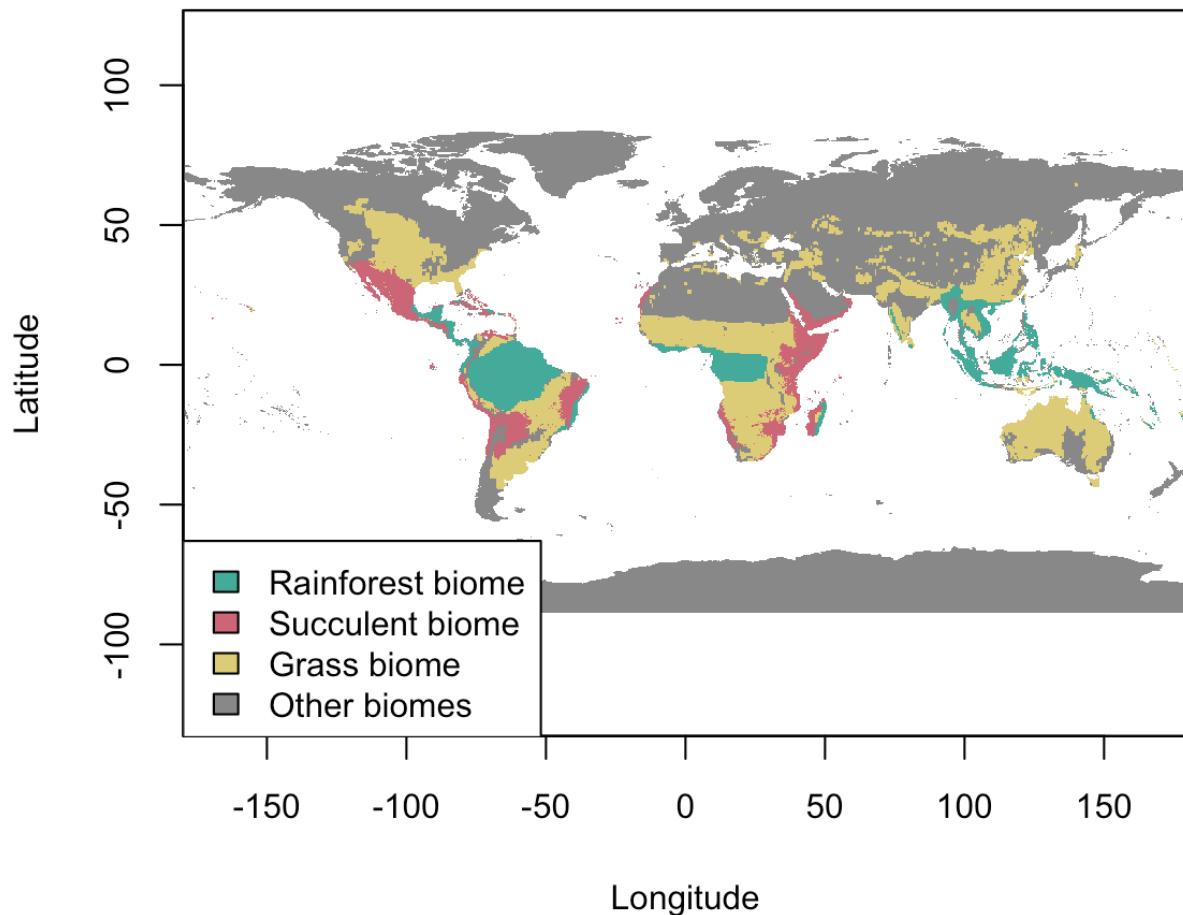


Fig. 2.1- Corlett & Primack's (2011) rainforest map without modifications (in green), Ringelberg et al.'s (2020) succulent biome map without areas of overlap with Corlett & Primack's (2011) rainforest biome map (in red) and Lehmann et al.'s (2019) grass biome map without areas of overlap with the succulent and rainforest maps (in yellow). Areas that are covered by none of these three biome maps correspond to other biomes, including the temperate biome.

Attributing species to biomes

Using the species occurrence datasets and the three biome maps, we calculated the number of occurrences for each species found within four areas: only succulent biome, only rainforest biome, only savanna biome and outside of these three biomes. Species-level maps of occurrences were produced for each biome and the proportions of occurrences in each were calculated (Annexe III). Finally, we produced generic-level maps of occurrences across these three biomes. Individual species are shown on these maps except for the large genera *Bauhinia*, *Schnella* and *Phanera* for which maps are shown only at the generic level (Annexe I).

Each species was assigned to one or several biomes by taking into account information found on herbarium specimen labels from digitized images, in floras, monographs and other literature using terms frequently encountered in literature for each of these biomes (Table 1). We also calculated the proportions of occurrences for each species in the four areas (Annexe III). We considered species to be potentially assigned to one or several biomes when more than 10% of occurrences for a species were found within the limits of the map of the biome (Annexe III).

There is support for allowing species to be assigned to multiple biomes in analyses of biome conservatism and biome shifts (Dale et al. 2021). Although most species were assigned to one or two biomes, a few species were assigned to three biomes (rainforest, succulent and savanna). For species with more than 10% of occurrences falling within the rainforest-succulent overlap, we compared the species occurrence maps with other more detailed regional vegetation maps and considered these additional sources of information when attributing species to these biomes. It is worth noting that a species with occurrences in areas of rainforest-succulent overlap isn't necessarily an indication that the species should be assigned to both of these biomes. In theory, we would expect a species occurring in both biomes to have occurrences within the areas of overlap as well as in the two individual biomes. We took this into account when attributing these species to biomes by looking at their overall distribution and the proportions of occurrences in the savanna, rainforest and succulent biome maps as well as the proportions outside of these three areas. When attributing biomes based on these proportions, we also took into account the total number of occurrences for each species, because we could expect this method to be less reliable with a smaller number of occurrence records.

Table 1: Terms frequently found in literature and used to assign species of Cercidoideae to biomes.

Biome	Terms
Succulent	thicket; scrub; thorn scrub; softwood scrub; caatinga; bushland (ex. <i>Acacia commiphora</i> bushland); scrubby; dry scrub;
Savanna	cerrado; pantanal; savanna; grassland; pampa; carrasco
Rainforest	tropical evergreen forest; ombrophilous forest; tropical rainforest; floresta Atlantica (Brazil); gallery forest; dipterocarp forest
(Unclear)	bushveld; carrasco; woodland; capoeira

Determining species habit

Species were assigned to one of three habit categories: tree/shrub, liana or herbaceous. Habit was attributed to species based on information found on herbarium specimen labels from digitized images, in floras, monographs and other literature.

Attributing species to continents

Species were assigned to one or several of eight continents based on our occurrence maps and information from literature. We considered Africa, Madagascar, Australia, Asia, Northern Asia, North America, Central America and South America. Species were assigned to Northern Asia when occurrences were found only within China. Only three species, all temperate species of the genus *Cercis*, were assigned to this region, as occurrences for all other Asian species in Cercidoideae were either more widespread across Asia or restricted to more Southern and tropical regions. (Biomes, habits and continents attributed to the 107 Cercidoideae species considered in our phylogenetic analyses are shown in SM IV.)

Time-calibrated phylogeny

As a basis for evaluating biome evolution in subfamily Cercidoideae, we used the concatenated DNA sequence alignments from Sinou et al. (2020), which included sequences for four loci (plastid *matK* and *trnL-F* and two copies of the nuclear gene *Legcyc*) and 169 accessions representing 114 species (Sinou et al, 2020). The study by Sinou et al. (2020) includes ~29% of the estimated ~396 Cercidoideae species, representing all genera and covering all continents and biomes in which Cercidoideae species occur. A total of 13 of these 114 species had multiple

accessions. For two of these species (*Barklya syringifolia* F.Muell. and *Bauhinia brachycarpa* Wall. ex Benth.), the sequences for the replicate taxa were merged using the ‘merge taxa’ function in Mesquite (Maddison and Maddison 2021) because the two accessions were sequenced for different loci. For the remaining species, the replicate with the most loci sequenced was selected. We removed two species from the Sinou et al. (2020) dataset: *Bauhinia porosa* Boivin ex Baill., because it is a synonym of *Bauhinia monandra* Kurz, and *Bauhinia x blakeana* Dunn, because it is an artificial hybrid and therefore, we are unable to assign it with certainty to a biome or continent. Five other species were removed because of identification and synonymy issues. This resulted in a dataset representing 107 species (and 107 accessions) out of ~396 species or ~27% of Cercidoideae species. The smaller genera *Adenolobus*, *Barklya*, *Brenierea* and *Tournaya* have 100% species coverage. *Cercis*, *Cheniella*, *Gigasiphon*, *Griffonia*, *Lysiphyllum*, *Piliostigma*, *Tournaya* and *Tylosema* represent 50%, 30%, 40%, 25%, ~67%, 40% and 80%, respectively, of the total numbers of species in the genus. The large genera *Bauhinia*, *Phanera* and *Schnella* represent ~29%, ~14% and ~19%, respectively, of the total numbers of species in the genus.

To reconstruct the phylogeny, we first performed a Bayesian analysis using MrBayes v. 3.2.7 (Ronquist et al. 2012), using the same parameters as in Sinou et al. (2020): a GTR+gamma model for three partitions (Legcyc1, Legcyc2, matK) and a GTR+invgamma model for trnLF partition. The analysis was run with four partitions (one for each locus) and for five million generations. Trees were sampled every 1000 generations with a burn-in of 0.25 (discarded first 1,250,000 generations). The genus *Cercis* was used to root the phylogeny as previous studies have supported *Cercis* as sister to the rest of the subfamily (Bruneau et al., 2008; LPWG, 2017; Wang et al., 2018).

A time-calibrated phylogeny was reconstructed using BEAST v. 2.6.3 (Bouckaert et al. 2019) with four partitions. We identified the TN93+F+G4 model based on the Akaike information criterion using Modelfinder (Kalyaanamoorthy et al. 2017) as implemented in IQ-TREE (Nguyen et al. 2015) as being the best model for Legcyc1, Legcyc2, and the TVM+F+G4 as being the best for matK and trnLF. However, the TVM model is not available in BEAST. We therefore decided to use the more complex GTR model. We ran the BEAST analyses using the TN93 model for the first two partitions and the GTR model for the last two partitions and compared these results with

those obtained using a GTR model for all four partitions. These changes seemed to make little difference on the age estimates, which is why we decided to use the more complex GTR substitution model for all four partitions. We used a gamma site model. Clock models and tree models were linked for these four partitions and their site models were not linked. We used two fossil priors: *Cercis* leaf and pod fossils found in Oregon with a minimum age of 36 Ma (Herendeen et al. 1992; Jia and Manchester 2014) placed on the stem node for the genus (Davis et al. 2002; Fritsch and Cruz 2012), and a *Bauhinia* leaf fossil found in Tanzania and dated to 46 Ma (Jacobs and Herendeen 2004), placed at the stem node of the clade including all Cercidoideae species except *Cercis* and *Adenolobus* (Sinou, 2015). We applied a log normal relaxed clock and a birth death model to these two fossil priors, and we rooted the tree with the *Cercis* clade.

Ancestral character reconstruction and biome evolution

While our distribution maps included all 340 species and subspecies for which occurrence records were found, our ancestral character reconstruction analyses were done only on the 107 species that were included in the phylogeny. These 107 species are representative of all biomes in which Cercidoideae clades are found. Ancestral biomes, habits and biogeography were inferred using BEAST v. 2.6.3 (Bouckaert et al. 2019). To accommodate species that had been attributed to more than one biome, we followed Gagnon et al. (2019) and manually edited the xml file to include ambiguity codes for characters with polymorphic states. Of the five taxa for which we were not able to establish biome states with certainty, four were *Bauhinia* species and were coded as polymorphic for rainforest, savanna and succulent (because *Bauhinia* species can be found in these three biomes and because these species are widely distributed, cultivated or invasive, making biome attribution difficult). The remaining taxon identified as *Phanera* sp. (*Du&al* HNK3467/CS55 (MT)) was assigned to the rainforest and savanna biomes as there are no *Phanera* species known to belong to the succulent biome. (Biomes, habits and continents assigned to the 107 species in the phylogeny can be found in Annexe IV.)

Parameters for the BEAST reconstruction analyses were set in BEAUTi. The three discrete characters ie. biomes, continents and habit, were added as three additional partitions sharing the same tree model with the other four partitions but not sharing the same clock and substitution (site) models. All three characters had their own clock and site models which were kept at default

parameters (gamma site model and strict clock model). The BEAST analysis included four replicate MCMC chains of 20 million generations, sampling every 1000 generations. Results of the four replicates were analyzed in Tracer v1.7.2 (Rambaut et al. 2018) to verify that the MCMC chains had converged and a burn-in was estimated to be 25%. The biome topologies, habit topologies and continent topologies resulting from the four replicates were combined in LogCombiner v2.6.6 (Bouckaert et al. 2019). The two maximum clade credibility trees were generated in TreeAnnotator v2.6.6 (Bouckaert et al. 2019) using median node heights and viewed in FigTree v1.4.4 (Bouckaert et al. 2019).

Biome conservatism

The number of biome shifts was evaluated using stochastic character mapping with the function `make.simmap` in the `phytools` R package (Revell 2012). This method is appropriate as it allows for polymorphic/missing character states. Species assigned to multiple biomes were given an equal probability of belonging to each of the biomes to which they were assigned, and these probabilities were used to simulate character mapping. Model fitting was performed using the `fitMk` function in `phytools` (Revell 2012); we considered an equal-rates model (ER), a symmetrical model (SYM) and an all-rates-different model (ARD) and chose the best-fitted model for biomes and habit using the Akaike Information Criterion (Akaike 1974). A total of 100 trees were randomly selected from the posterior distribution of the BEAST output. We then performed stochastic character mapping for biomes on these trees using `make.simmap` with 100 simulations. To test for biome conservatism, we followed Gagnon et al. (2019) and compared the number of shifts per tree with the number of shifts per tree obtained with randomly reordered tip states using the `sample` function in R (null distribution) and repeating this analysis five times (using a sample of ten trees and ten `make.simmap` simulations). A lower number of shifts obtained with our data compared with the number of shifts with randomized data can indicate that the considered trait has some historical inertia (Maddison and Slatkin 1991), providing evidence for biome conservatism. This analysis was performed using the `geiger` (Pennell et al. 2014) and `phytools` R packages (Revell 2012).

The number of biome shifts obtained by randomizing the tip states was also compared with the number of shifts determined through stochastic character mapping with `make.simmap` using the biome states determined using the proportions of occurrences belonging to each biome or area that

we considered (“savanna”, “succulent”, “rainforest”, “temperate” and/or “other”) as a prior probability distribution of the tip states (probabilistic approach). Stochastic character mapping was performed using the `make.simmap` function in `phytools` with 500 simulations and the maximum clade credibility tree reconstructed with `MrBayes`.

Phylogenetic signal for biomes was calculated using two different measures: Pagel’s lambda (Pagel 1999) using the `fitDiscrete` function in the `geiger` R package (Pennell et al. 2014) and the Delta statistic (Borges et al. 2023). `fitDiscrete` was run using the ER, SYM and ARD models. Because `fitDiscrete` does not allow for missing or polymorphic character states, and 55 taxa were attributed to multiple biomes, we repeated this analysis 100 times (on 100 trees), each time randomly assigning these 55 taxa to one of their biomes. The Delta statistic was calculated using our data and using reshuffled data (ten times for biomes and 100 times for habit). We obtained a p-value by computing the probability that the delta statistic for reshuffled data is superior to the delta for real data. A p-value of less than 0.05 can provide evidence for phylogenetic signal (Pennell et al. 2014). High phylogenetic signal for biomes constitutes evidence for phylogenetic biome conservatism (Losos 2008).

2.3 Results

Geographic distribution of Cercidoideae across biomes

Our maps (Annexe I) produced with cleaned and quality-controlled occurrence data show that the two *Adenolobus* species are restricted to the succulent biome of South-West Africa. The single species of *Barklya*, *B. syringifolia* F.Muell., is found along the southeastern South-Eastern coast of Australia in the savanna biome. *Bauhinia* species are found primarily throughout Central America, South America and the Caribbean, many species occur in Africa south of the Sahara Desert, in Madagascar, throughout Southern Asia and along the northeastern coast of Australia. The 166 *Bauhinia* species included (of a total of ~200 species) are found in the rainforest (~64 spp.), succulent (~65 spp.) and savanna (~68 spp.) biomes. The single species of *Brenierea*, *B. insignis* Humbert, is found in the succulent biome of southern Madagascar. The five *Cercis* species occur in the temperate biome, primarily in North America (southern Canada to Mexico) and China, with two species occurring across Europe. The nine *Cheniella* species included (of a total of 11-

12 spp.) occur in both rainforest (8 spp.) and savanna (3-4 spp.) biomes from Southern China to Indonesia. *Gigasiphon* includes four species, one occurring in the succulent biome of Eastern Africa and three occurring in the rainforest biome: one in Madagascar, one in the Philippines and one in Papua New Guinea. All four *Griffonia* species occur primarily in the rainforest biome of Western Africa. The nine *Lysiphyllum* species occur primarily in Northern and Central Australia, with a few species occurring in Southeast Asia, and are primarily savanna species (6-7 spp.), with a few occurring in both savanna and rainforest biomes (1-2 spp.). The 74 *Phanera* species included (of a total of ~95 species) are found throughout rainforest (~63 spp.) and savanna (~21) biomes of South-East Asia and Southern China, with one species occurring on the rainforest coast of Brazil. Of the three species in *Piliostigma* for which we have occurrence records (two missing), two occur across the savanna biome of Africa and one occurs in the savanna biome in Southern Asia and Northern Australia. The 48 *Schnella* species included (of a total of ~48) occur from southern Mexico to southern Brazil across rainforest, succulent and savanna biomes (but most species in rainforest). The single species of *Tournaya*, *T. gossweileri* (Baker f.) A.Schmitz, is found in the rainforest biome of western Africa. The four *Tylosema* species included occur in the savanna (3 spp.) and succulent biomes (2 spp.) of Southern and Western Africa. Biomes attributed to the species included in the Sinou et al. (2020) Cercidoieae phylogeny are shown in Fig. 2.3 and Fig. 2.4 as boxes at branch tips, and those for additional species not included in Sinou et al. (2020) are given in Annexe III.

Time-calibrated phylogeny

Our analysis estimated the crown age of Cercidoieae in the early Eocene at 48.74 Ma (95% highest posterior density: 46.12-54.75 Ma) (Fig. 2.2, Table 2). Using *Cercis* to root the phylogeny, our analysis shows strong support for two large lineages: a Bauhinia clade (Bayesian posterior probability (BPP) of 1) including species of the genera *Piliostigma* sister to *Brenierea* + *Bauhinia* (BPP of 1), and a *Phanera* clade (BPP of 1) including the genera *Gigasiphon*, *Tournaya*, *Tylosema*, *Barklya*, *Schnella*, *Lysiphyllum* and *Phanera* (*Gigasiphon* as sister to the rest of the clade, BPP of 1). *Adenolobus* is resolved as sister to the rest of Cercidoieae excluding *Cercis* (BPP of 1). *Griffonia* is resolved as sister to the clade comprising the Bauhinia and *Phanera* clades. Most genera are supported as monophyletic, with the exception of *Cheniella* which is resolved as polyphyletic and embedded in *Phanera*, and *Schnella*, which is resolved as paraphyletic because

of the nested position of *Barklya syringifolia*. These relationships are very similar to those found in the phylogeny of Sinou et al. (2020).

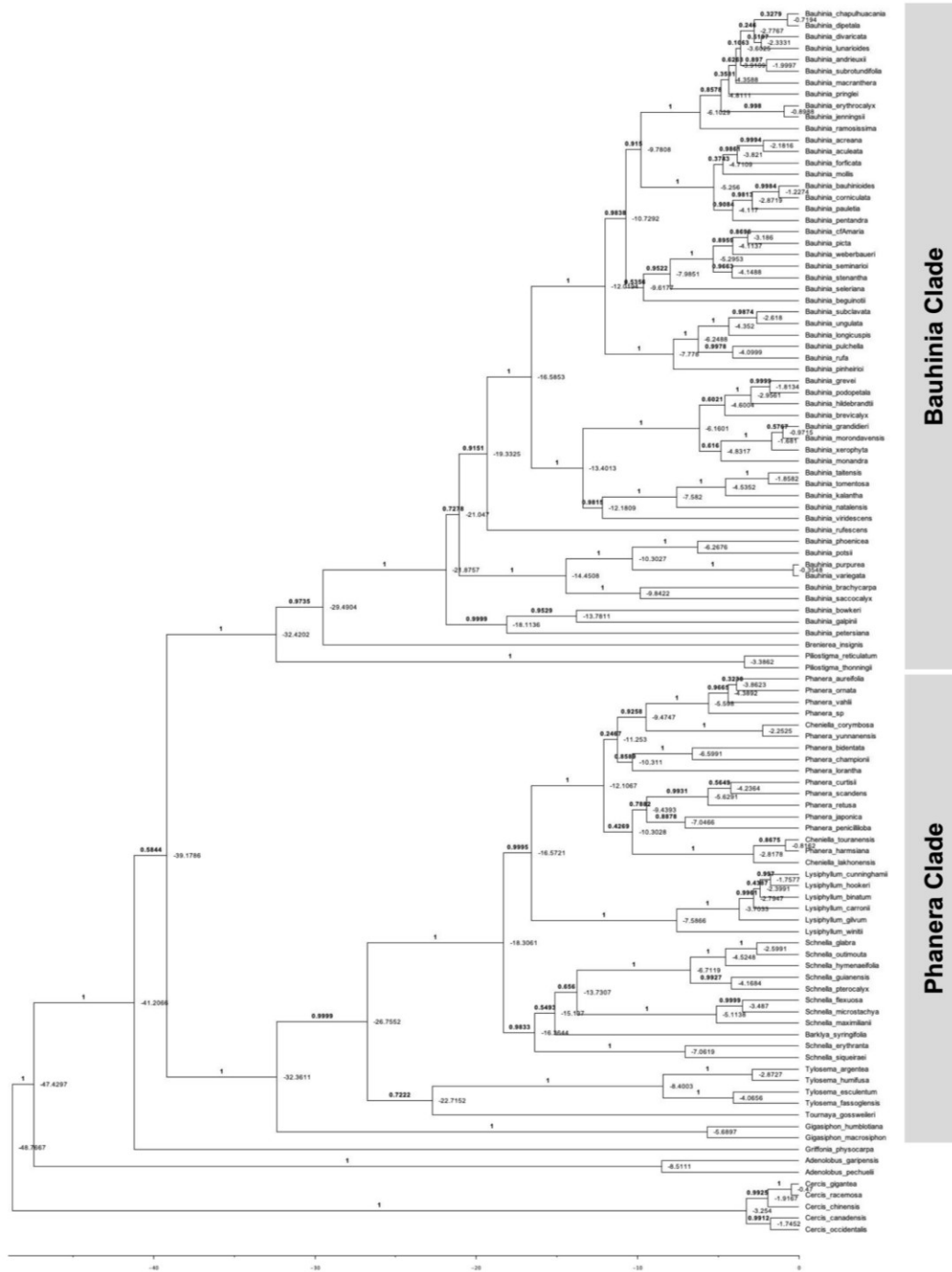


Fig. 2.- Time-calibrated phylogeny of Cercidoideae (maximum clade credibility tree), generated in BEAST v. 2.6.3. Values at nodes represent estimated node ages and values above branches represent Bayesian posterior probability values. Time scale is displayed below in millions of years.

Ancestral biomes and habits

Our BEAST ancestral biome reconstructions indicate that the rainforest biome is the most likely ancestral biome to all Cercidoideae (Fig. 2.3). (The probabilities of biome and habit states at nodes are shown in Annexes V and VI.) The genus *Cercis*, which is concentrated in the temperate biome, could be associated with a shift from rainforest to temperate (Table 2). The analyses suggest a minimum of 17 biome shifts (Figs 2.3, 2.5) (this is the number of shifts at nodes, when we consider the most probable states reconstructed at nodes over all possible trees where changes can occur anywhere along branches). The most common direction of biome shifting is from rainforest to savanna and the six shifts of this type occurred throughout the phylogeny (one is characteristic of the genus *Lysiphyllum*, two occur in *Phanera* species, one in *Piliostigma* and two in *Bauhinia*) (Table 2). Five shifts from rainforest to succulent can be identified: two occur in the genus *Bauhinia*, one is characteristic of *Brenierea insignis*, one subtends the genus *Adenolobus* and one subtends the genus *Tylosema*. Five shifts from the succulent to rainforest biomes are also observed, all within *Bauhinia*. There were no shifts from the savanna biome and no shifts from the temperate biome. Biome shifts occurred between 48.74 Ma (95% HPD: 46.12 - 54.74 Ma) and 4.23 Ma (95% HPD: 1.88 - 6.93 Ma). Our analyses indicate that shifts to the savanna biome are all more recent compared to shifts into other biomes, the earliest occurring in genus *Piliostigma* at 32.42 Ma (95% highest posterior density (HPD): 26.23 - 38.60 Ma) and the most recent occurring at 4.23 Ma (95% HPD: 1.88 - 6.93 Ma) in *Phanera curtisii* (Prain) Bandyop. & Ghoshal.

Using stochastic character mapping as implemented in the `make.simmap` function (Phytools), four types of shifts occurred: from succulent to rainforest, rainforest to succulent, temperate to succulent and succulent to savanna (Fig. 2.6). Using proportions of occurrences in biomes as prior probabilities of biome states for taxa, the four types of shifts that occurred were: succulent to rainforest, rainforest to savanna, from another biome to succulent, and from temperate to another biome (Fig. 2.7). Other types of shifts are non-existent in our analysis. In contrast to the BEAST reconstructions, the analysis using biomes attributed based on both occurrence records and literature as well as the analysis using proportions of occurrences both suggest that the common ancestor to the Cercidoideae clade, excluding *Cercis*, most likely belonged to the succulent biome. A shift to the rainforest biome likely occurred in the *Phanera* clade, followed by more recent shifts to the savanna biome.

BEAST analyses estimate that the tree/shrub habit is the ancestral habit for Cercidoideae, with a shift to lianescent habit in the *Phanera* clade (32.36 Ma; 95% HPD: 25.85 - 38.79 Ma), followed by five shifts back to the tree/shrub habit: in *Barklya syringifolia* F.Muell. (16.44 Ma; 95% HPD: 12.27 - 21.31 Ma), in *Lysiphyllum* (16.60 Ma; 95% HPD: 12.65 - 20.97 Ma), and in three *Phanera* species (*P. lorantha* Pierre ex Gagnep. (10.27 Ma; 95% HPD: 7.25 - 14.06 Ma), *P. retusa* Benth. (5.60 Ma; 95% HPD: 2.91 - 8.65 Ma) and *P. yunnanensis* (Franch.) Wunderlin (2.25 Ma; 95% HPD: 0.78 - 4.58 Ma)). Within the *Phanera* clade, a shift from the lianescent habit to a herbaceous habit occurs in *Tylosema* (22.82 Ma; 95% HPD: 16.72 - 28.90 Ma). In the *Bauhinia* clade, species are all trees or shrubs, and no shifts in habit were observed.

Using stochastic character mapping as implemented in the `make.simmap` function (Phytools), four types of habit shifts occurred: from liana to tree/shrub, herbaceous to tree/shrub, herbaceous to liana, and liana to herbaceous (Fig. 2.8). Other types of shifts were not observed in our analysis. In contrast to the BEAST reconstructions, this analysis indicates that the lianescent habit is the ancestral habit for Cercidoideae, with a shift to the tree/shrub habit in the *Bauhinia* clade.

While the tree/shrub habit is found in Cercidoideae species across all four biomes, all 24 lianescent species were assigned to the rainforest biome (10 of which were attributed to both rainforest and savanna biomes). Of the mostly lianescent genera in the *Phanera* clade, three of the four shifts to the tree/shrub habit are associated with a shift in biome from rainforest to savanna, and similarly in *Lysiphyllum*, the lianescent to tree/shrub habit shift is also associated with a shift from rainforest to savanna. In *Tylosema* the lianescent habit to herbaceous habit shift is associated with a shift from the rainforest to the succulent biome.

Biogeographical reconstructions

Our ancestral continent reconstruction analysis indicates that Cercidoideae (excluding the genus *Cercis*) originated in Africa and that many long-distance dispersal events have occurred throughout the evolution of lineages. We see a total of 13 continent shifts (Fig. 2.4): five occur within the succulent biome (in *Bauhinia*), five within the rainforest biome (in both the *Bauhinia* and *Phanera* clades), two are associated with shifts from succulent to rainforest biomes (in the

Bauhinia clade) and one occurs within the savanna biome (in *Lysiphyllum*). (The probabilities of continent states at nodes are shown in Annexe VII.) Conversely, our biome and continent reconstruction analyses (Fig. 2.4) show that biome shifts are rarely associated with continental disjunctions. Lineages that disperse to other continents tend to remain within the same biome and biome shifts tend to occur within the same continents. The only notable occurrence of a shift in both biome and continent occurs in the genus *Lysiphyllum* in which we see a shift characteristic of the entire genus from a rainforest liana to a savanna tree or shrub at approximately 16.6 Ma that occurred within Asia, but that is shortly followed by a dispersal event to Australia (characteristic of the entire genus excluding *Lysiphyllum winitii* (Craib) de Wit, the sister species in our phylogeny). Our analyses reveal only one occurrence of a shift in habit coinciding with dispersal to a new continent: the divergence of the species *Barklya syringifolia* (nested within the rainforest genus *Schnella*) is associated with a shift from liana to tree/shrub habit and with dispersal from South America to Australia. We also note a recent shift in the clade comprising *Bauhinia jenningsii* P. Wilson and *Bauhinia erythrocalyx* Wunderlin from the succulent biome in North America to the rainforest biome in Central America. Ancestral continent reconstruction analyses also reveal that all shifts from succulent to rainforest biomes occur in the New World, whereas shifts in the opposite direction occur mainly in Africa (and once in South America). Shifts from rainforest to savanna biomes all occur within Africa and Asia.

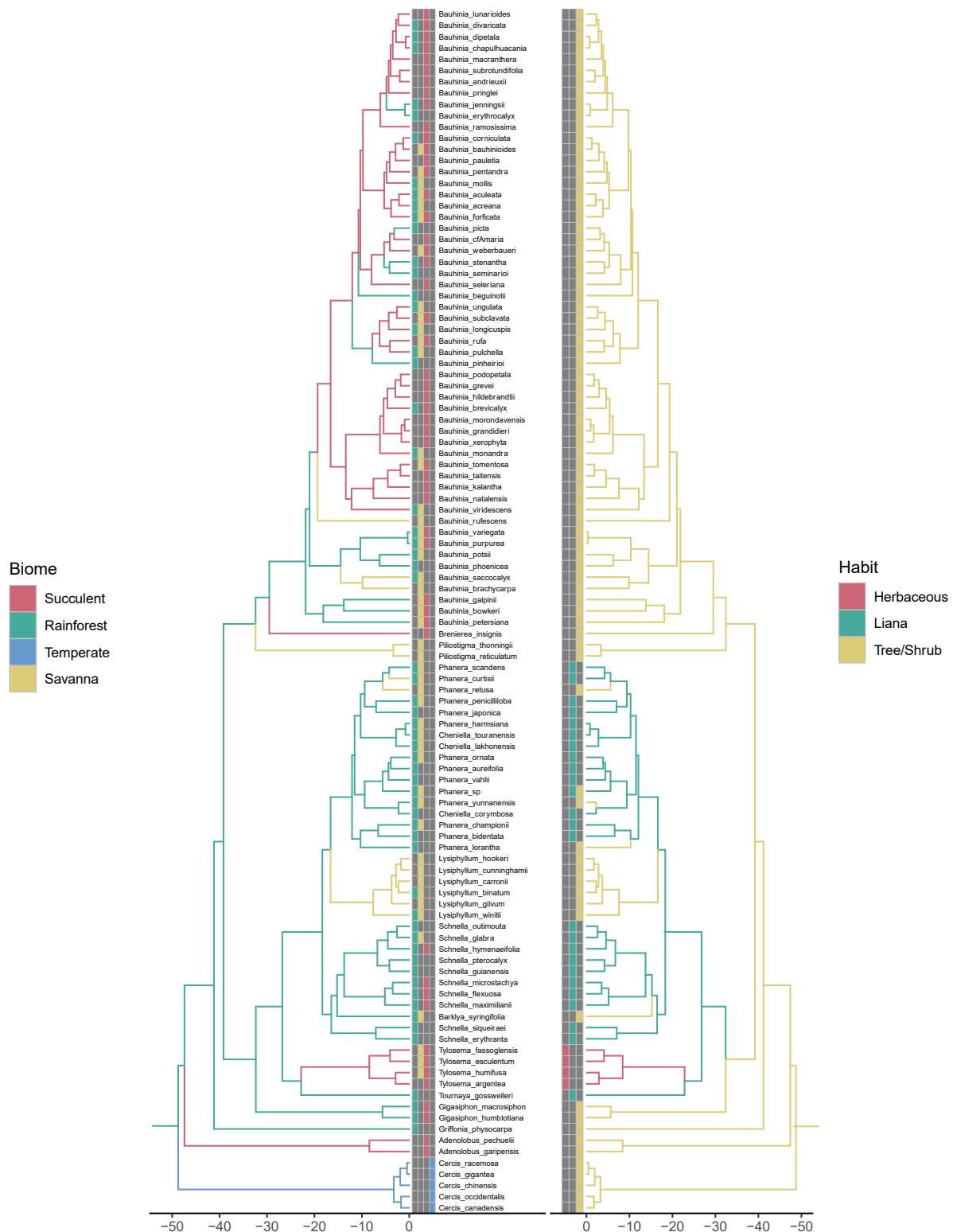


Fig. 2.3- Bayesian ancestral state reconstruction for biomes (left) and habit (right) displayed on the time-calibrated phylogeny of Cercidoideae (maximum clade credibility tree), generated in BEAST v. 2.6.3. Boxes at the tips represent the biomes and habits attributed to taxa, gray boxes indicate an absence of the character state for a taxon.

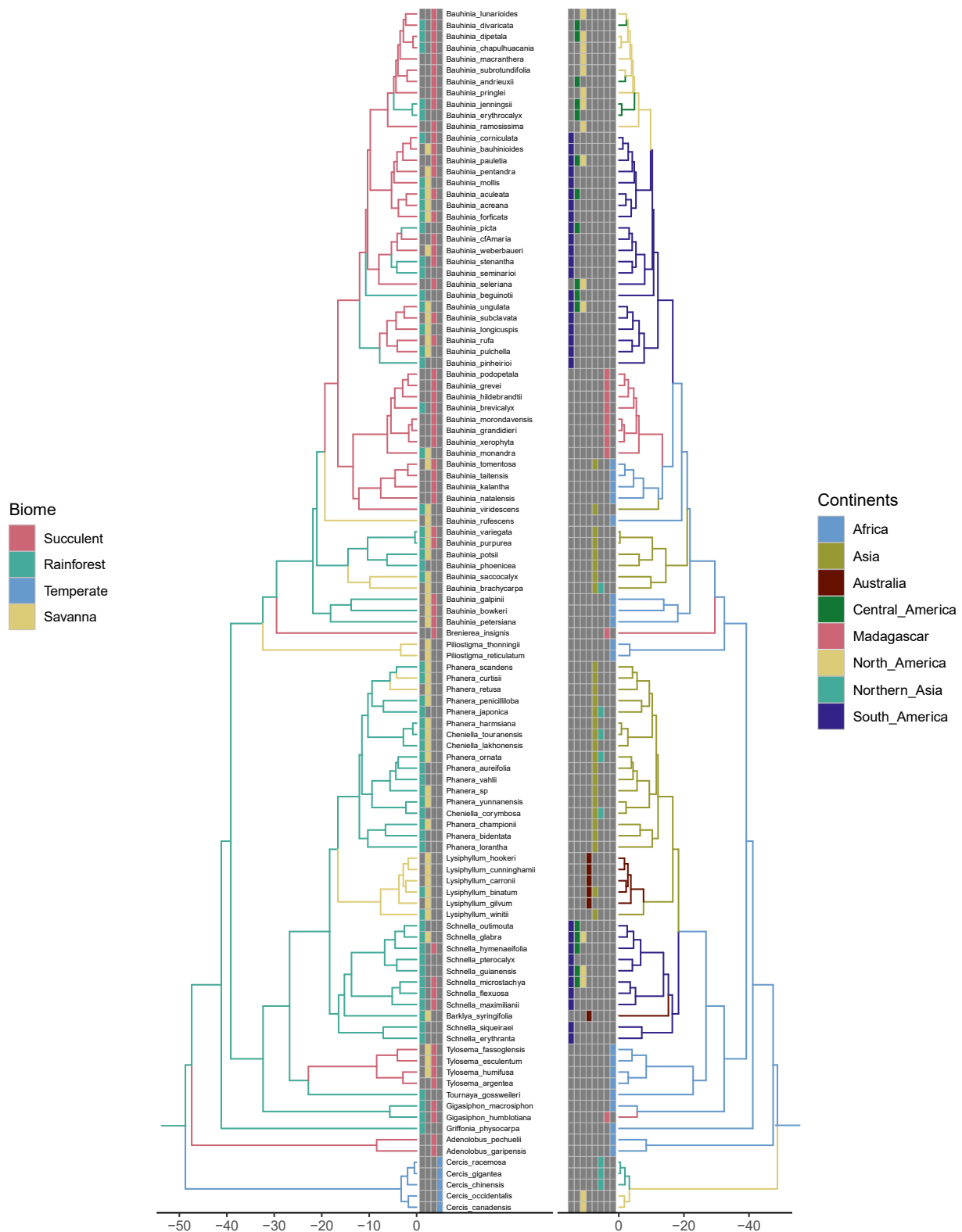


Fig. 2.4- Bayesian ancestral state reconstruction for biomes (left) and continents (right) displayed on the time-calibrated phylogeny of Cercidoideae (maximum clade credibility tree), generated in BEAST v. 2.6.3. Boxes at the tips represent the biomes and continents attributed to taxa, gray boxes indicate an absence of the character state for a taxon.

Table 2-All biome shifts occurring in our ancestral character reconstruction analyses with BEAST: direction of biome shifts, taxa in which they occur, the age of the nodes at which they occur, whether they are associated with a change in habit and whether they are associated with a change in continent. The BEAST analysis reconstructed the rainforest biome as the ancestral biome to Cercidoideae. Rows in gray indicate shifts in more than one reconstructed character.

Direction of biome shift	Taxon	Node age (Ma)	Node age (Ma 95% HPD)	Change in habit	Change in continent
Rainforest to temperate	Genus <i>Cercis</i>	48.41	[46.12-54.75]	Tree/shrub is ancestral habit	Africa is ancestral continent
Succulent to rainforest	<i>Bauhinia pinheiroi</i> , <i>B. pulchella</i> , <i>B. rufa</i> , <i>B. longicuspis</i> , <i>B. subclavata</i> , <i>B. unguolata</i> (clade)	12.02	[9.32-15.15]	No change	Occurs within South America
	<i>Bauhinia beguinotii</i>	10.72	[8.11-13.49]	No change	Occurs within South America
	<i>Bauhinia erythrocalyx</i> , <i>B. jenningsii</i>	4.83	[3.20-6.55]	No change	Shift from North America to Central America
	<i>Bauhinia seminarioi</i> , <i>B. stenantha</i>	5.30	[3.35-7.66]	No change	Occurs within South America
	<i>Bauhinia picta</i>	3.20	[1.57-5.24]	No change	Occurs within South America
Rainforest to savanna	Genus <i>Piliostigma</i>	32.42	[26.23-38.60]	No change	Occurs within Africa
	<i>Bauhinia rufescens</i>	19.34	[15.08-23.55]	No change	Occurs within Africa
	Genus <i>Lysiphyllum</i>	16.60	[12.65-20.97]	Liana to tree/shrub	Occurs within Asia, but is followed by a shift to Australia
	<i>Bauhinia brachycarpa</i> , <i>Bauhinia saccocalyx</i> (clade)	14.46	[5.20-14.97]	No change	Occurs within Asia
	<i>Phanera retusa</i>	5.60	[2.91-8.66]	Liana to tree/shrub	Occurs within Asia
	<i>Phanera curtsii</i>	4.23	[1.88-6.93]	No change	Occurs within Asia

Rainforest to succulent	Genus <i>Adenolobus</i>	47.41	[46.03-52.64]	No change	Occurs within Africa
	Genus <i>Brenierea</i>	29.51	[23.64-35.47]	No change	Shift from Africa to Madagascar
	Genus <i>Tylosema</i>	22.82	[16.72-28.90]	Liana to herbaceous	Occurs within Africa
	Genus <i>Bauhinia</i>	19.34	[15.08-23.55]	No change	Occurs within Africa
	Genus <i>Bauhinia</i>	7.77	[5.03-10.51]	No change	Occurs within South America

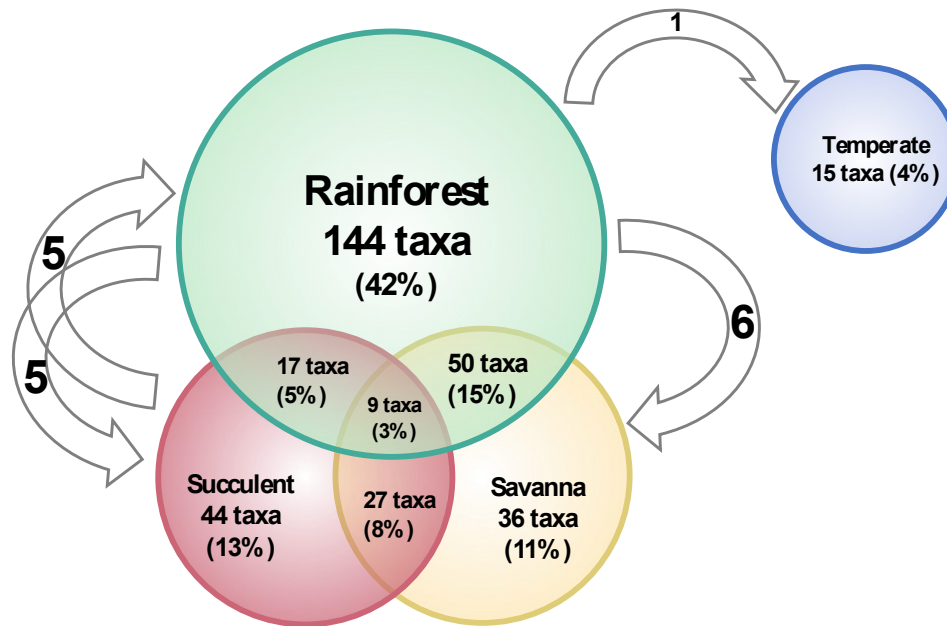


Fig. 2.5- Number of biome shifts in each direction based on the BEAST Bayesian ancestral character reconstruction analysis, number of Cercidoideae species and subspecies assigned to each of the four biomes and percentage of taxa assigned to each biome or to multiple biomes, out of a total 342 taxa (340 for which we had occurrence data and two for which we didn't have occurrence data but that were included in our phylogeny), of which 103 were assigned to more than one biome (50 taxa were assigned to both rainforest and savanna biomes, 27 taxa were assigned to both succulent and savanna biomes, 17 taxa were assigned to both rainforest and succulent biomes and nine taxa were assigned to all three of these biomes). Grey arrows represent biome shifts and direction of shifts.

Phylogenetic biome conservatism

The ARD model was the best-fitted model for both biomes and habit based on the Akaike information criterion and was therefore used to compute both the number of biome shifts with `make.simmap` and Pagel's lambda. The numbers of biome shifts obtained with our data were significantly different from those obtained with reshuffled data (Table 3), meaning that we can reject the null hypothesis that there are as many changes in these two traits as we could expect if they were randomly distributed. The median Pagel's lambda was 0.874 for biomes and 0.998 for habit (Table 4). The delta statistic was higher for our data compared to reshuffled data, for both biomes and habit ($p\text{-value} < 0.05$) (Table 4). These values suggest biome conservatism and habit conservatism. (Because of time constraints, the delta statistic for biomes was calculated 10 times with reshuffled data, while it was calculated 100 times for habit.)

Table 3- Number of biome and habit shifts in Cercidoideae obtained with real and reshuffled data using stochastic character mapping as implemented in `phytools` (`make.simmap` function) and an all rates different (ARD) model (best-fitted model for biomes and habit). Numbers of shifts using real data were obtained using a sample of 100 trees and 100 `make.simmap` simulations. Numbers of shifts with reshuffled data were obtained by reshuffling the data five times per tree, using 10 trees and 10 `make.simmap` simulations. 1st quartiles, 3rd quartiles and medians of numbers of shifts are shown in this table.

	Biomes		Habit	
	Real data	Reshuffled data	Real data	Reshuffled data
1st quartile	29.175	506.6	11.335	565.075
Median	30.155	964.9	11.84	1146.25
3rd quartile	32.47	1041.4	13.2375	54665.025

Table 4-Phylogenetic signal for biomes and habit using Pagel’s lambda (Pagel 1999) and the delta statistic (Borges et al., 2023) calculated using an ARD model (best-fitted). Pagel’s lambda for biomes was obtained by reshuffling the biome data 100 times and calculating the median of these 100 trees. Pagel’s lambda for habit was obtained without reshuffling the data. The delta statistics for biomes and habit were obtained using our data and using reshuffled data (10 times for biomes and 100 times for habit), then calculating a p-value as the probability that the delta statistic for reshuffled data is superior to the delta statistic for real data. A p-value of less than 0.05 indicates conservatism for a trait. P-values are null for both biomes and habit because the delta statistics for reshuffled data were always inferior to the delta statistics for real data.

	Biomes	Habit
Median Pagel’s lambda	0.874 (ARD model); 0.900 (ER model)	0.998 (ARD model)
Delta statistic for real data	2.417	39.736
Median delta statistic for reshuffled data	0.577	1.074
P-value for delta statistic	0	0

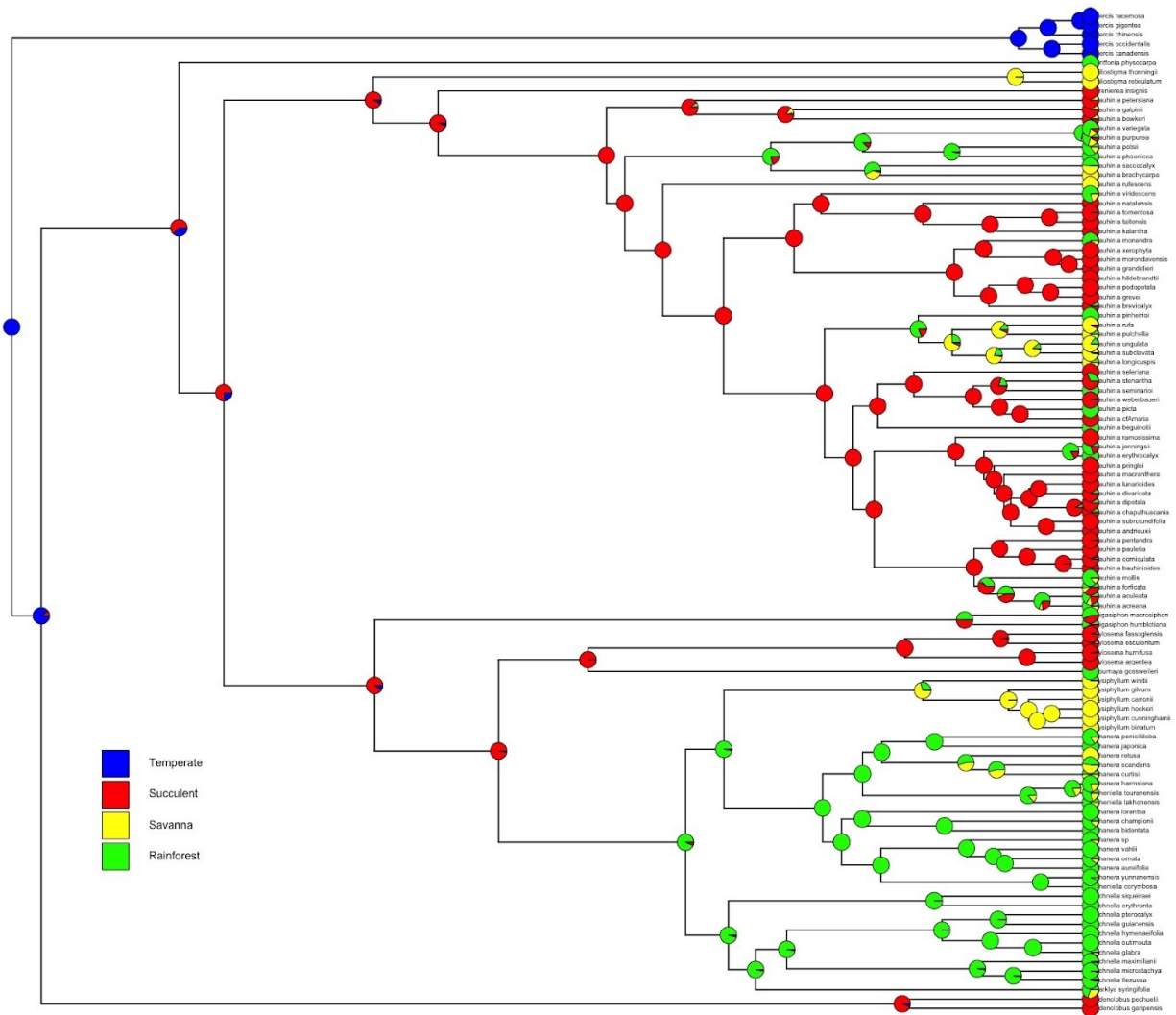


Fig. 2.6- Stochastic character mapping for biomes using make.simmap (Phytools), using the maximum clade credibility tree generated in BEAST, an all-rates-different model and 500 make.simmap simulations. Species assigned to multiple biomes were given an equal probability of belonging to each of the biomes to which they were assigned. Trees have 28.636 changes between states on average and four types of shifts occurred: across 500 trees, an average of 16.379 shifts occurred from succulent to rainforest, 8.53 from rainforest to savanna, 2.812 from temperate to succulent and 0.916 from succulent to savanna.

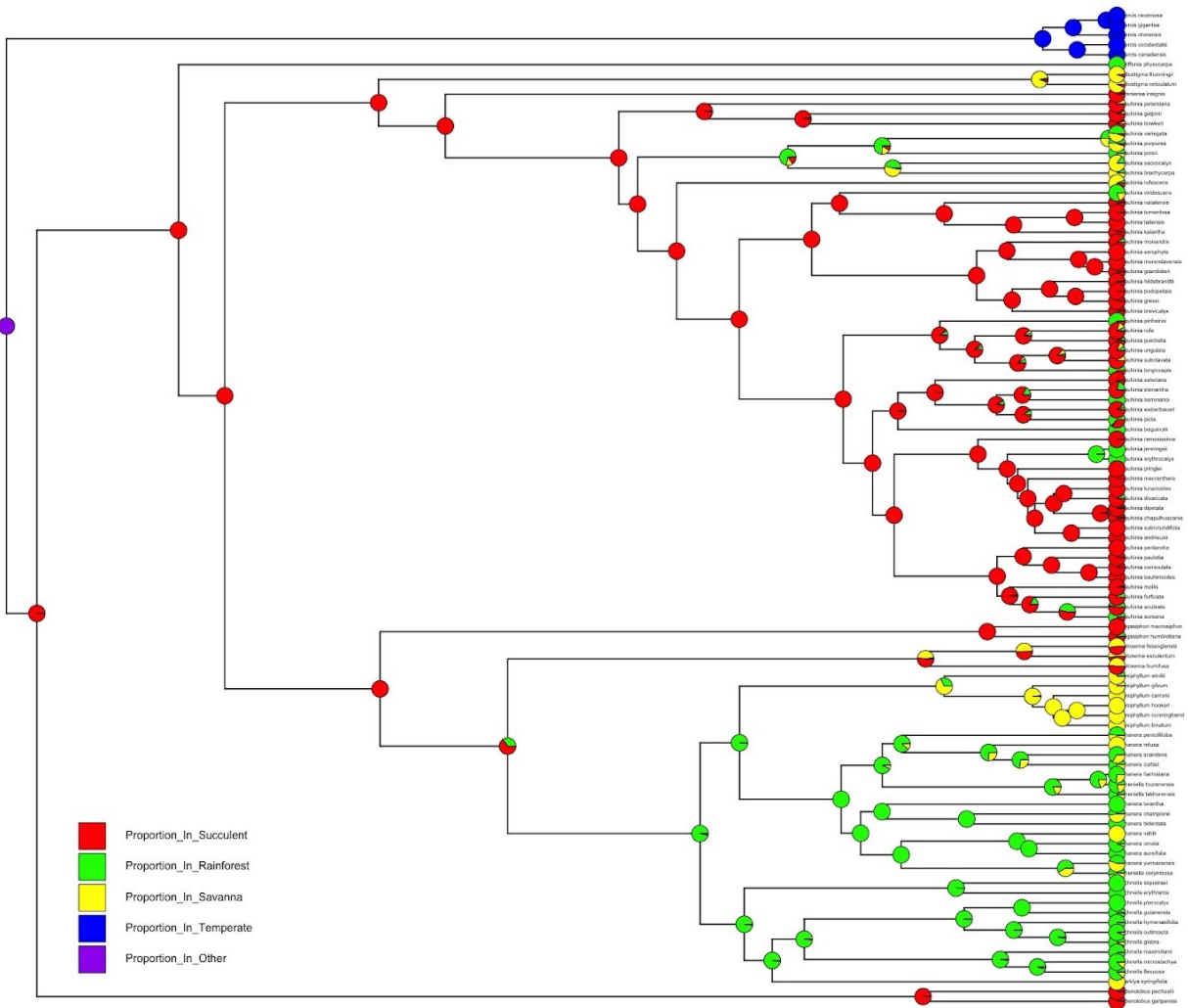


Fig. 2.7- Stochastic character mapping for biomes using make.simmap (Phytools), using the maximum clade credibility tree generated in BEAST, an all-rates-different model and 500 make.simmap simulations. Proportions of species occurrences in the savanna biome, the succulent biome, the rainforest biome and outside of these three biomes were used as prior probabilities of biome states for taxa, except for *Cercis* species which were attributed to the temperate biome (probability of 1 for temperate biome). Trees have 26,458 changes between states on average and four types of shifts occurred: across 500 trees, an average of 13.282 shifts occurred from succulent to rainforest, 11.174 from rainforest to savanna, 1.002 from other to succulent and 1 from other to temperate.

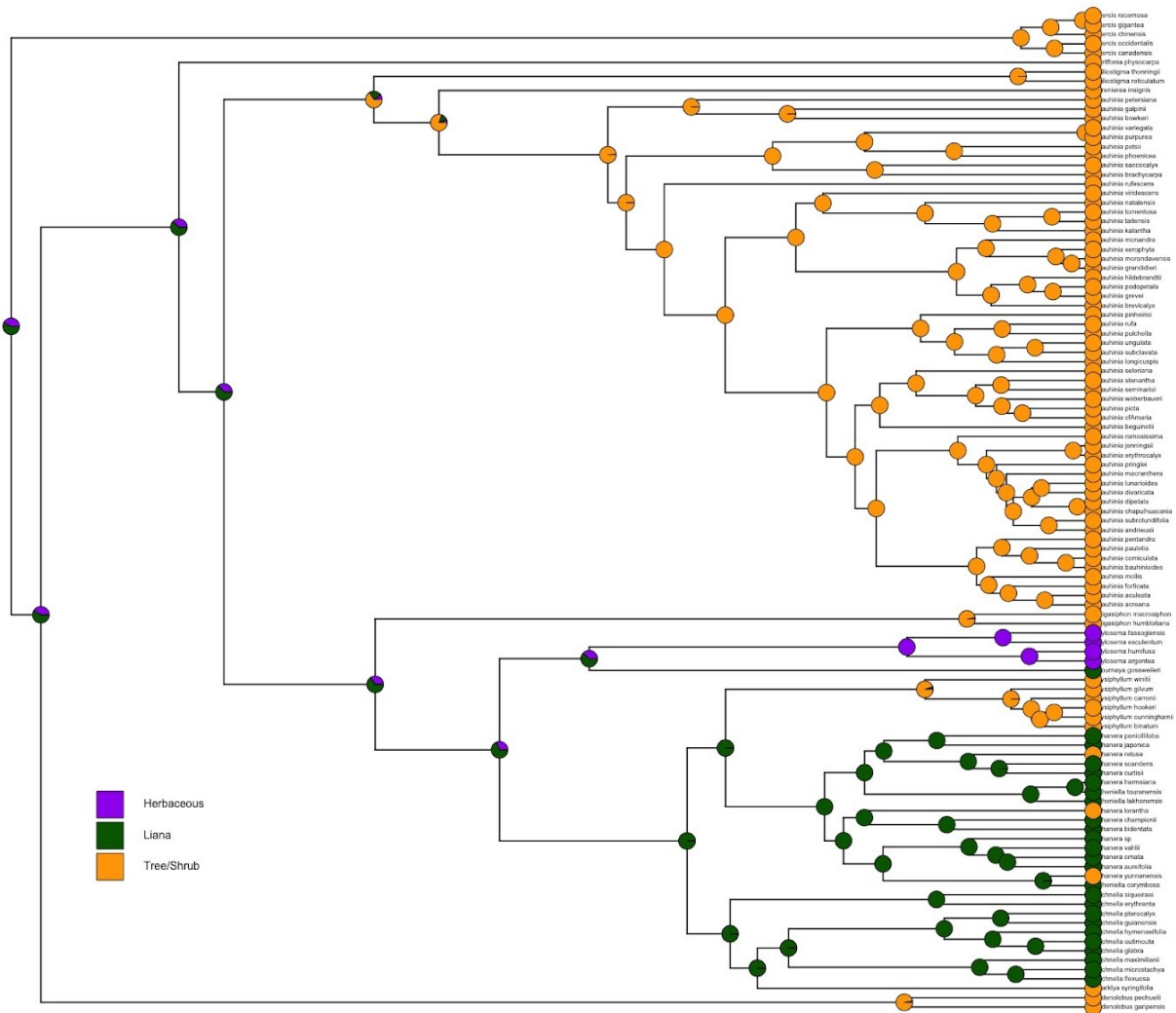


Fig. 2.8- Stochastic character mapping for habit using make.simmap (Phytools), using the maximum clade credibility tree generated in BEAST, an all-rates-different model and 500 make.simmap simulations. Trees have 13.236 changes between states on average and four types of shifts occurred: across 500 trees, an average of 8.846 shifts occurred from liana to tree/shrub, 1.812 from herbaceous to tree/shrub, 1.528 from herbaceous to liana and 1.06 from liana to herbaceous.

2.4 Discussion

Subfamily Cercidoideae is characterized by a primarily pantropical distribution with complex patterns across several wet and dry tropical biomes. While our analyses indicate that biomes are phylogenetically conserved in Cercidoideae, these diverse distribution patterns suggest both that long distance dispersal is prominent in the evolutionary history of the group and that over time Cercidoideae have been able to adapt to different environments. However, these distribution

patterns differ between the two major clades. Phanera clade species are found in Africa, Asia, Australia, South America and Central America and are mostly rainforest lianas (approximately 75%), except for *Tylosema*, a succulent biome herbaceous genus, and *Lysiphyllum*, a savanna genus including semi-scandent shrubs and lianas, with or without tendrils, as well as trees (Wunderlin et al., 1987; Lewis & Forest, 2005; POWO, 2022). Bauhinia clade species are similar to Phanera clade species in their distribution (except that they are not found in Australia) but more diverse in terms of biome distributions as they occur in all three major biomes (rainforest, savanna and succulent) and display less variation in habit as species are all small trees or shrubs, without tendrils (Lewis & Forest, 2005; POWO, 2022). The temperate genus *Cercis* is sister to the rest of the subfamily, followed by the genus *Adenolobus* which is restricted to the succulent biome of south-western Africa (Annexe I-Carte I). These two early-diverging lineages of small trees or shrubs are somewhat more geographically isolated from the rest of Cercidoideae, are relatively species-poor and may represent vestigial lineages that have poorly adapted to changing environmental conditions, including climate. Comparison of the differing transcontinental distribution patterns and habits between major clades in Cercidoideae can help provide insights for understanding what may determine the distribution of these clades, including the importance of factors such as dispersal limitations and the ability to adapt to new environments. To answer these questions, we looked at the prevalence of biome shifts throughout the history of Cercidoideae and the relative frequencies of shifts between different biome types. Our analyses show that biome shifts have occurred in both major clades and on almost all continents where Cercidoideae species are found (Asia, Africa, South America, Central America). However, while shifts have occurred throughout Cercidoideae, some biome pairs and directions of shifts are more common than others. Our analyses show three types of biome shifts which are relatively more frequent and discussed below.

Shifts from the rainforest to succulent biomes occur throughout the evolution of Cercidoideae lineages (early Eocene to late Miocene) and all occur within Africa and within tree/shrub lineages, except for one shift in the genus *Tylosema* that coincides with a shift to a herbaceous habit (some species with tendrils), and one shift within the genus *Bauhinia* which occurs within South America. Several studies have provided evidence for succulent biome conservatism (Pennington, 2009; Gagnon et al. 2019; Ringelberg et al., 2020). However, our results indicate a total of six shifts into

the succulent biome. A possible explanation for some of these shifts out of the rainforest biome could be that they were driven by the climate cooling that occurred during the Oligocene and changed the global distribution of biomes, including retraction of rainforests, resulting in less connectivity between Old World and New World tropical forests (Bush et al. 2011; Landis et al. 2020). This loss of connectivity is supported by our observation that shifts from rainforest to succulent biomes occur within the same continents (within Africa/Madagascar or South America), none of these shifts coinciding with a shift in continents.

Shifts in the opposite direction, from the succulent to rainforest biomes, occur only in the New World and are the most recent types of shifts in Cercidoideae (middle Miocene-Pliocene; Fig. 2.3). Because these shifts are more recent relative to other types, it is more probable that the distribution of biomes at this time resembled that of our maps, which show that these two biomes are adjacent and often interconnected in South and Central America. Spatial adjacency or connectivity of biomes has been suggested as a factor that could increase the probability of shifts between biomes, due in part to the higher geographic opportunity for shifts as well as the fact that adjacent biomes are often more climatically similar (Donoghue & Edwards, 2014). However, while the succulent and savanna biomes are adjacent and share similarities in climate, both being seasonally dry (Pennington et al. 2009; Ringelberg et al. 2020), our analyses do not show any shifts between these two biomes. Shifts from succulent to savanna biomes could be limited by a lack of adaptations in succulent biome species to the frequent fires that are characteristic of the savanna biome, such as thick corky bark and the ability to resprout from rhizomes (Pennington et al. 2009; Simon et al. 2009; Simon & Pennington 2012).

Shifts from rainforest to savanna biomes occur in both Asia and Africa, at varying times and in both major tropical clades. Many other studies have indicated frequent and recent shifts in plant lineages between moist forests and savanna (Schrire et al. 2005; Estrella et al. 2017; Antonelli et al. 2018; Gagnon et al. 2019). Shifts between these two biome types were shown to be some of the most common types of shifts in Detarioideae (Estrella et al., 2017; similar age to Cercidoideae) and in the Pterocarpus clade (Schley et al, 2022), which also occur in Africa and Asia. The expansion of grasslands during the late Miocene and Pliocene has been suggested as a driver of these shifts from wet biomes to savannas (Donoghue & Edwards, 2014) and could also help explain

shifts of this type in Cercidoideae. Two of six of these shifts involve changes in habit from liana to tree/shrub. Overall, our analysis shows one early occurring shift (early Oligocene) from a tree/shrub habit to a lianescent habit in the *Phanera* clade, followed by many more recent shifts back to the tree/shrub habit (in *Lysiphyllum*, *Barklya* and some *Phanera* species) or a change to the herbaceous habit (in *Tylosema*). This could suggest that it is easier to shift from a liana to another habit but difficult for tree/shrub lineages to shift habits (and this could be consistent with the observed stability in habit throughout the evolution of the *Bauhinia* clade lineages which remain trees or shrubs). These results are somewhat similar to those of Gagnon et al. (2019) which showed that the ancestral habit of the *Caesalpinia* group (Fabaceae) (which is of comparable age to Cercidoideae) was also the tree/shrub habit, with one early shift to a lianescent habit followed by a more recent shifts back to the tree/shrub habit. The shift back to the tree/shrub habit in *Lysiphyllum* (and in *Phanera retusa*) could suggest that the lianescent habit is not well adapted to the fire-prone savanna biome and that shifts to the savanna biome are more likely for species with a woody habit.

Our observation that while liana species in Cercidoideae belong primarily to the rainforest biome, arborescent and shrubby species occur in all four biomes that we've considered, could bring further support to the idea that the tree/shrub habit is more adaptable to both wet and dry biomes in comparison to the lianescent habit, which tends to occur in the wet biome. This could help explain why we observe more biome shifts to occur in the widespread tree/shrub *Bauhinia* clade, which includes several invasive species, than in the rest of Cercidoideae. Donoghue and Edwards (2014) suggested that the presence of certain "enabler" traits could be a significant factor influencing the probability of niche evolution. Lohmann et al. (2013) suggested that the variety of both wet and dry niches occupied by the neotropical clade Bignoniaceae (Bignoniaceae), including the savanna, succulent and rainforest biomes, could be related to the variation in growth form as Bignoniaceae, like Cercidoideae, includes both shrubby and lianescent species, while this type of variation in habit is otherwise relatively rare in neotropical plant groups (Lohmann et al. 2013).

Another factor that has been suggested as having an influence on the frequency of biome shifts is the age of biomes and their connectivity through time (Donoghue & Edwards, 2014). The rainforest biome is suggested to have originated in the Cretaceous-Eocene (Bush et al. 2011;

Landis et al. 2020) and the succulent biome in the Oligocene (Gagnon et al., 2019), whereas the savanna biome appeared in the late Miocene-early Pliocene (Edwards et al. 2010; Pennington and Hughes 2014). The more recent appearance of the savanna biome could also help explain why we observe no shifts from the savanna biome, yet we see many shifts between the much older rainforest and succulent biomes as well as an early-occurring shift between temperate and rainforest biomes. Indeed, our analyses indicate that the genus *Cercis*, sister to the rest of Cercidoideae, is restricted to the temperate biome in the Northern Hemisphere, while the rest of Cercidoideae is reconstructed as having originated in the rainforest biome, which suggests that at least one shift has occurred early-on in the evolution of Cercidoideae between rainforest and temperate biomes and possibly through an intermediary ancestor that is no longer extant (considering that our time-calibrated phylogeny shows that ~45 Ma separate the basal and crown nodes of *Cercis*). Tropical rainforests and temperate forests were more interconnected during the Eocene than in more recent eras (Bush et al. 2011), which could help explain this shift in Cercidoideae during this time as well as the absence of shifts between these two biomes in subsequent diversifications in Cercidoideae. Schrire et al. (2005) suggested that legumes originated in a dry tropical biome (succulent biome) around the Tethys Sea in the early tertiary and that lineages subsequently shifted to moist tropical forests. However, our analyses indicate a rainforest origin for Cercidoideae. While this is possible given the relative estimated ages of biomes, a succulent biome origin for Cercidoideae is also possible considering that the genus *Adenolobus*, which is the sister lineage to all Cercidoideae except *Cercis*, is restricted to the succulent biome. Furthermore, stochastic character mapping analyses with make.simmap (Fig. 2.6 and Fig. 2.7) reconstructed the succulent biome as the ancestral biome for Cercidoideae.

Cercis is known to be a temperate clade with a distribution range spanning dry to mesic climates in the Northern Hemisphere (Davis et al. 2002; Fritsch et al. 2018). *Cercis* is also the only temperate clade in Cercidoideae (Sinou et al., 2020) and has been suggested to have avoided extinction (unlike other taxa in these regions) through leaf adaptations to xeric and mesic habitats (Fritsch et al., 2018). However, the occurrence of some *Cercis* species in the succulent biome (ANNEXE I-Carte 5) as well as the temperate biome could potentially provide support for a succulent biome origin for Cercidoideae, in line with Schrire et al.'s dry tropical biome origin hypothesis for legumes. It is also worth noting that by assigning *Cercis* to only the temperate biome

in our reconstruction analyses, we have probably underestimated the number of possible biome transitions. Coding *Cercis* as polymorphic for both temperate and succulent biomes may have resulted in analyses suggesting additional shifts between these two biomes within the *Cercis* clade. Additionally, because *Cercis* is sister to all other Cercidoideae, this decision could also affect the reconstructed ancestral biome to all of Cercidoideae, meaning that coding *Cercis* as polymorphic could also result in reconstruction analyses favoring different ancestral biomes for Cercidoideae than those suggested by our analyses.

Our ancestral character reconstruction analyses show that biome shifts tend to occur within the same continent and that dispersals to new continents tend to occur within the same biome. This appears to be true across different continents and biomes, except in the case of the genus *Lysiphyllum* in which the shift from the rainforest to the savanna biome which subtends the entire genus is followed by dispersal from Asia (*L. wintii* (Craib) de Wit) to Australia (*L. gilvum* (F.M.Bailey) Pedley, *L. binatum* (Blanco) de Wit, *L. carronii* (F.Muell.) Pedley, *L. hookeri* (F.Muell.) Pedley and *L. cunninghamii* (Benth.) de Wit). This biome shift in *Lysiphyllum* also coincides with a shift from a lianescent to a semi-scandent shrubby habit (with some species having tendrils). Similarly, a habit shift from a lianescent to arborescent habit (non-climbing) occurring in *Barklya syringifolia* coincides with dispersal from South America to Australia, however, the placement of *Barklya syringifolia* is weakly supported. Our analyses indicate six continent shifts within the succulent biome, but only two within the rainforest biome and one within the savanna biome. While our analyses show six shifts from rainforest to succulent biomes, the high number of continent shifts within the succulent biome relative to the three other biomes could be consistent with the results of Ringelberg et al. (2020) and Gagnon et al. (2019) that indicated high levels of succulent biome conservatism in non-succulent plant clades.

2.5 Conclusion

Overall, our analyses suggest that multiple biome shifts have occurred throughout the evolution of Cercidoideae lineages, in particular between the rainforest and succulent biomes and from the rainforest to the savanna biome. While our analyses show two major shifts in both biomes and habit (*Lysiphyllum* and *Tylosema*), we do not find that lianescent lineages have shifted biomes more frequently. Indeed, many biome shifts have occurred between all three tropical biomes within

the Bauhinia clade in which the lianescent habit is absent. We also find that while biome shifts tend to occur within continents, multiple long-distance dispersals to new continents have occurred, most often within the same biome. The frequent shifts in Cercidoideae indicate that species have been able to adapt to significantly different environments over time. However, in the case of *Lysiphyllum* and *Tylosema*, for example, our analyses do not indicate whether biome shifts occur before habit shifts, or vice versa. The question remains whether species capable of shifting biomes have adapted *in situ*, or whether shifts to new biomes were facilitated by pre-existing adaptations such as more suitable habits for the new environment.

Chapitre 3- Conclusion générale

En reconstituant l'évolution des biomes, du port et de la biogéographie des Cercidoideae, il a été possible d'apporter de nouvelles perspectives sur l'histoire évolutive de cette sous-famille et sur les corrélations potentielles entre les changements de biomes et un trait fonctionnel particulier, le port. Il nous semblait que le port soit le seul trait fonctionnel chez les Cercidoideae leur apportant un avantage adaptatif assez significatif pour qu'une corrélation avec les changements de biomes soit identifiable avec nos analyses, qui s'intéressent à des patrons à très grande échelle (à l'échelle des continents). Il existe évidemment des traits fonctionnels connus comme étant caractéristiques des biomes qu'on a considéré, le biome succulent étant caractérisé par les plantes grasses qui sont adaptés à la sécheresse (Pennington et al. 2009; Simon et al. 2009) et la savane étant caractérisée par les graminées qui sont adaptés aux feux et à l'herbivorie (Charles-Dominique et al. 2016; Jardine et al. 2020), mais les Cercidoideae n'appartiennent pas à ces groupes fonctionnels. Nous considérerons dans ce dernier chapitre l'importance éventuelle d'autres traits fonctionnels chez les Cercidoideae, ainsi que des limites à l'étude de biomes.

Au niveau des modes de dispersion et de la morphologie florale, il a été suggéré que les fleurs zygomorphes de *Cercis* pourraient constituer une adaptation à la pollinisation par les insectes (Wunderlin et al. 1987). Le reste des Cercidoideae présentent d'autres morphologies florales, à part *Adenolobus* qui présente aussi des fleurs légèrement zygomorphes et qui est le groupe-frère des Cercidoideae excluant *Cercis* (Sinou et al. 2020). Les fleurs distinctes de *Cercis* pourraient constituer un autre indice qui soutient une histoire évolutive différente des autres clades et associée au biome tempéré. D'ailleurs, la grande distance autant géographique qu'évolutive entre le genre tempéré *Cercis* et le reste de la sous-famille pourrait aussi indiquer une tolérance aux basses températures (et peut-être le gel) chez *Cercis* qui est absente chez le reste des espèces (Fritsch et al. 2018). Cependant, nous n'avons pas considéré la morphologie florale dans cette étude parce qu'il existe peu d'indications dans la littérature que ce trait soit d'importance évolutive chez les Cercidoideae et plus généralement, qu'il existe des liens entre la morphologie florale et les changements de biomes. Les Cercidoideae sont principalement pollinisés par le vent et les insectes, et bien qu'il existe des différences morphologiques entre pollens de différents clades (Wunderlin et al. 1987), il ne semble pas y avoir de différences fonctionnelles significatives. Toutefois, une

étude plus poussée de la morphologie des fleurs et du pollen des clades tropicaux pourrait élucider des adaptations à certains types de pollinisateurs (Wunderlin et al. 1987), ce qui pourrait aider à mieux comprendre la répartition de certaines espèces à travers leurs habitats. En particulier, plusieurs études suggèrent une association entre la morphologie des fleurs et la spécialisation des interactions entre plantes et pollinisateurs (Neal et al. 1998; Joly and Schoen 2021).

À travers l'étude du port chez les Cercidoideae, il semblerait que la présence de vrilles, un trait plutôt associé à des plantes grimpantes, peuvent toutefois être présentes non seulement chez les espèces lianescentes de Cercidoideae, mais aussi chez certaines espèces arbustives (par exemple, chez des espèces du genre *Lysiphyllum*, selon Wunderlin et al. (1987)). Il est donc possible que des espèces arbustives de Cercidoideae possédant des vrilles constituent un état intermédiaire entre les lianes et les arbustes ou petits arbres sans vrilles. L'étude de certains traits plus spécifiques liés au port pourrait élucider des patrons plus détaillés d'évolution des biomes chez les Cercidoideae, possiblement à travers un "gradient" de ports où un changement entre ports lianescents et arborescents/arbustives passerait par un arbuste grimpant avec des vrilles (et possiblement d'autres traits liés à la capacité à grimper, comme les vrilles adhésives vs. non-adhésive et les capacités à grimper à partir de racines, de tiges ou de pétioles). Il existe aussi d'autres traits liés au port qui pourraient être d'intérêt évolutif dans le contexte des changements de biomes. Puisqu'il semblerait que la plus grande différence écologique à l'origine des différences fonctionnelles entre biomes succulent et savane soit les feux fréquents, il pourrait être pertinent de considérer des adaptations au feu, tels que l'épaisseur des tiges ou des troncs, l'apparence et l'épaisseur de l'écorce et la présence d'organes souterrains de réserve (rhizomes) (Pennington et al. 2009; Ringelberg et al. 2020). Plus spécifiquement, on pourrait considérer le clade *Bauhinia*, où les espèces se trouvent dans les biomes savane et succulent mais ont tous un port arborescent ou arbustif, et se demander s'il existe des différences morphologiques significatives entre les espèces de ces deux biomes, afin de comprendre comment ce clade non-lianescent a pu s'établir dans une telle variété de conditions environnementales. Cependant, la disponibilité d'informations sur les organes souterrains est limitée comparativement à la morphologie florale et foliaire, ce qui fait partie des raisons pour lesquelles nous n'avons considéré que trois catégories pour le port.

Une grande limite à ce type d'étude en biogéographie historique est qu'on connaît avec peu de certitude comment les biomes étaient distribués et interconnectés par le passé. Les découvertes et datations de nouveaux fossiles peuvent apporter des informations supplémentaires sur les biomes ancestraux des Cercidoideae, en plus d'augmenter la précision des âges estimés. Les nouvelles techniques d'imagerie satellite et l'apprentissage automatique permettent de faire des cartes de biomes et de végétation de plus en plus précises. Toutefois, même les cartes de biomes les plus récentes ont des limites de précision, ces incertitudes pouvant être dues par exemple à des perturbations récentes comme la déforestation et les feux (Aleman et al. 2020). Il y a certainement aussi un biais avec les données d'occurrences, puisque beaucoup de régions du monde sont sous-échantillonnées. En particulier, nous avons remarqué un manque de ressources et de données d'occurrences pour de nombreuses d'espèces se trouvant en Afrique et particulièrement en Asie.

De plus, bien qu'il existe une grande variété de biomes et de façons de les définir (Mucina, 2019), on peut remettre en question l'intérêt de définir des biomes à l'échelle mondiale. Par exemple, l'observation que les espèces lianescentes de Cercidoideae appartiennent tous au biome forêt tropicale humide, tandis que les espèces arborescentes et arbustives semblent se retrouver majoritairement dans les biomes secs, pourrait indiquer que ces patrons d'évolution et de répartition à travers les biomes pourraient régir de limites adaptatives à la sécheresse et dans certains cas, aux feux. C'est une des raisons pour lesquelles, en plus de considérer des cartes de biomes, il serait pertinent de considérer des gradients d'humidité et de température, ou même les types de sols. Une étude récente sur le clade des Mimosoides, un autre groupe pantropical de légumineuses dont des espèces se trouvent dans des milieux secs et dans la forêt tropicale humide, indique qu'un gradient de disponibilité d'eau (précipitations) explique le renouvellement des lignées au sein de continents (Ringelberg et al. 2022). Il se pourrait que la répartition des Cercidoideae, et même d'autres groupes de plantes dont les espèces se trouvent à travers plusieurs continents et des habitats variés, soit mieux expliquée par des facteurs environnementaux que par des définitions de biomes qui peuvent être légèrement arbitraires. En considérant ces facteurs plus précis et en utilisant des données d'occurrences, il serait possible d'effectuer de la modélisation de répartition d'espèces dans l'objectif de mieux identifier des facteurs climatiques et édaphiques à l'origine de certains patrons de répartition d'espèces.

Finally, even though we have considered in this study three major components of plant biogeography, the biomes encompassing a variety of environmental and climatic factors, the port constituting an adaptation to these factors, and the movement of continents over time being important to understand dispersal events, our analyses do not allow us to estimate whether a change of port occurs as a result of dispersal of a species to a new biome, or if species that change biomes are pre-adapted to their new environment by possessing specific traits that confer a competitive advantage. Research focused on the genetic processes and implications at the origin of these port changes could help answer questions that remain unanswered: what are the mechanisms and factors necessary to trigger these changes (easy/probable or difficult/improbable) and on what time scales can they occur? These are the kinds of knowledge that could help us better understand the changes in biomes identified and to elucidate the potential intermediate ports in the Cercidoideae.

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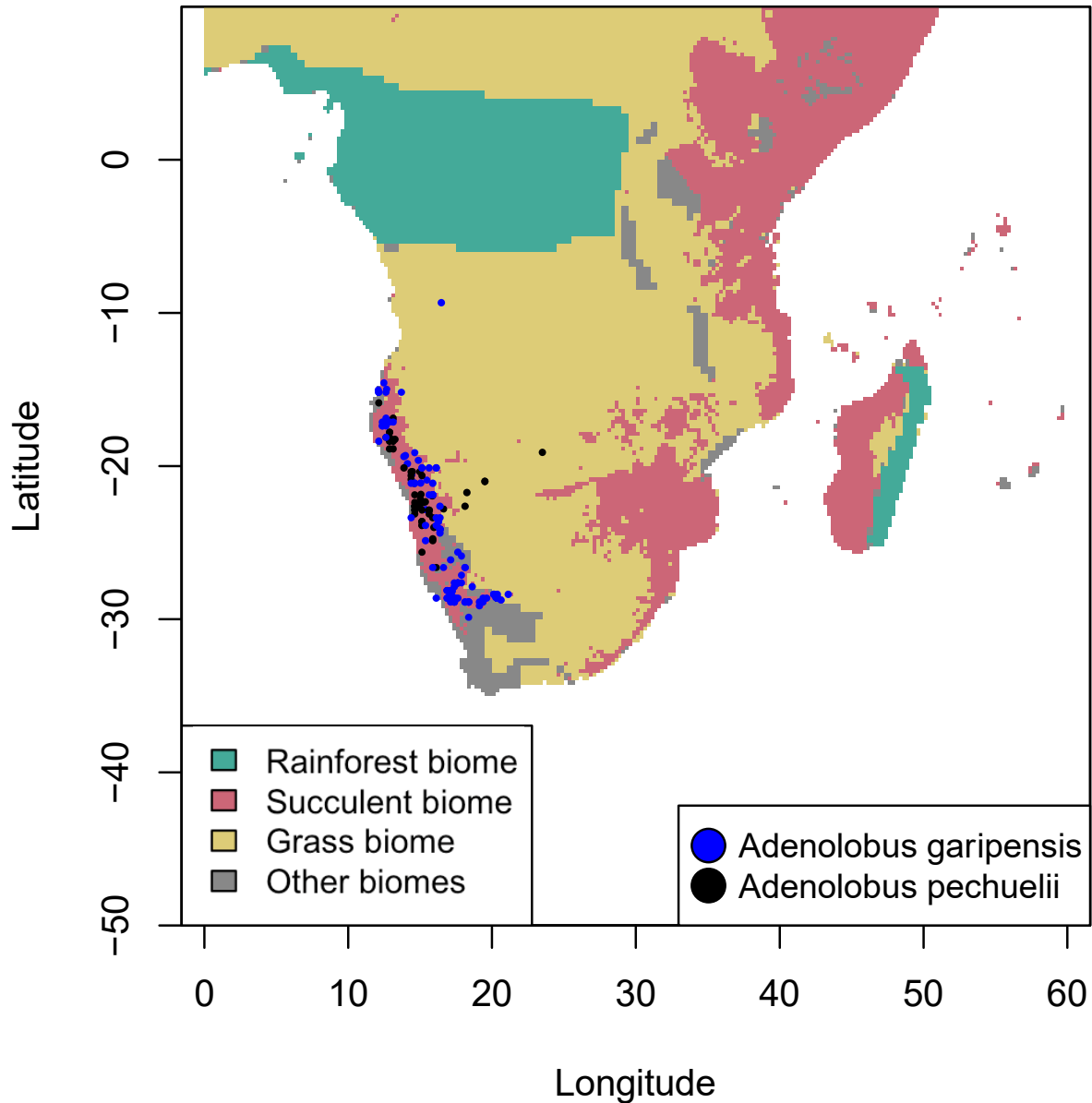
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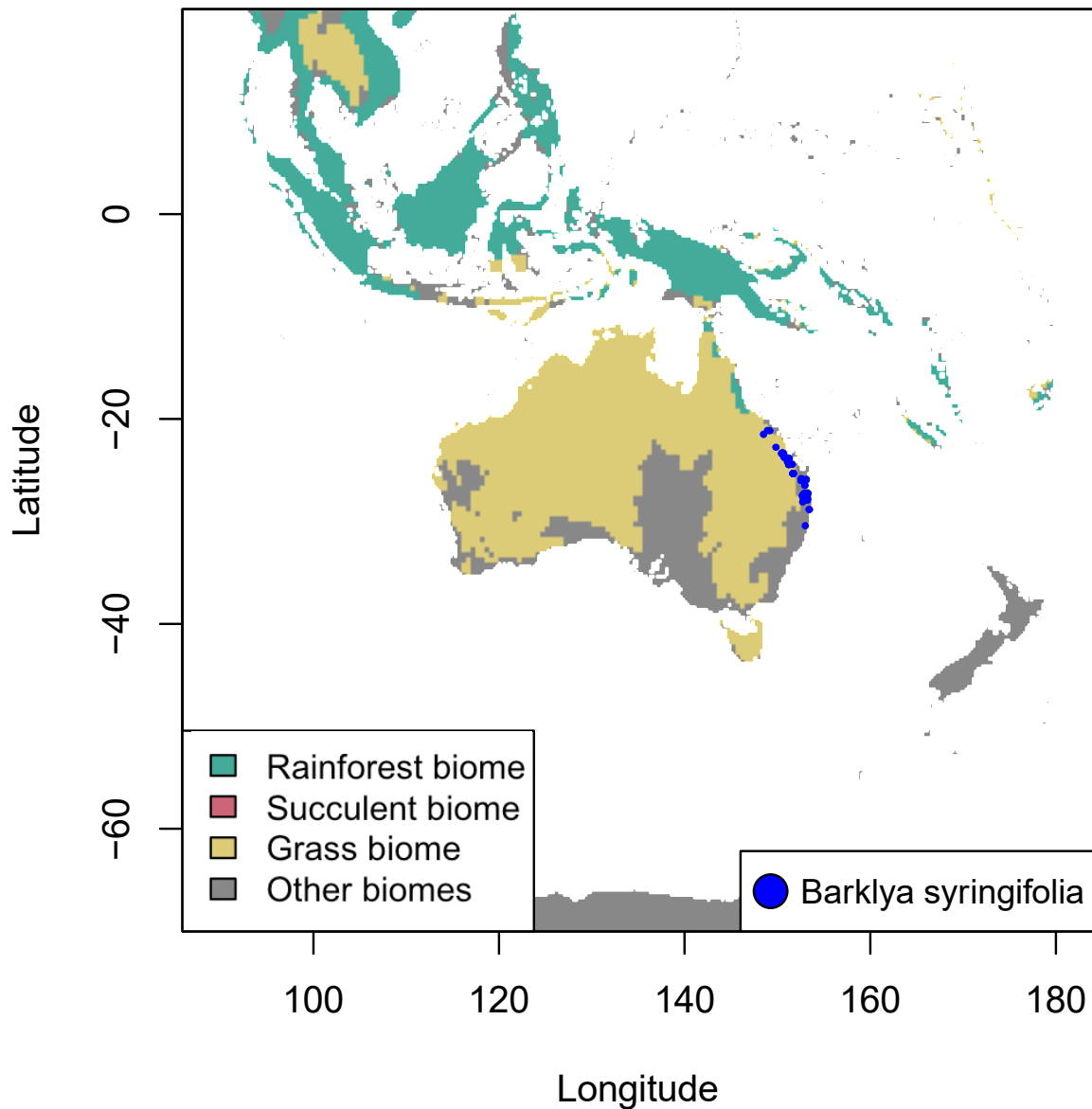
Annexe I- Cartes de répartition des espèces de Cercidoideae à travers les biomes savane, succulent et forêt tropicale humide.

***Adenolobus* spp. occurrences across biomes**



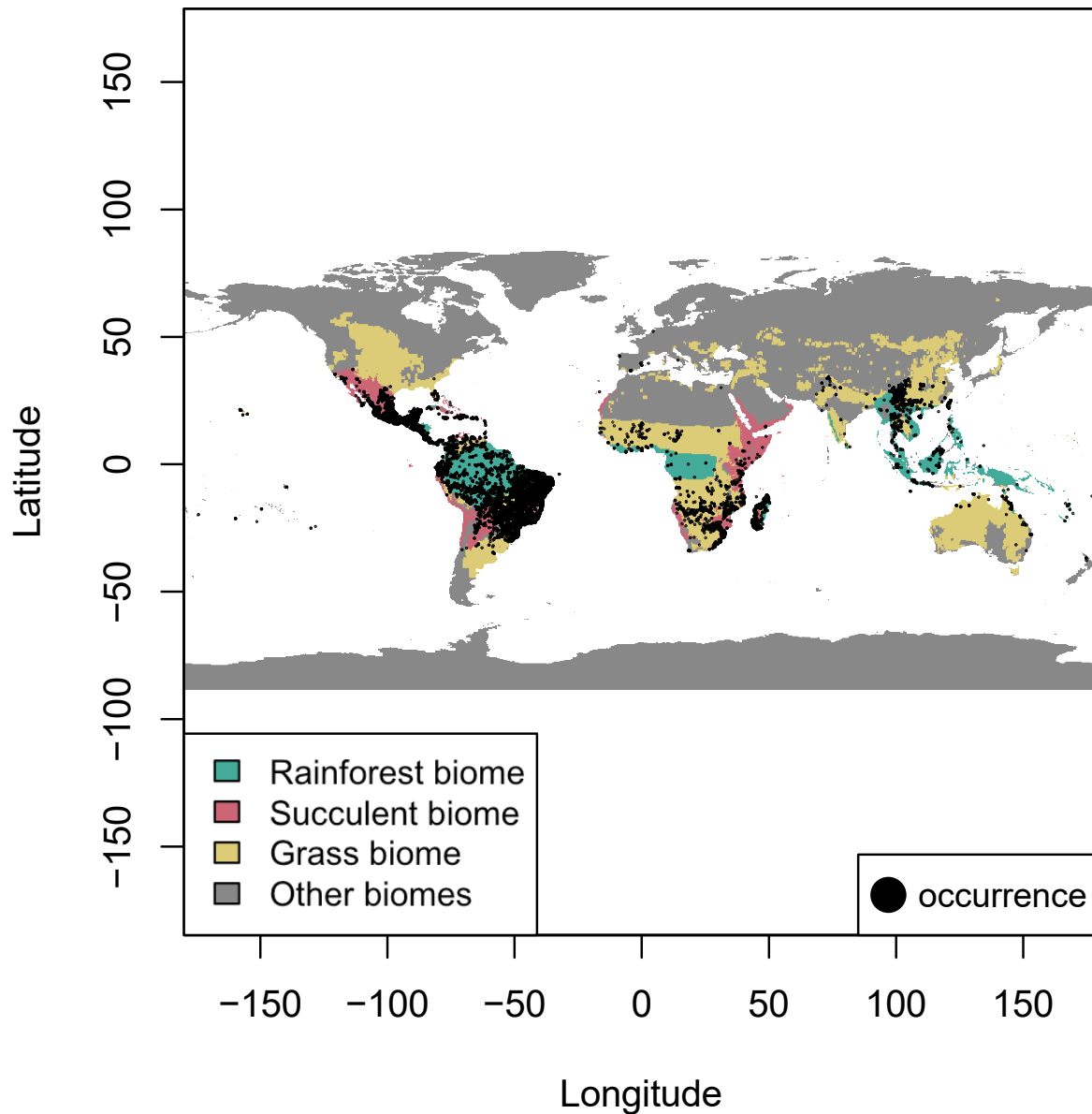
Carte 1: Répartition des deux espèces d'*Adenolobus* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2019; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 137 points pour deux espèces).

Barklya sp. occurrences across biomes



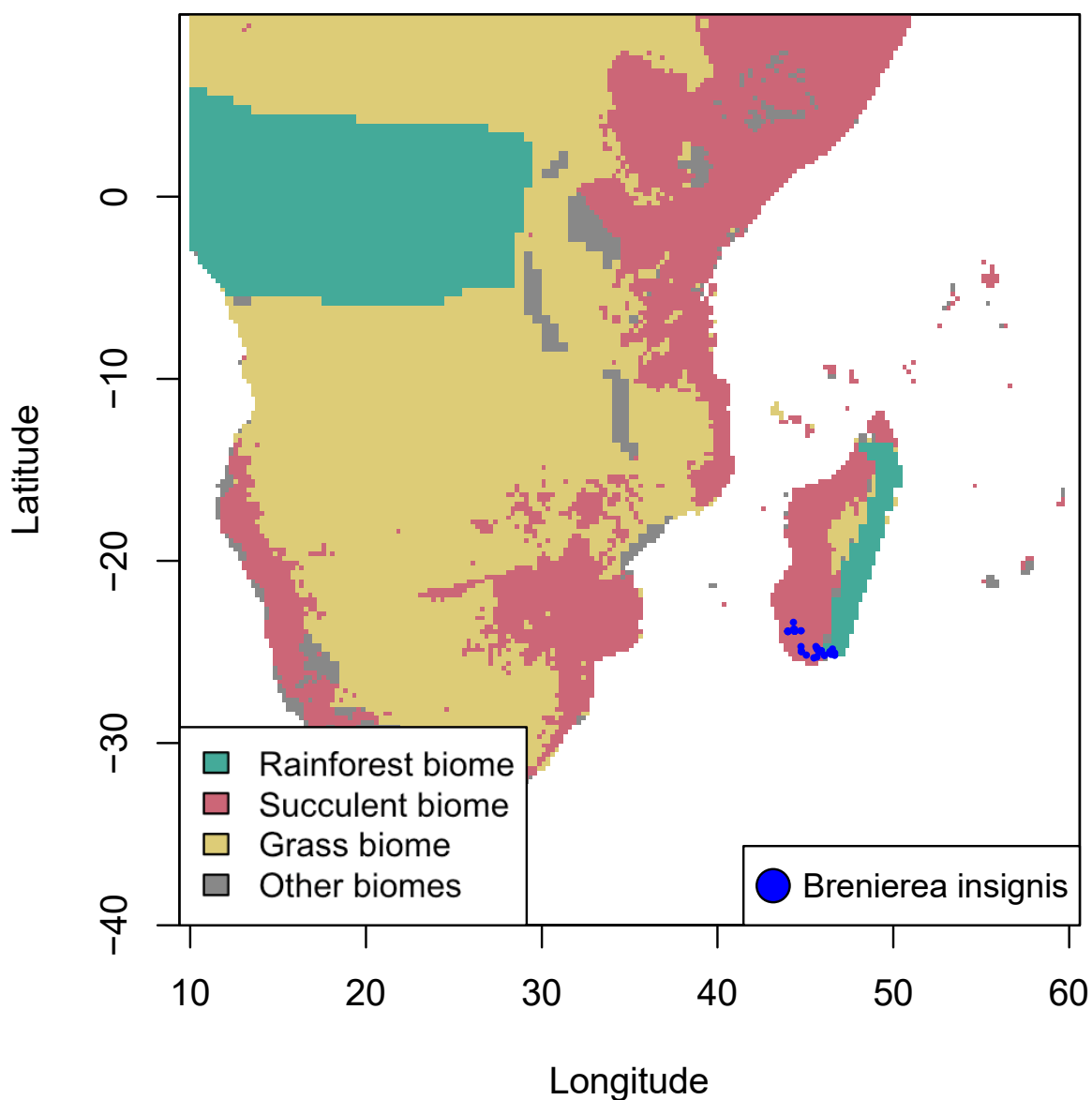
Carte 2: Répartition de *Barklya syringifolia* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2019; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 71 points pour une espèce).

Bauhinia spp. occurrences across biomes



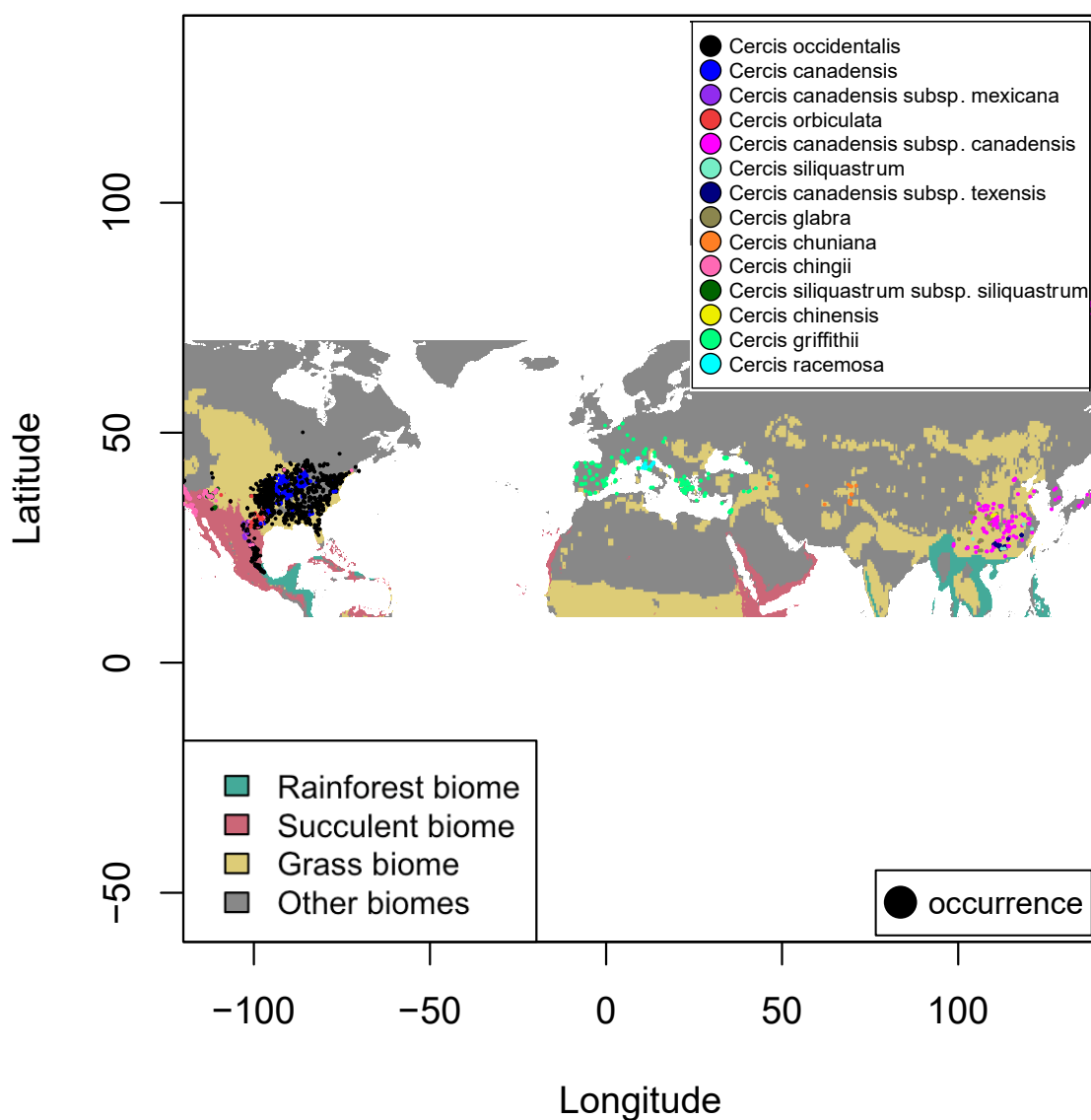
Carte 3: Répartition des espèces de *Bauhinia* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2019; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 16092 points pour 166 espèces).

Brenierea sp. occurrences across biomes



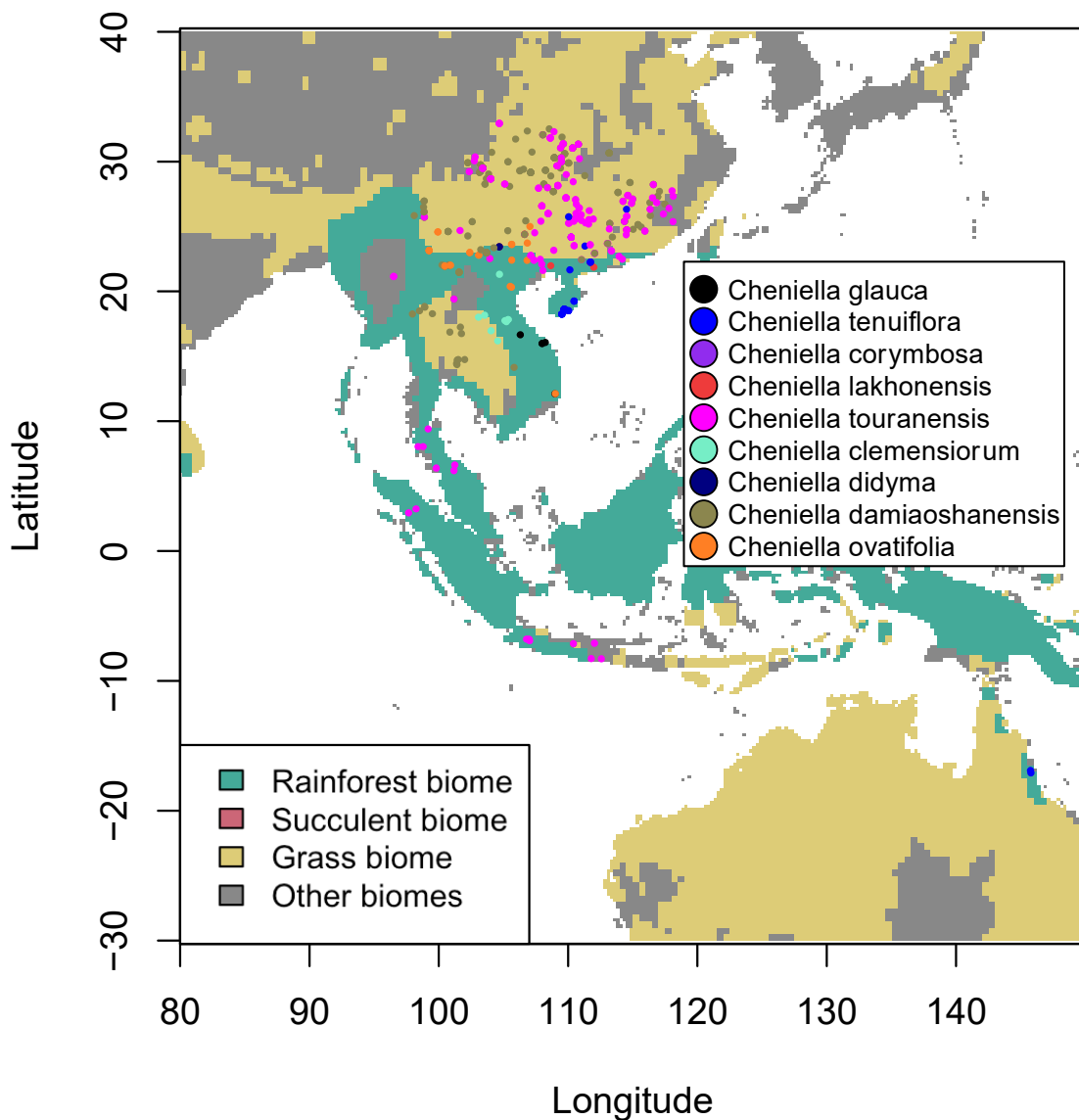
Carte 4: Répartition de *Brenierea insignia* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2020; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 35 points pour une espèce).

Cercis spp. occurrences across biomes



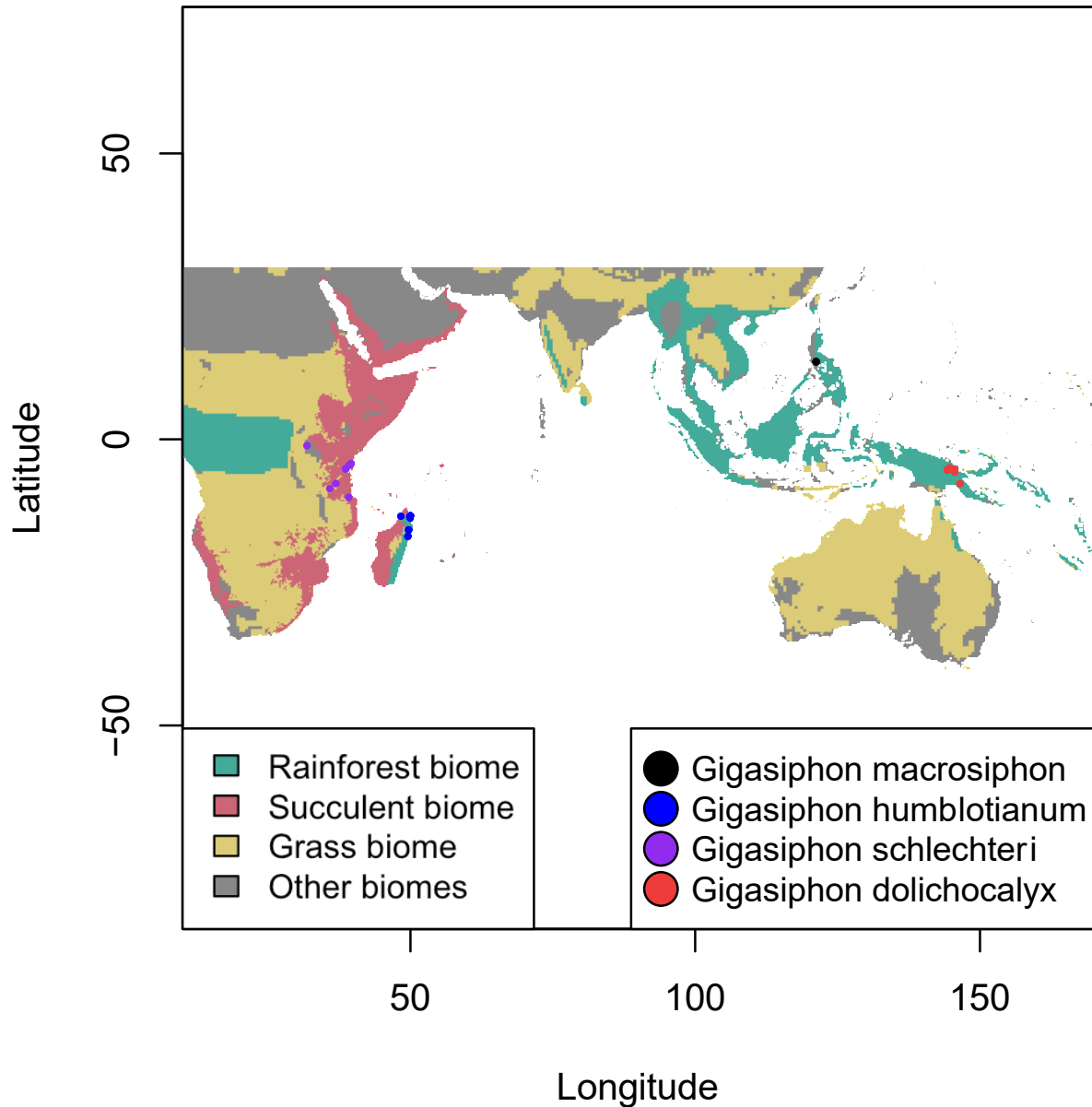
Carte 5: Répartition des 14 espèces de *Cercis* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2019; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 3156 points pour 14 espèces).

Cheniella spp. occurrences across biomes



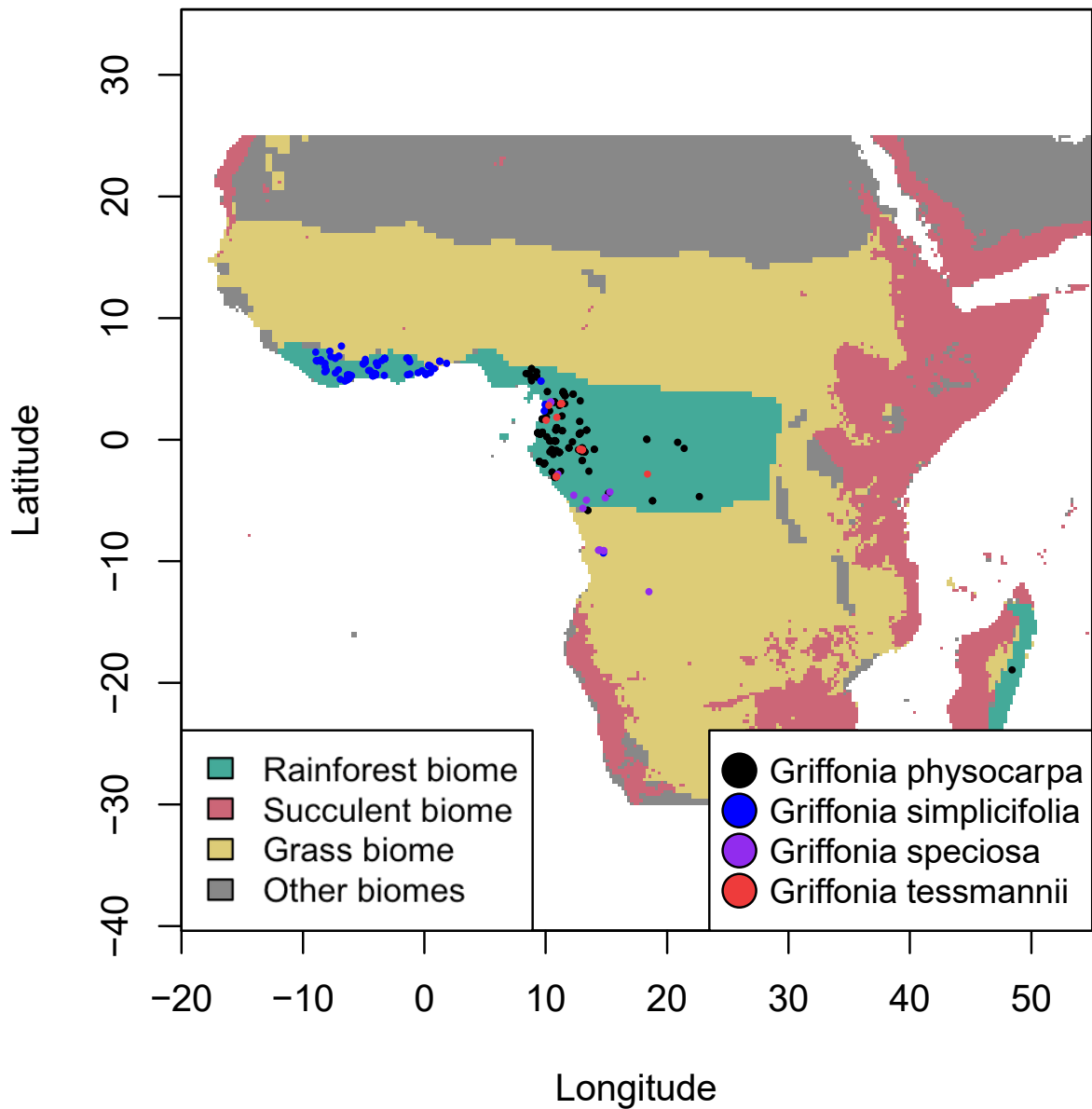
Carte 6: Répartition des neuf espèces de *Cheniella* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2020; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 288 points pour 9 espèces).

Gigasiphon spp. occurrences across biomes



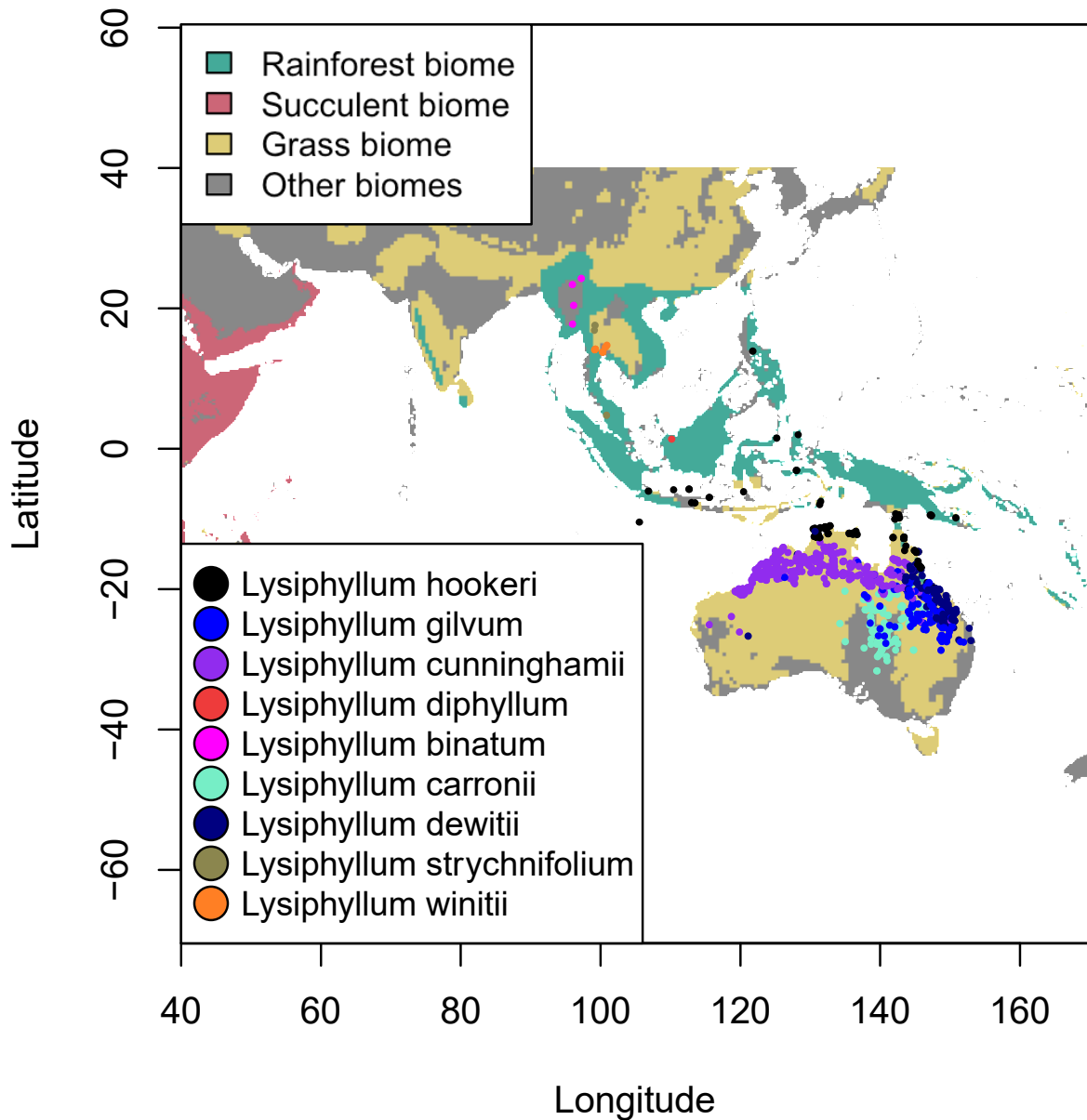
Carte 7: Répartition des quatre espèces de *Gigasiphon* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2019; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 40 points pour quatre espèces).

Griffonia spp. occurrences across biomes



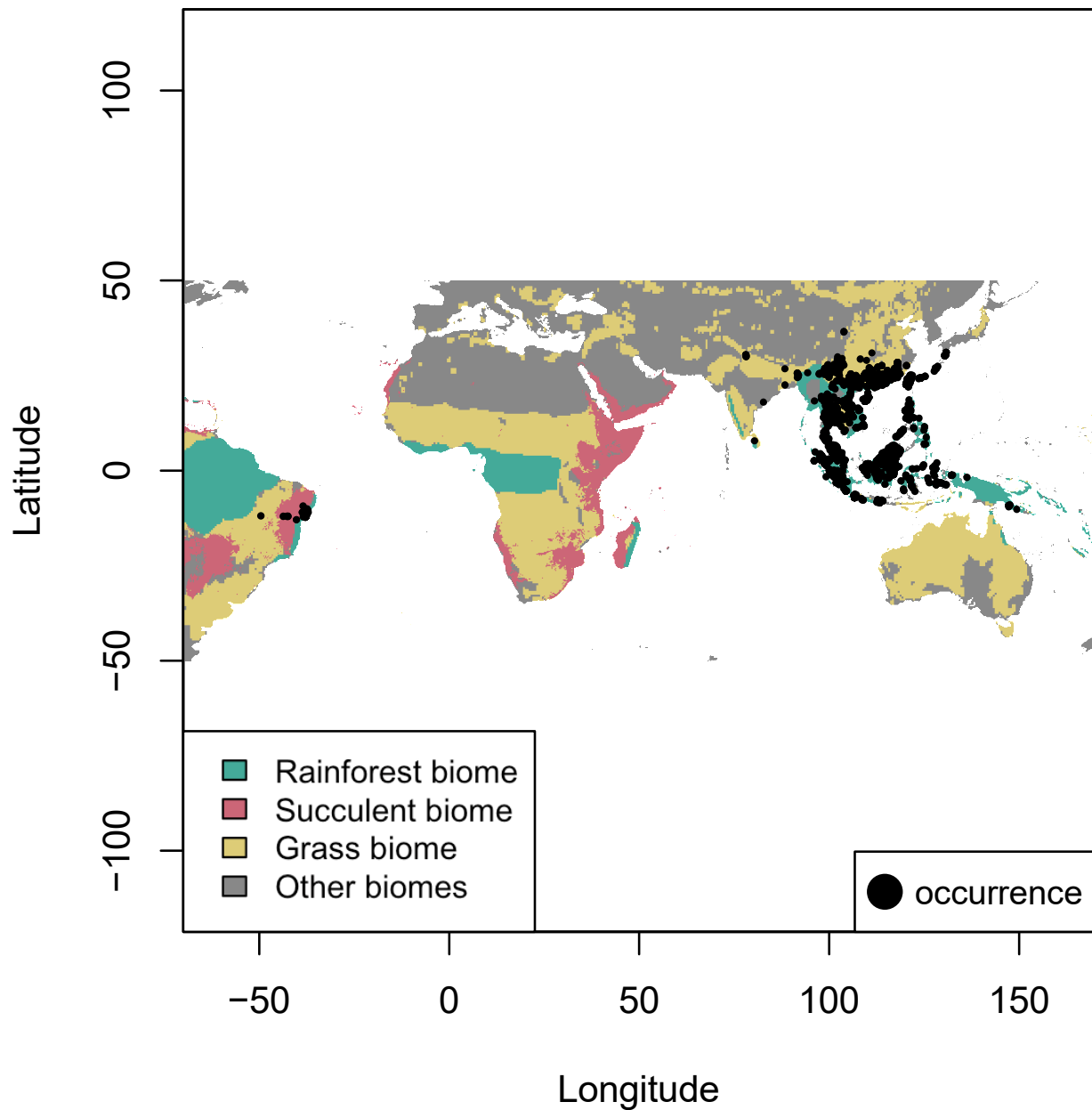
Carte 8: Répartition des quatre espèces de *Griffonia* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2019; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 191 points pour quatre espèces).

Lysiphyllum spp. occurrences across biomes



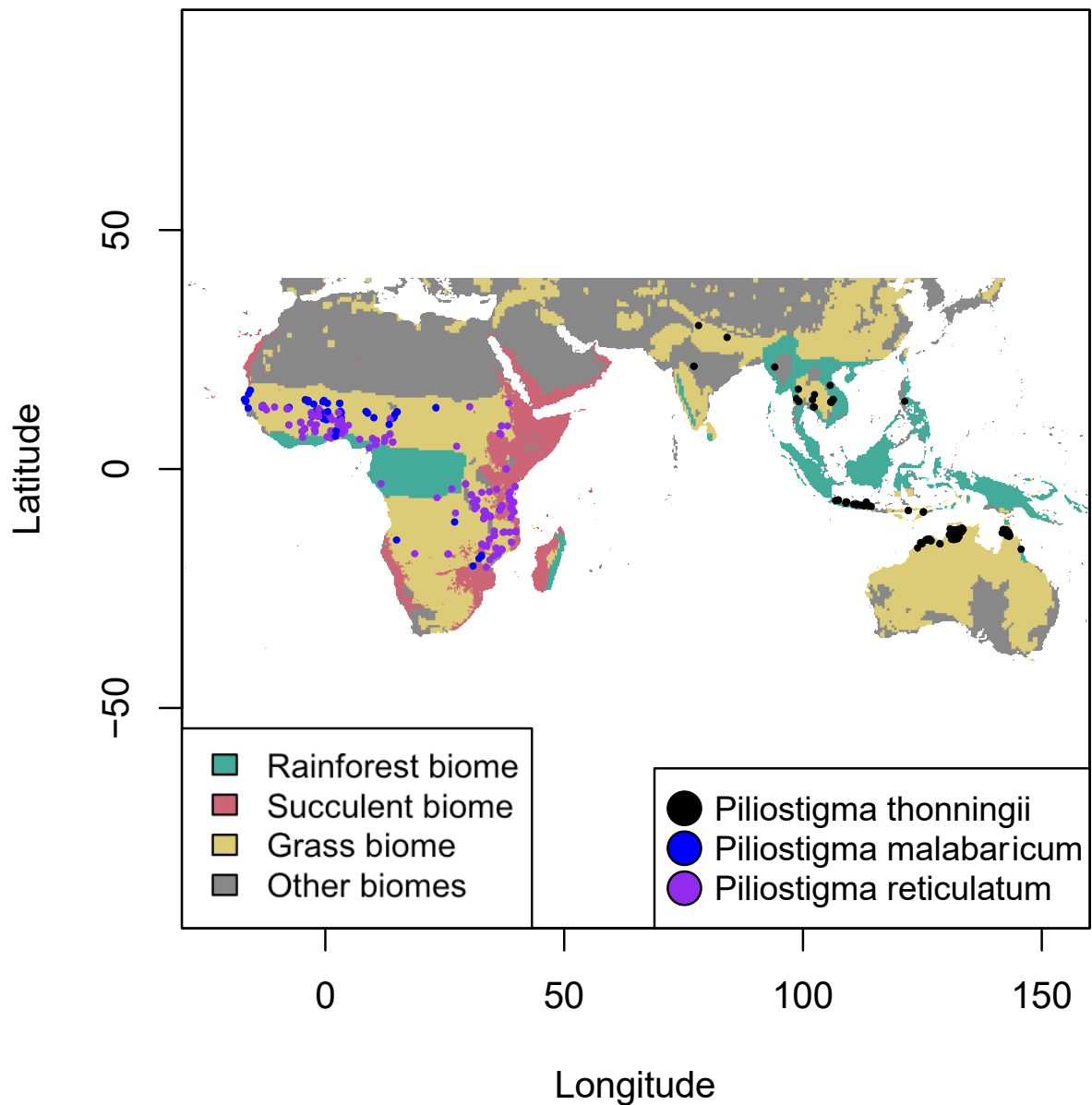
Carte 9: Répartition des quatre espèces de *Lysiphyllum* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2019; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 1107 points pour neuf espèces).

Phanera spp. occurrences across biomes



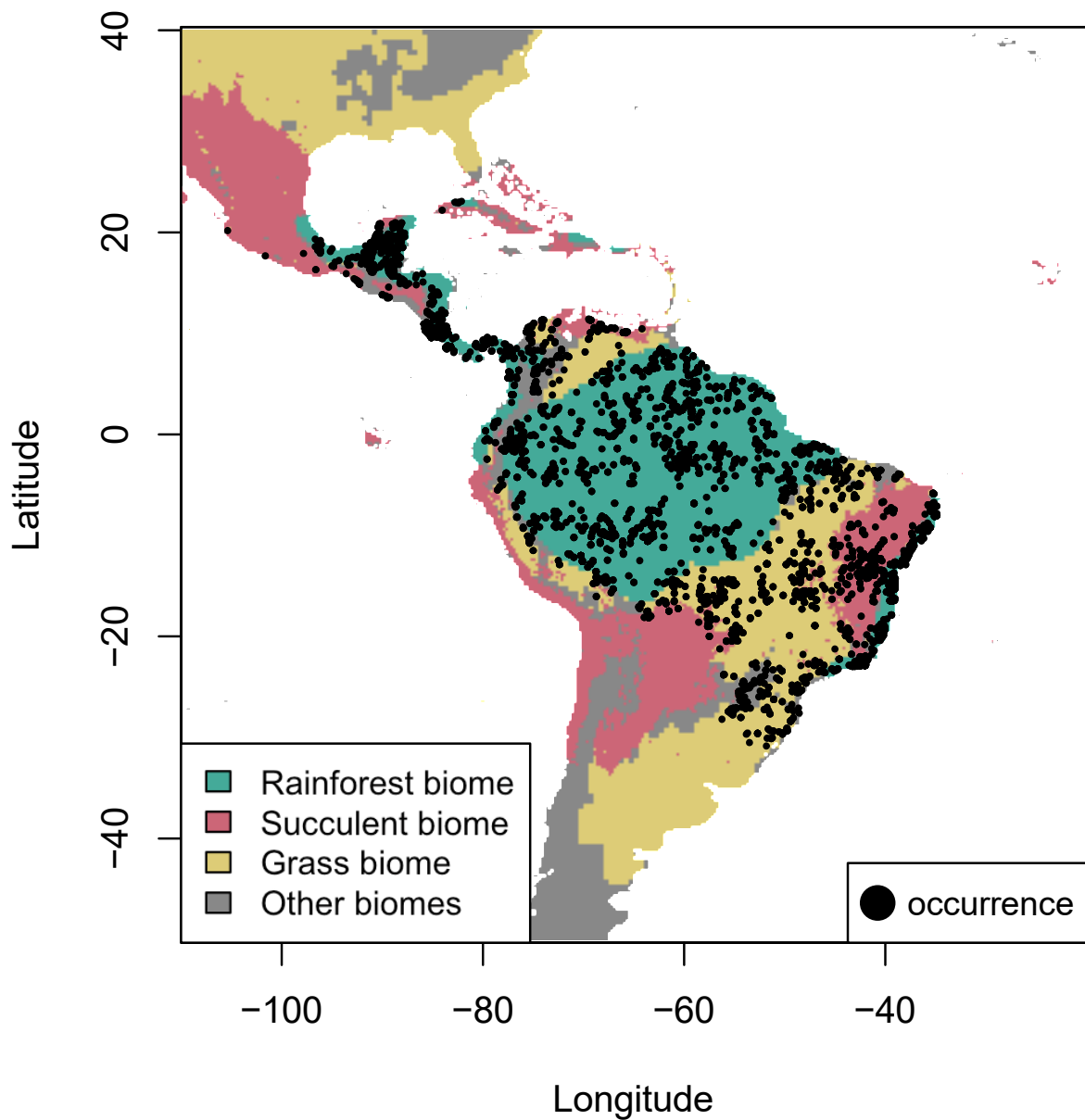
Carte 10: Répartition des espèces de *Phanera* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2019; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 1460 points pour 74 espèces).

Piliostigma spp. occurrences across biomes



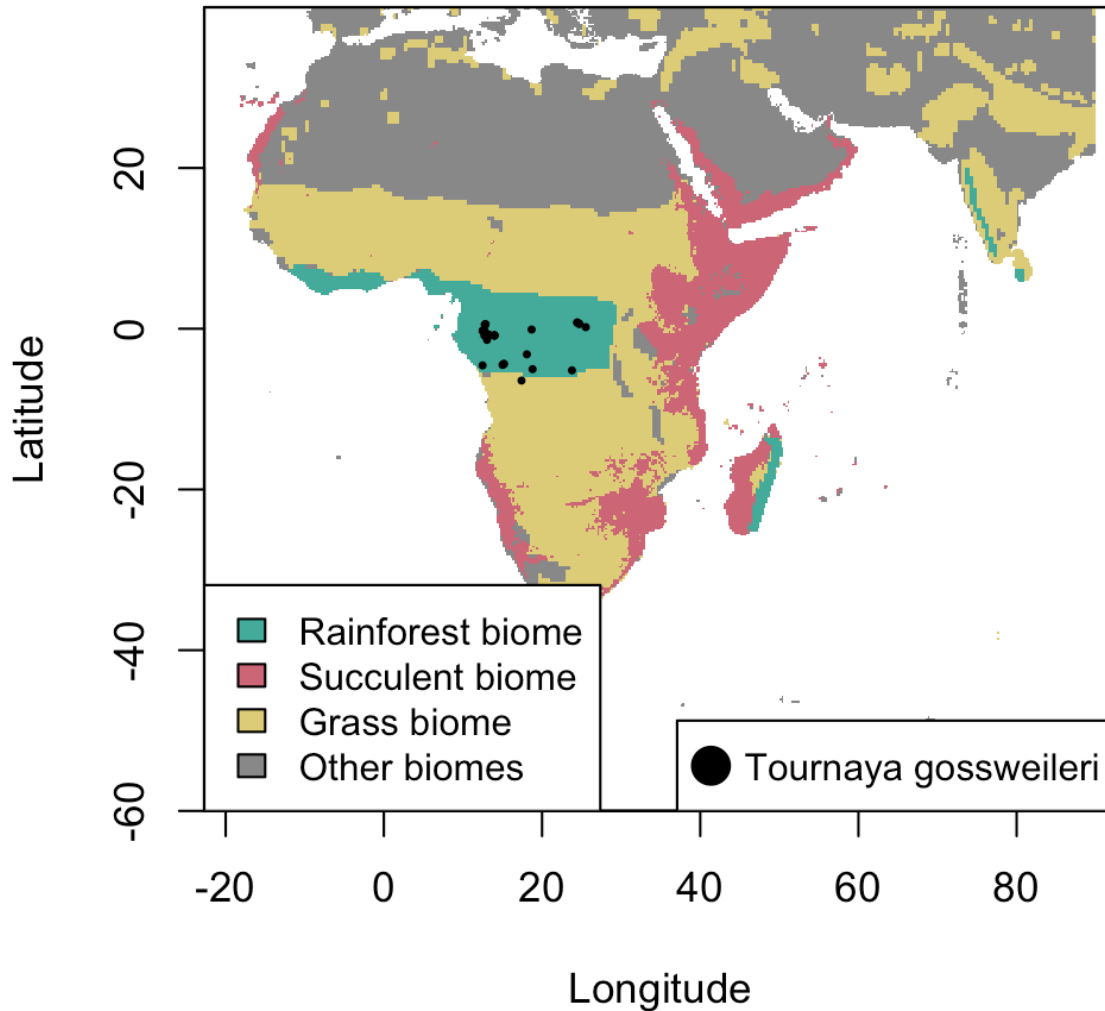
Carte 11: Répartition des trois espèces de *Piliostigma* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2019; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 366 points pour six espèces).

Schnella spp. occurrences across biomes



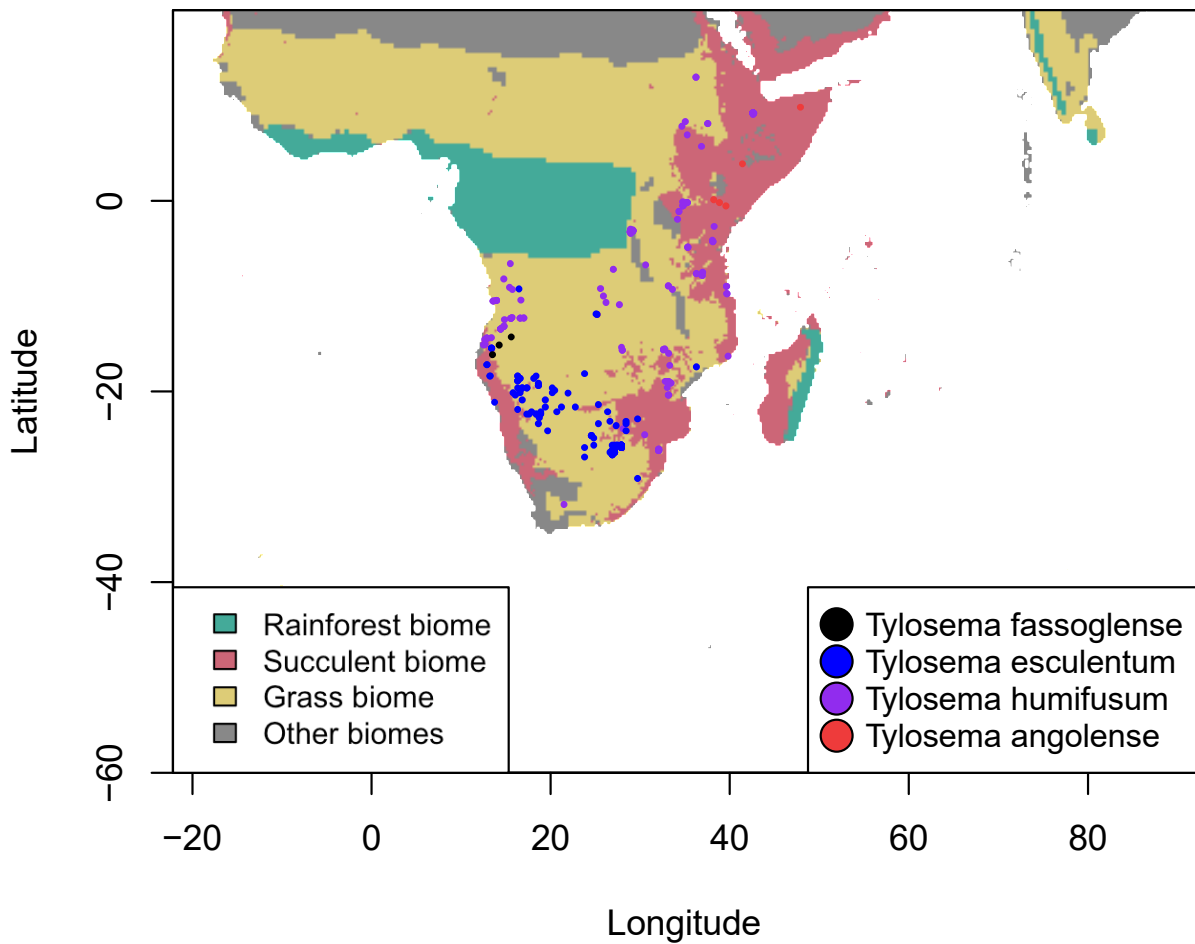
Carte 12: Répartition des espèces de *Schnella* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2019; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 4142 points pour 48 espèces).

Tournaya sp. occurrences across biomes



Carte 13: Répartition de *Tournaya gossweileri* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2020; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 25 points pour 1 espèce).

Tylosema spp. occurrences across biomes



Carte 14: Répartition des quatre espèces de *Tylosema* à travers les cinq régions considérées: le biome savane (Lehmann et al. 2019; représenté en jaune), le biome succulent (Ringelberg et al., 2020; représenté en rouge), le biome forêt tropicale humide (Corlett & Primack, 2011; représenté en vert) et les régions couvertes par aucun de ces biomes (représentées en gris). Chaque point représente une occurrence provenant d'un spécimen d'herbier (total de 181 points pour quatre espèces).

Annexe II- Cartes des occurrences générées dans R (avec ‘ggplot2’ (Wickham 2016) et ‘maps’ (Becker and Wilks 2021)) pour chacune des 340 espèces et sous-espèces de Cercidoideae pour lesquelles des données d’occurrences ont été obtenu.

Disponibles sur :

https://github.com/CharHR/Cercidoideae_Biome_Evolution_C_Hagelstam_Renshaw

Annexe III- Nombres et proportions d’occurrences dans les biomes succulent, forêt tropicale humide, savane et dans aucun de ces trois biomes, pour les 340 espèces et sous-espèces de Cercidoideae pour lesquelles des données d’occurrences ont été obtenu. Pour chaque espèce, les biomes (succulent, forêt tropicale humide et/ou savane) dans lesquels plus de 10% de ses occurrences se trouvent, les biomes attribués aux espèces selon la littérature uniquement et les sources.

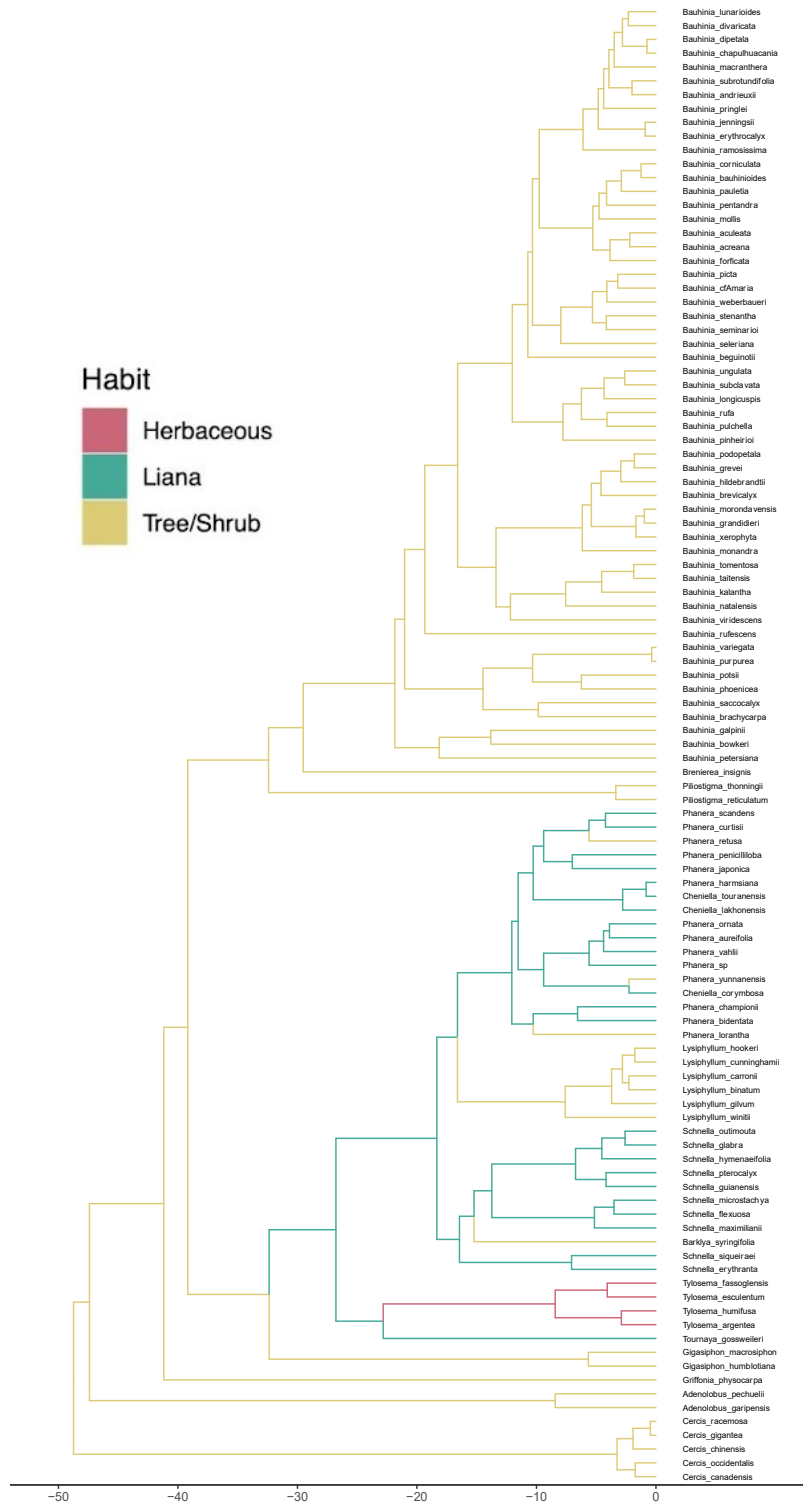
Disponibles sur :

https://github.com/CharHR/Cercidoideae_Biome_Evolution_C_Hagelstam_Renshaw

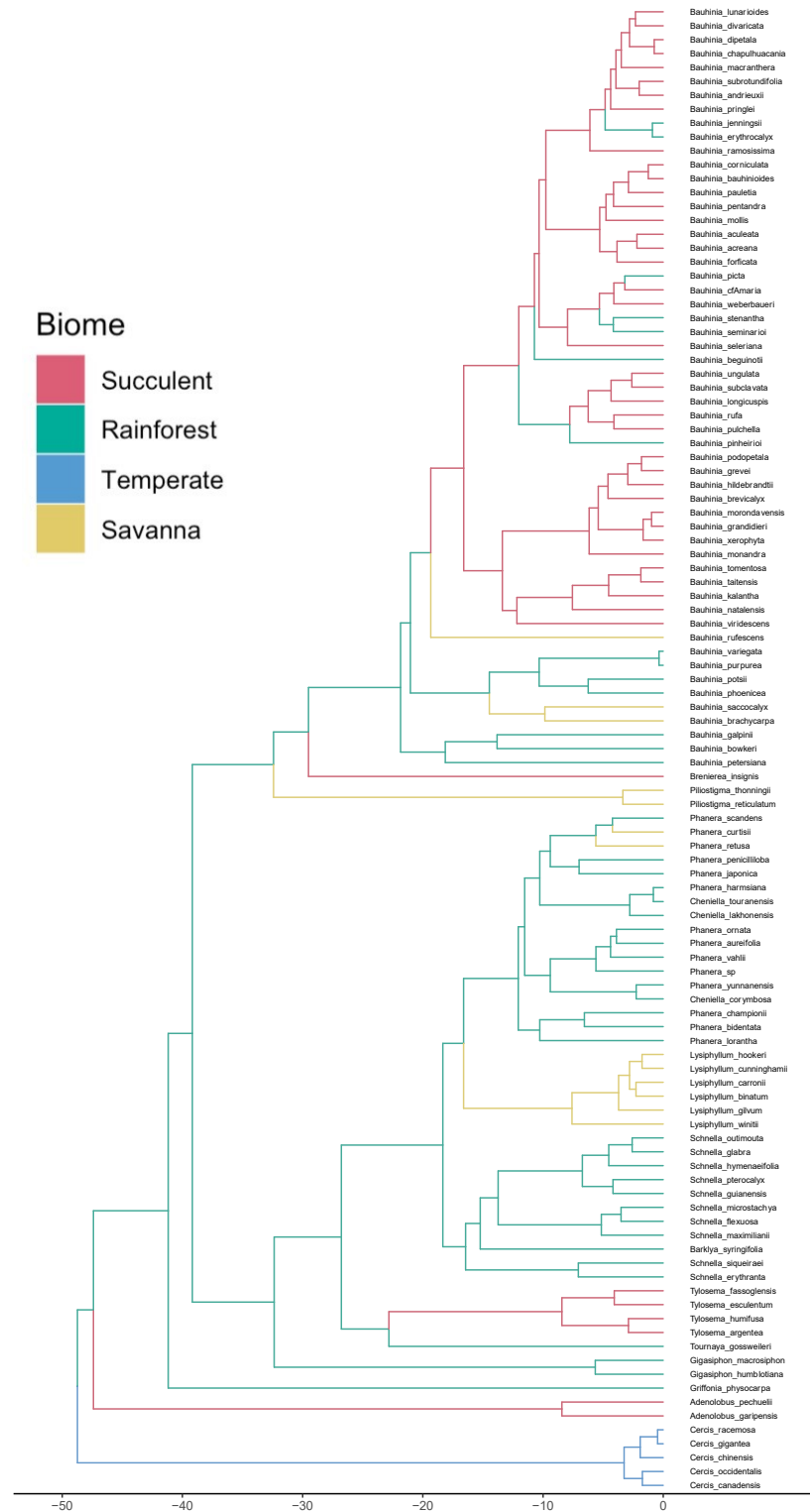
Annexe IV- Biomes, port et continents attribués aux 107 espèces de Cercidoideae considérées dans les analyses phylogénétiques, numéros de collection associés à ces espèces et sources pour les ports et continents attribués aux espèces.

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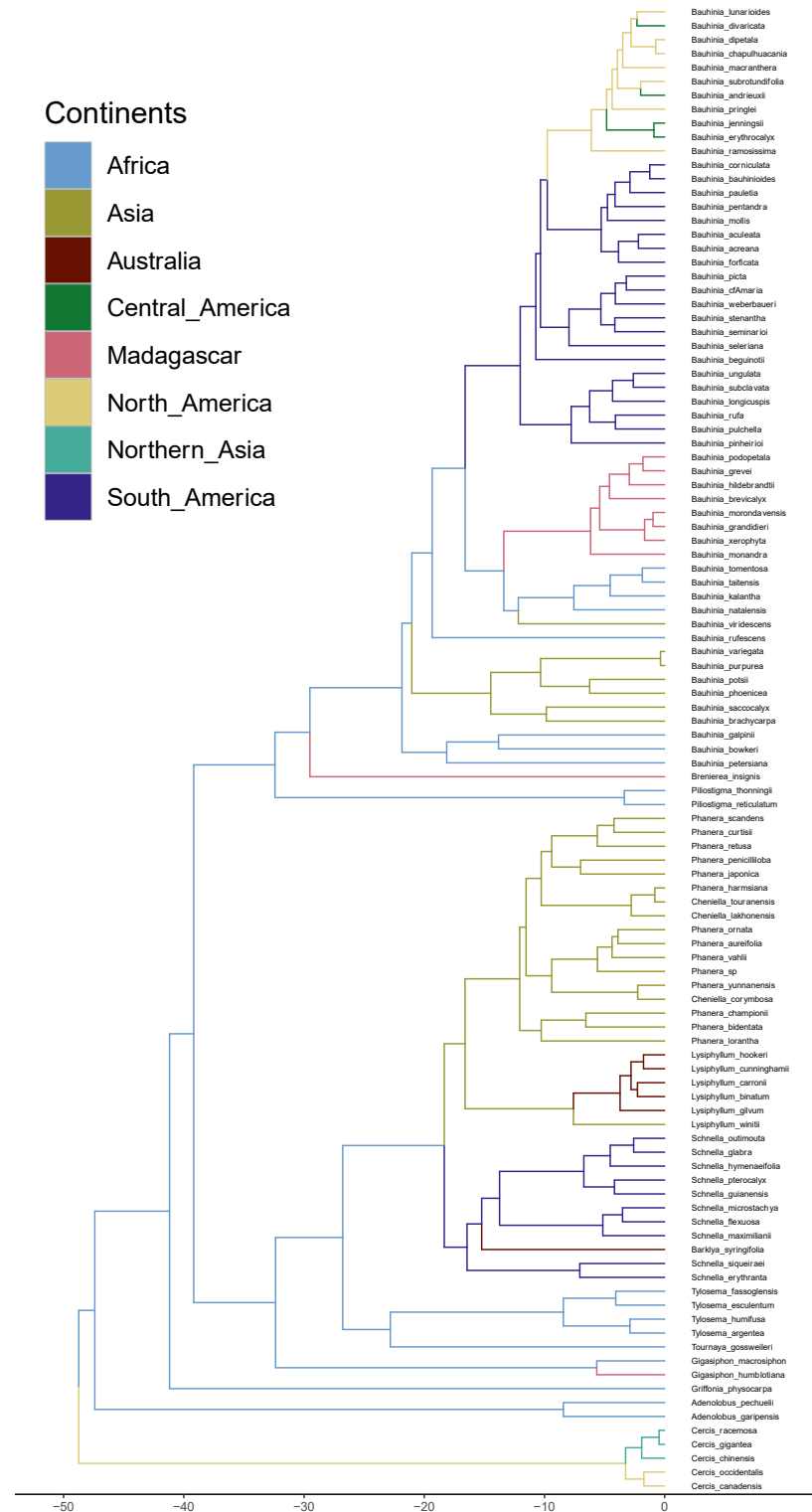
https://github.com/CharHR/Cercidoideae_Biome_Evolution_C_Hagelstam_Renshaw



Annexe V - Reconstruction bayésienne de ports ancestraux pour Cercidoideae, sur la phylogénie calibrée dans le temps (maximum clade credibility tree) générée avec BEAST v. 2.6.3. Les diagrammes circulaires représentés aux nœuds représentent les probabilités des états de biomes d’avoir été reconstruits aux nœuds sur l’ensemble des 80 000 arbres échantillonnés lors de l’analyse. Les ports attribués aux espèces sont présentés dans la figure 2.3.



Annexe VI- Reconstruction bayésienne de biomes ancestraux pour Cercidoideae, sur la phylogénie calibrée dans le temps (maximum clade credibility tree) générée avec BEAST v. 2.6.3. Les diagrammes circulaires représentés aux nœuds représentent les probabilités des états de biomes d’avoir été reconstruits aux nœuds sur l’ensemble des 80 000 arbres échantillonnés lors de l’analyse. Les biomes attribués aux espèces sont présentés dans la figure 2.3.



Annexe VII- Reconstruction bayésienne de continents ancestraux pour Cercidoideae, sur la phylogénie calibrée dans le temps (maximum clade credibility tree) générée avec BEAST v. 2.6.3. Les diagrammes circulaires représentés aux nœuds représentent les probabilités des états de biomes d’avoir été reconstruits aux nœuds sur l’ensemble des 80 000 arbres échantillonnés lors de l’analyse. Les continents attribués aux espèces sont présentés dans la figure 2.4.