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Diversity, Ecology and Evolution of Monocaulous Plants in New Caledonia

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Diversité, Ecologie et Evolution des Plantes Monocaules de Nouvelle-Calédonie

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Résumé: L'évolution convergente des formes de croissance est un phénomène fondamental reliant l'écologie et l'évolution des plantes. Remarquablement illustré dans plusieurs systèmes insulaires, ce phénomène n'a jamais été clairement identifié en Nouvelle-Calédonie, pourtant connue pour la richesse et l'originalité de sa flore. Par une approche combinant architecture des plantes, traits fonctionnels, taxonomie, phylogénie et données environnementales, cette thèse analyse l'histoire évolutive de la monocaulie, une forme de croissance mal connue, en Nouvelle-Calédonie. Les monocaules sont des plantes autoportantes ligneuses dont les fonctions majeures sont assurées par une seule tige apparente. En Nouvelle-Calédonie, elles sont représentées par 182 espèces dicotylédones appartenant à 41 genres et 30 familles et sont souvent menacées d'extinction. L'évolution répétée de la monocaulie en Nouvelle-Calédonie, issue d'au moins 31 événements d'apparition, est l'un des cas les plus remarquables de convergence en milieu insulaire. Dans le genre *Atractocarpus*, la monocaulie est apparue récemment deux à trois fois via diverses réductions des branches en inflorescences, montrant l'importance des processus hétérochroniques dans l'évolution des formes de croissance. La monocaulie est fortement corrélée à plusieurs traits démontrant des contraintes majeures dans la coordination fonctionnelle. L'évolution de la monocaulie est fortement associée aux forêts denses humides et au substrat ultramafique, et pourrait avoir contribué à la diversification des lignées par des phénomènes de partitionnement de niche. La remarquable convergence de la monocaulie en Nouvelle-Calédonie peut s'expliquer par quatre hypothèses majeures liées (i) à la structure particulière des forêts denses humides (en lien avec les cyclones) favorisant l'exploration unidirectionnelle de l'espace, (ii) aux contraintes édaphiques liées aux substrats ultramafiques induisant une paupérisation architecturale, (iii) à l'absence historique de grands brouteurs, auxquels les monocaules sont particulièrement sensibles, et (iv) à la persistance des forêts denses humides lors des épisodes glaciaires (servant de refuges pour ces espèces sensibles) et leur expansion post-glaciaire (fournissant de nombreuses opportunités écologiques).

Mots-clés : Architecture des plantes, Convergence évolutive, Forme de croissance, Îles, Phylogénie, Traits fonctionnels

Abstract: Convergent evolution in growth habit is a fundamental phenomenon linking plant ecology and evolution. Remarkably illustrated in island biotas, this phenomenon has not clearly been identified in the distinctive and megadiverse New Caledonian biodiversity hotspot. Through an approach combining plant architecture, functional traits, taxonomy, phylogeny and environmental data, this thesis analyses the evolutionary history of the poorly known monocaulous growth habit in New Caledonia. Monocauls are self-supporting woody plants whose cardinal functions rely on a single visible stem. In New Caledonia, they are represented by 182 dicotyledonous species belonging to 41 genera in 30 families and are often endangered. The repeated evolution of monocauly in New Caledonia, resulting from at least 31 independent events, is one of the most remarkable cases of convergence in insular environments. In the genus *Atractocarpus* (Rubiaceae), monocauly evolved recently two or three times through branch reductions into inflorescences, emphasizing the importance of heterochronic processes in the evolution of growth habit. Monocauly is strongly correlated with several traits illustrating major constraints in functional coordination. The evolution of monocauly is strongly associated with rainforests and ultramafic substrate, and could have contributed to the diversification of lineages through niche partitioning. The remarkable convergence toward monocauly in New Caledonia can be explained by four major hypotheses: (i) structural features of rainforests (related to cyclone frequency and intensity) favoring unidirectional exploration of space, (ii) the edaphic constraints associated with ultramafic substrates inducing architectural pauperization, (iii) the historical absence of large native browsers to which monocauls are particularly sensitive, and (iv) the persistence of rainforest during glacial episodes – and expansion afterward – that served as refugia and further provided ecological opportunities.

Keywords: Convergent evolution, Functional traits, Growth habit, Islands, Phylogeny, Plant architecture

Avant-propos :

Cette thèse de doctorat est le fruit de trois années de travail menées à l'Unité Mixte de Recherche botAnique et Modélisation de l'Architecture des Plantes et des végétations (UMR AMAP) au sein du Centre IRD de Nouméa qui accueille l'Herbier de Nouvelle-Calédonie (NOU).

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Certains des chapitres présentés ici ont fait ou vont faire l'objet de publications scientifiques. Ces publications doivent être citées préférentiellement au présent document, notamment pour les actes taxonomiques.

Le document est rédigé en anglais pour le rendre accessible au plus grands nombre. Un résumé étendu en français est disponible à la fin du document.

Foreword:

This PhD Thesis is the result of three years of research conducted within the Joint Research Unit "botAnique et Modélisation de l'Architecture des Plantes et des végétations" (UMR AMAP) at the French National Research Institute for Sustainable Development (IRD) from Nouméa, which hosts the Herbarium of New Caledonia (NOU).

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Several chapters of this PhD have been or will be published in scientific journals. These publications should be cited rather than this PhD document, especially for taxonomic acts.

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« C'est l'île aux mille rivières limpides prenant leur source dans des forêts primitives, l'île des falaises et des cimes empanachées de pins colonnaires, l'île des kaoris, des palmiers, des fougères géantes, comme c'est l'île des maquis aux floraisons d'une infinie variété et des niaoulis chatoyant soir et matin aux rayons obliques du soleil. […] mais plus encore, ce sont les détails qui retiennent l'attention, l'architecture étrange d'un arbre, le dessin d'un feuillage, la couleur d'une fleur. On est surpris de la richesse et de la fantaisie de la décoration, car chaque massif a sa flore, chaque forêt recèle des plantes rares. »

Maurice Schmid (1981)

À la Nouvelle-Calédonie et ses habitants,

Terre de Parole, Terre de Partage

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Chapter 1 — General Introduction

1.1 Islands as models in ecology and evolution

Most of major ecological and evolutionary theories have been influenced by works on island biotas (Darwin, 1859; Wallace, 1880; MacArthur and Wilson, 1967; Warren et al., 2014; Whittaker et al., 2017). Given their isolation and particular environmental conditions and history, oceanic islands are exceptionally suited for the investigation of convergent evolution and adaptive radiation (Elmer and Meyer, 2011; Whittaker et al., 2017). One of the most famous and remarkable adaptations of insular floras, involved in both convergent evolution (Givnish, 2010; Lens et al., 2013) and adaptive radiation (Bramwell, 1975; Jorgensen and Olesen, 2001), is the so-called "secondary woodiness" (i.e. the evolution of woodiness in herbaceous lineages). This notable pattern was formerly described by Darwin (1859), extensively studied by Carlquist (1974), and remains a hot topic in plant science (e.g. Lens et al., 2012a; Rowe and Paul-Victor, 2012). Though first described from islands, the phenomenon also occurs in continental floras, leading to a generalization of concepts (Lens et al., 2012b; Lens et al., 2013; Kidner et al., 2016; Whittaker et al., 2017).

Islands, as natural laboratories for the study of ecology and evolution, continue to provide opportunities for understanding general patterns and processes of plant evolution (Whittaker et al., 2017). In particular, information on functional traits and phylogenetic relations of island species represent gaps that need to be filled (Santos et al., 2016; Keppel et al., 2018).

Among islands, New Caledonia has been recognized as a particularly promising model for ecological and evolutionary studies (Grandcolas et al., 2008; Murienne, 2009; Jaffré et al., 2013;

Grandcolas, 2017). The long-term isolation and particular history of New Caledonia have resulted in a flora that harbors many peculiarities, including the outstanding richness in endemic and microendemic species (Lowry, 1998; Grandcolas et al., 2008; Morat et al., 2012; Wulff et al., 2013; Ibanez et al., 2017b), a high incidence of relictual lineages, which remains puzzling (Pillon, 2012; Pillon et al., 2017), and an exceptional diversity of some globally rare lineages (Jaffré, 1995; Pillon et al., 2010; Pouteau et al., 2015). Recent biogeographic and phylogenetic studies failed to find much evidence for old *in situ* radiations and rather indicates that the island's richness might result from a combination of relictual lineages, repeated colonization events, and recent speciation (Grandcolas et al., 2008). This led some authors to consider New Caledonia as an "old Darwinian island" (Grandcolas et al., 2008; Swenson et al., 2014) and one of the world's main biogeographical regions (Guillaumin, 1934; Good, 1964; Takhtajan, 1969; van Balgooy, 1971; Morat et al., 1994). Despite these peculiarities, virtually no example of remarkable convergence has been demonstrated to date, in contrast with striking cases of convergent evolution and adaptive radiation found in other islands (Elmer and Meyer, 2011; Whittaker et al., 2017).

1.2 Convergence and adaptive value of traits

An important feature of insular biota is their taxonomic and functional disharmony (Carlquist, 1974; Cody and Overton, 1996; Gillespie, 2001; Pillon et al., 2010; Lens et al., 2013; Schlessman et al., 2014). Taxonomic disharmony, i.e. the uneven representation of some lineages, is widely regarded as a strong evidence of long-distance dispersal and has been largely documented (e.g. Carlquist, 1974; Loope et al., 1995; Pillon et al., 2010). Functional disharmony, i.e. the uneven representation of functional trait attributes, has rather been studied through the concept of "island syndromes" (Whittaker et al., 2017). Among frequently cited trait attributes, those over-represented on islands are woodiness (Carlquist, 1974; Shmida and Werger, 1992; Lens et al., 2013), sexual dimorphism (Sakai and Weller, 1999; Jorgensen and Olesen, 2001; Schlessman et al., 2014), heterophylly (Cockayne, 1919; Friedmann and Cadet, 1976; Givnish, 1994), monocarpy (Jorgensen and Olesen, 2001; Read et al., 2008), and loss of dispersability (Carlquist, 1974; Cody, 1986; Fresnillo and Ehlers, 2007). The high frequency of a trait attribute in islands could result from (i) preferential establishment of species presenting the attribute, (ii) repeated *in situ* independent evolution of the attribute, and/or (iii) *in situ* diversification of lineages presenting the attribute (Figure 1.1). Identifying which mechanisms account for the high incidence of a given trait attribute is thus crucial for understanding which ecological and evolutionary processes have driven the development of the current taxonomic and functional diversity.

Among the important phenomena of evolutionary theory stands convergent evolution, i.e. the appearance of a similar trait attribute under similar selection pressures but not inherited from a common ancestor (McGhee, 2011; Givnish, 2016). While the term “convergence” has been expanded in community ecology, where it concerns plant association rather than plant evolution (e.g. Cody, 1973; Lamont et al., 2002; Díaz et al., 2004; Fukami et al., 2005; Grime, 2006), a phylogenetical approach is needed to demonstrate evolutionary convergences. Convergence provides the most powerful line of evidence for adaptive evolution, i.e. the selective advantage of traits in a given environment (Endler, 1986; Grime, 2006; Wake et al., 2011; Givnish, 2016). Convergent evolution is particularly striking when environmental conditions are constraining, as in arid (e.g. Arakaki et al., 2011), frost-prone (e.g. Givnish, 2010; Boucher et al., 2016) or nutrient poor environments (e.g. Albert et al., 1992; Ellison and Gotelli, 2001). By contrast, when the environment is less constraining (or at smaller phylogenetic scale), biotic factors (i.e. competition) prevail, leading to divergent selection among close relatives (Weiher and Keddy, 1995; Givnish, 2016). Divergent selection, sometimes leading to adaptive radiation (i.e. the rise of a diversity of

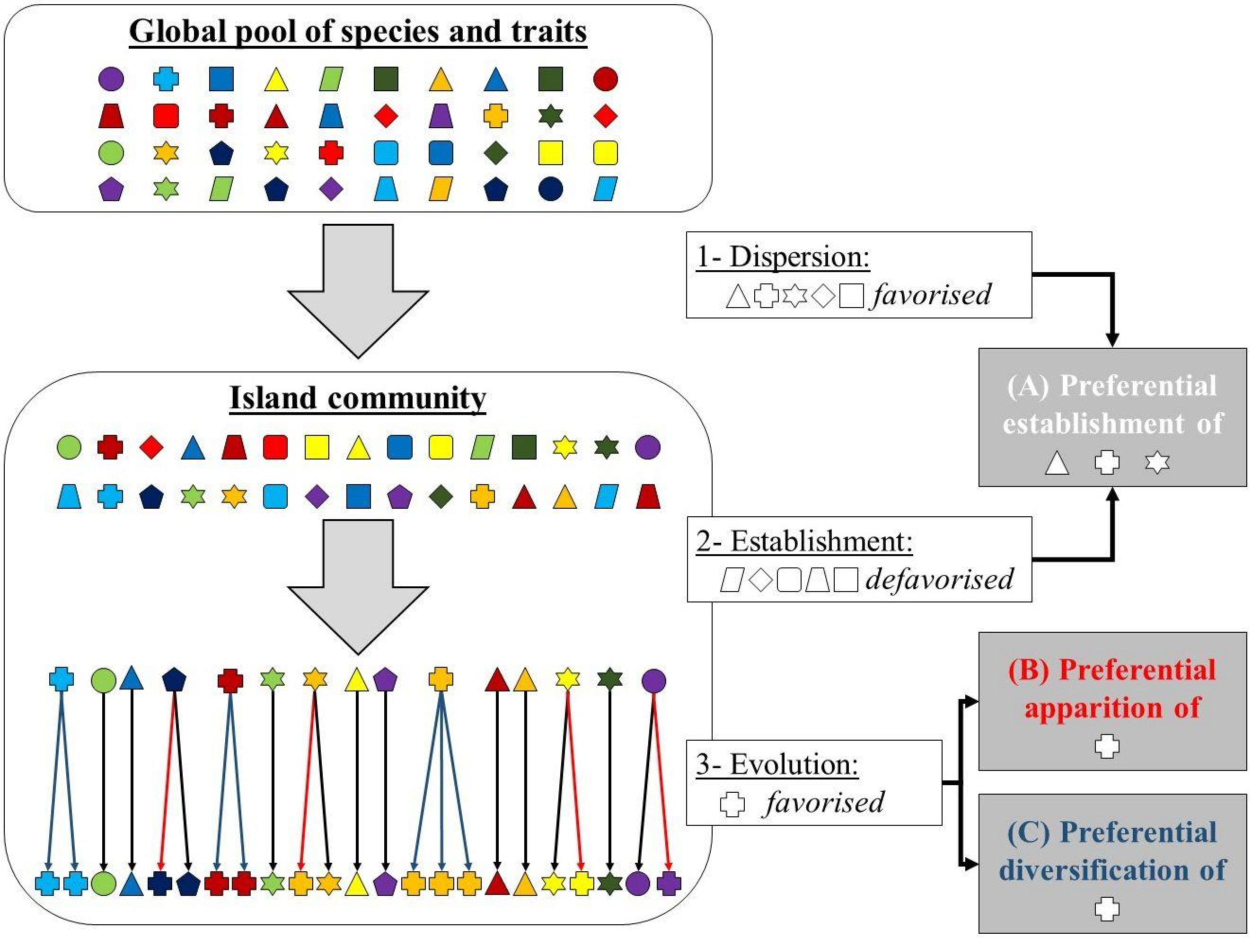


FIGURE 1.1 – Illustration of theoretical mechanisms leading to island syndromes. Each form represents a hypothetical attribute and each color represents a hypothetical lineage. High occurrence of an attribute (here ✚) in the island could be due to **(A)** establishment of species presenting the trait (dispersion filter and establishment filter), **(B)** repeated evolution of the trait and/or **(C)** diversification of lineages presenting the trait.

ecological roles, Givnish, 2016) results from different exploitation of resources among closely related species (Schluter, 2000; Grime, 2006). However, while convergent and divergent evolution are opposite evolutionary phenomena, divergent selection, when occurring repeatedly in distinct lineages, can also lead to convergence (Thomson and Wilson, 2008).

Some authors consider that convergence is related to the concept of evolutionary constraint, i.e. that evolutionary pathways are constrained by a limited set of functional and developmental possibilities (Thomson and Wilson, 2008; McGhee, 2011). Convergence has often been used as a key argument against stochasticity in evolutionary theories (Patterson, 1988; Wake, 1991; Kreitman and Akashi, 1995; Schluter and Nagel, 1995). Physical laws and phylogenetic background are though to impose functional constraint, while environment provides an overall standard value (McGhee, 2011; Díaz et al., 2016; Olson et al., 2018). Convergence thus provides a framework for elucidating evolutionary constraints and prerequisites of some trait associations. This might especially pertain to functional traits that are widely represented in global plant spectra (Westoby et al., 2002; Reich et al., 2003; Westoby and Wright, 2003; Wright et al., 2004; Wright et al., 2007; Díaz et al., 2016) and whose correlated evolution leads to more integrative plant traits such as growth habit.

1.3 Convergence in growth habit

Most of the striking examples of convergence in the plant world concern growth habit, illustrated for instance by rosette-trees in high-elevation tropical regions (Givnish, 2010, 2016), cactoid trees in deserts (Arakaki et al., 2011; Hernàndez-Hernàndez et al., 2011), cushion plants in high-alpine mountains (Boucher et al., 2012; Boucher et al., 2016), and lianas in tropical (seasonal) rainforests (Gianoli, 2015; Isnard and Feild, 2015).

Growth habit, the general physiognomical appearance of a plant, results from the combination of morphological and anatomical traits, with a particular importance of structural traits (see Du Rietz, 1931; Lacza and Fekete, 1969; Millan, 2016 for reviews). The term is used in this study as a synonym for other widely used terms with similar definitions (e.g. vegetative form, life form, growth form… Warming, 1909). Despite different terminologies, the notion of growth habit reflects specific strategies of resource acquisition and use, and consequently involves strong relations with the environment. Such integrative plant traits are of ecological and evolutionary interest (Eriksson and Bremer, 1992; Dodd et al., 1999; Gianoli, 2004; Bonser and Geber, 2005) because they involve a set of underlying traits, potentially reinforcing the effect on fitness (Arakaki et al., 2011). For instance, convergence toward a liana habit implies correlated evolution of a suite of traits at the morphological scale (e.g. climbing organs, Isnard and Silk, 2009; Couvreur et al., 2015; Sousa-Baena et al., 2018), anatomical scale (e.g. heteroxylly, Angyalossy et al., 2015; Isnard and Feild, 2015) and physiological scale (e.g. high specific hydraulic conductivity, Ewers et al., 1989; Zhu and Cao, 2009; Santiago et al., 2015). Hence, the liana growth habit is present in at least 130 plant families (Gentry, 1991; Isnard and Feild, 2015) and can account for up to 40% of species and stems in some tropical forests (Pérez-Salicrup and Sork, 2001; Schnitzer, 2005; Schnitzer et al., 2015). The evolution of the liana growth habit was shown to increase clade diversification rates (Gianoli, 2004; Couvreur et al., 2015; Gianoli, 2015), as found for other growth habits (e.g. Roquet et al., 2013; Frenzke et al., 2016).

Convergence toward a particular growth habit often preferentially occurs in some clades (Arakaki et al., 2011; Boucher et al., 2016), showing the importance of prerequisites and evolutionary constraints for growth habit evolution (Rowe and Speck, 2005). For instance, some anatomical constructions and morphological attributes facilitate the evolution of a climbing habit

(Isnard et al., 2003; Isnard and Rowe, 2008). By contrast, anatomical characteristics associated with the evolution of a climbing habit can constrain evolution toward self-supporting shrubs and trees (Rowe and Speck, 2005; Wagner, 2010; Wagner et al., 2012). As we move forward in developing our understanding of plant habit evolution (e.g. Dubuisson et al., 2003; Verboom et al., 2004; Bonser and Geber, 2005; Rowe and Speck, 2005; Mort et al., 2007; Wagner et al., 2012; Givnish et al., 2014), the integrative, and yet relevant, framework provided by plant architecture lags behind other approaches (see Bateman, 1994; Bateman, 1999; Meyer-Berthaud et al., 2010; Isnard et al., 2012).

1.4 Linking functional traits and plant architecture

Growth habit results from the integration of a combination of several individual traits (e.g. branching pattern, body size and shape, position of inflorescences, anatomy…) that have often been studied separately (e.g. Carlquist, 1984; Givnish et al., 2009; Isnard et al., 2012; Wagner et al., 2014). As such, growth habit provides some evidence for the correlated evolution (*sensu* Pagel, 1994) of two or more traits across lineages. Some of these trait associations, known as global spectra (e.g. Reich et al., 2003; Wright et al., 2004; Chave et al., 2009; Díaz et al., 2016), are considered as primary drivers of plant evolution and functional diversity worldwide (Díaz et al., 2004; Poorter and Bongers, 2006; Díaz et al., 2016). Among the oldest and best documented are Corner's rules (Corner, 1949, 1953-1954) describing a universal correlation between branching intensity, leaf size, stem size, fruit size, and inflorescence complexity (Corner, 1949; White, 1983b; Bond and Midgley, 1988; Lauri, 1988; Brouat et al., 1998; Cornelissen, 1999; Brouat and McKey, 2001; Westoby et al., 2002; Preston and Ackerly, 2003; Westoby and Wright, 2003; Pickup et al., 2005; Sun et al., 2006; Normand et al., 2008). As such, selection on a single trait is likely to affect whole plant form and function (Figure 1.2). In this context, evolution of growth habit needs to be

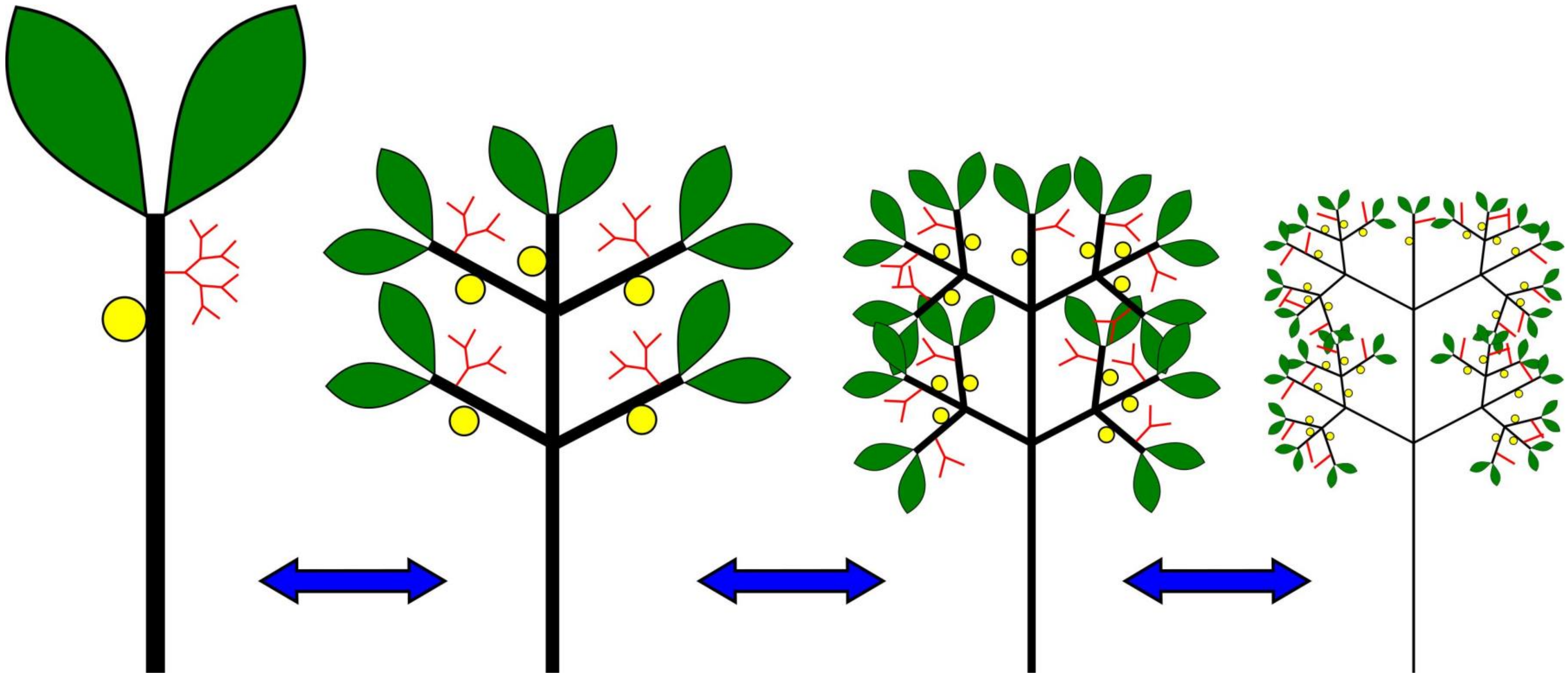


FIGURE 1.2 – Schematic illustration of Corner's rules (Corner 1949) corresponding to two principles; (i) "*Axial conformity*. The stouter, or more massive, the axis in a given species, the larger and more complicated its appendages" and (ii) "*Diminution on ramification*. The greater the ramification, the smaller become the branches and their appendages". Following these principles, a negative correlation is expected between branching intensity and leaf size, fruit size and inflorescence size.

studied through an integrative approach merging functional traits and plant structural construction.

Plant architecture characterizes the spatial arrangement and specialization of structures (morphological origin, branching pattern, axis categorization) and their evolution during ontogeny (Hallé et al., 1978; Barthélémy and Caraglio, 2007, see Chapter 2 for more details). It can consequently highlight how plant structure correlates with function and help identify the evolutionary processes behind plant evolution (see Bateman, 1994; Bateman, 1999; Sussex and Kerk, 2001; Meyer-Berthaud et al., 2010). Architectural studies have taught us that plants are modular organisms composed of structural elements that can differ in their organization and function (Hallé et al., 1978; Barthélémy and Caraglio, 2007). For instance in many tree and treelet species, the trunk mainly assumes exploration and support functions while branches are, in comparison, more specialized in assimilation and reproduction. As such, plant architecture provides integrative tools to understand plant spatial and temporal exploitation of resources (Barthélémy and Caraglio, 2007; Smith et al., 2014). Architectural traits have been shown to impact plant fitness either directly (Küppers, 1989; Millet et al., 1999; Charles-Dominique et al., 2010; Charles-Dominique et al., 2012; Millan, 2016; Charles-Dominique et al., 2017) or in interaction with other functional traits (Pérez-Harguindeguy et al., 2013; Trueba et al., 2016). Plant architecture thus has much to offer in comparative studies that aim to decipher the evolution of plant growth habits and their associated traits.

1.5 The monocaulous growth habit

From the above architectural background, we know that plant functions are generally partitioned into different axis categories. However, among the diversity of extant and past known architectures (see Galtier and Hueber, 2001; Hallé, 2004; Meyer-Berthaud and Decombeix, 2009; Chomicki et al., 2017), some trees that have been referred to as “monocaulous” have such a simple structure that they are constituted by a single stem (Hallé et al., 1978).

Monocauly classically characterizes woody plants constituted by a single unbranched trunk supporting a distal rosette of large leaves (Corner, 1949). The term was used in various domains, and formal definitions – when provided – often differ among studies (see Chapter 3 for a more detailed review). This growth habit, particularly atypical for non-monocots, has fascinated naturalists for a long time (e.g. Von Humboldt, 1808; Cotton, 1944; Corner, 1949; D'Arcy, 1973; Hedberg and Hedberg, 1979) and is at the center of highly discussed ecological and evolutionary theories. Monocaulous species were long considered as relicts of the ancestral form for Angiosperms (Corner, 1949). Recent molecular phylogenies have indicated multiple recent evolution of monocauly in Angiosperms (e.g. Chomicki et al., 2017) but the evolutionary history of extant monocauls remains unclear. Monocaulous plants were also at the inception of Corner's rules (Corner, 1949, 1953-1954) (Figure 1.2), whose statements are today among the most widely documented global spectra (leaf – stem scaling or foliage – stem scaling, e.g. Westoby and Wright, 2003; Olson et al., 2009; Yang et al., 2009). Probably because of their global rarity and restriction to tropical areas, monocaulous species have rarely been included in ecological and evolutionary studies. The most famous case of the evolution of monocauly is represented by "unbranched shrubs with massive leaf rosettes that dominate equatorial alpine zones in many part of the world" (Givnish, 2016). In these rosette-tree species, architecture, anatomy, and leaf features represent adaptation to nightly frost and very high diurnal fluctuations in temperature (Goldstein and Meinzer, 1983; Meinzer and Goldstein, 1986; Melcher et al., 1994; Givnish, 2016). Other monocaulous species are restricted to dry areas, particularly on islands, where their ecology and evolution have been indirectly investigated through secondary woodiness (Mabberley, 1974b, a; Böhle et al., 1996; Mort et al., 2007; Lens et al., 2013). But the majority of monocaulous species seem to occur in tropical rainforests where other abiotic conditions likely favor the evolution of this habit (e.g. Corner, 1949; D'Arcy, 1973; Hallé et al., 1978). This other kind of monocauly has been much less studied, although it has been noted – sometime as highly diversified – in rainforests worldwide such as in New Guinea (Hallé, 1974), Gabon (Hallé and Hallé, 1965), Panama (D'Arcy, 1973), Madagascar (Koechlin et al., 1997), and especially New Caledonia, where monocauly has long attracted the attention of botanists (Carlquist, 1974; Veillon, 1976; Schmid, 1979, 1981, 1990).

Carlquist (1974) was probably the first to note that, in New Caledonia, "there is a modal tendency for smaller, sparsely branched shrubs". Schmid (1981) considered that the preponderance of this growth habit is among the main physiognomical characteristics of New Caledonian rainforest understory. He estimated that at least 20 families include monocaulous or pachycaulous (i.e. sparsely branched) species (Schmid, 1990). A more accurate quantification of the diversity of monocaulous plants in New Caledonia was provided by the work of Veillon (1976), who described the architectural models of 575 vascular plant species. His results indicated that ca. 19% of the studied flora was monocaulous and that this growth habit was found to occur in 23 families. While this study did not include all of the non-monocot flora, the frequency of monocauly in so many different families suggests a potentially remarkable case of convergent evolution.

1.6 Problematic and objectives

Convergence in growth habit is a key evolutionary pattern linking plant architecture, functional traits and the abiotic environment. While the phenomenon is a fascinating particularity of island biotas, it has never been deeply described in the megadiverse and distinctive flora of New Caledonia. Monocauly represents a growth habit whose ecology and evolutionary history remain poorly known and the repeated observations of its frequency in several distantly related families could clearly exemplify the first case of evolutionary convergence for the archipelago. The objectives of this thesis are to investigate the diversity, ecology and evolution of monocaulous species in New Caledonia. More precisely, the rationale and design of the study were developed around the following questions:

- What is monocauly? How many non-monocot monocaulous species are there in New Caledonia?
- How many times did monocauly evolve? What are the evolutionary correlates of monocauly? Are there prerequisites or environmental contingencies that appear to have facilitated its evolution?
- Can we use an architectural approach to depict the evolution of monocauly in a species-level phylogeny? What are the functional and ecological implications of shifts in growth habit? Has monocauly been involved in the diversification of lineages?
- What are the morpho-anatomical traits associated with the monocaulous habit? Do we find evidence that supports Corner's rule?
- Which hypotheses could explain convergence toward monocauly in New Caledonia?

1.7 Thesis outline

This thesis comprises seven chapters of which four are presented under an article format. For these four chapters, only the layout was edited from the original manuscripts articles to provide better consistency within the document. Each chapter depicts different and complementary approaches to characterizing monocauly and analysing the diversity, ecology and evolution of monocaulous plants in New Caledonia.

Chapter 2 presents the general methodology used throughout this work. It describes in particular the study sites, the architectural approach, and how it was used to compile a list of New Caledonian monocaulous species.

Chapter 3 presents a bibliographic synthesis of the concept of monocauly and hypotheses about its evolution and associated life history and environmental traits. This chapter does not follow an article format but is planned to be the starting point of a review paper.

In **Chapter 4** we describe a new monocaulous species encountered during this thesis. By illustrating architectural diversity in the endemic genus *Bocquillonia* (Euphorbiaceae), we also aim to show possible variation in growth habit around a single architectural model.

The aim of **Chapter 5** is to study the evolutionary history of monocaulous species throughout the phylogeny of New Caledonian woody genera. In particular, we quantified repeated evolution, phylogenetic signal and evolutionary correlates of monocauly in the island. IUCN risk of extinction status and threats to the New Caledonian flora were used to evaluate the major threats to monocaulous species.

Chapter 6 aims to illustrate in detail the evolution from a branched habit toward the monocaulous habit and the functional implication of this transition in the genus *Atractocarpus* (Rubiaceae). We furthermore investigated how growth habit transition could affect species diversification in the genus.

The aim of **Chapter 7** is to analyse morpho-anatomical traits of monocaulous species through a comparative approach that also includes branched close relatives and to provide insights into the functional implications of Corner’s rules.

Finally, the results of these chapters are summarized, combined and discussed in **Chapter 8**. This general discussion deals in particular with the functional attributes and adaptive significance of monocauly, evolutionary pathways leading to monocauly, inferences about the evolution and conservation of the New Caledonian flora, and the general interest of plant architecture to depict plant ecology and evolution.

Chapter 2 — General methodology

2.1 Study location: the New Caledonian archipelago

2.1.1 Geography and abiotic environment

New Caledonia is a French archipelago located in the Southwest Pacific Ocean slightly north of the Tropic of Capricorn (20-23°S, 164-167°E, Figure 2.1), east of Australia (ca. 1400 km) and north of New Zealand (ca. 2000 km). The total land area is about 18,500 km², of which the largest island (*Grande Terre*) covers 89%. The remaining land area is divided between the Loyalty Islands (*Ouvéa*, *Lifou* and *Maré*), *Belep*, the *Ile des Pins* and several smaller islands (Figure 2.1). *Grande Terre* (ca. 400 km long and 50 km wide on average) is divided lengthwise (from Northwest to Southeast) by a continuous mountain range that reaches 1628 m in the North (*Mont Panié*) and 1618 m in the South (*Mont Humboldt*). This mountain range is closer to the east coast, where it drops steeply into the sea, while the west coast is characterized by relatively broad plains, except on the Northwest, where large isolated mountains occur.

The subtropical climate of New Caledonia is strongly influenced by a marked orography; mean annual precipitation ranges from 800 mm.yr^{-1} in the lowlands of the leeward west coast to more than 4000 mm.yr^{-1} on the windward east coast and mountain tops (Météo-France, 2007; Maitrepierre, 2012). A dry season (precipitation < 100 mm.month^{-1}) occurs from August to November. Mean annual temperatures are comprised between ca. 20 and 25 °C, and frost is supposed to rarely occurs, even on mountain tops (Maitrepierre, 2012). New Caledonia is frequently subject to cyclones and tropical depressions (3 or 4 per year on average) that can be very intense (Maitrepierre, 2012; Ibanez et al., 2018a). The climate is highly variable from one year to another due to the influence of larger climatic events such as ENSO (El Niño-Southern Oscillation,

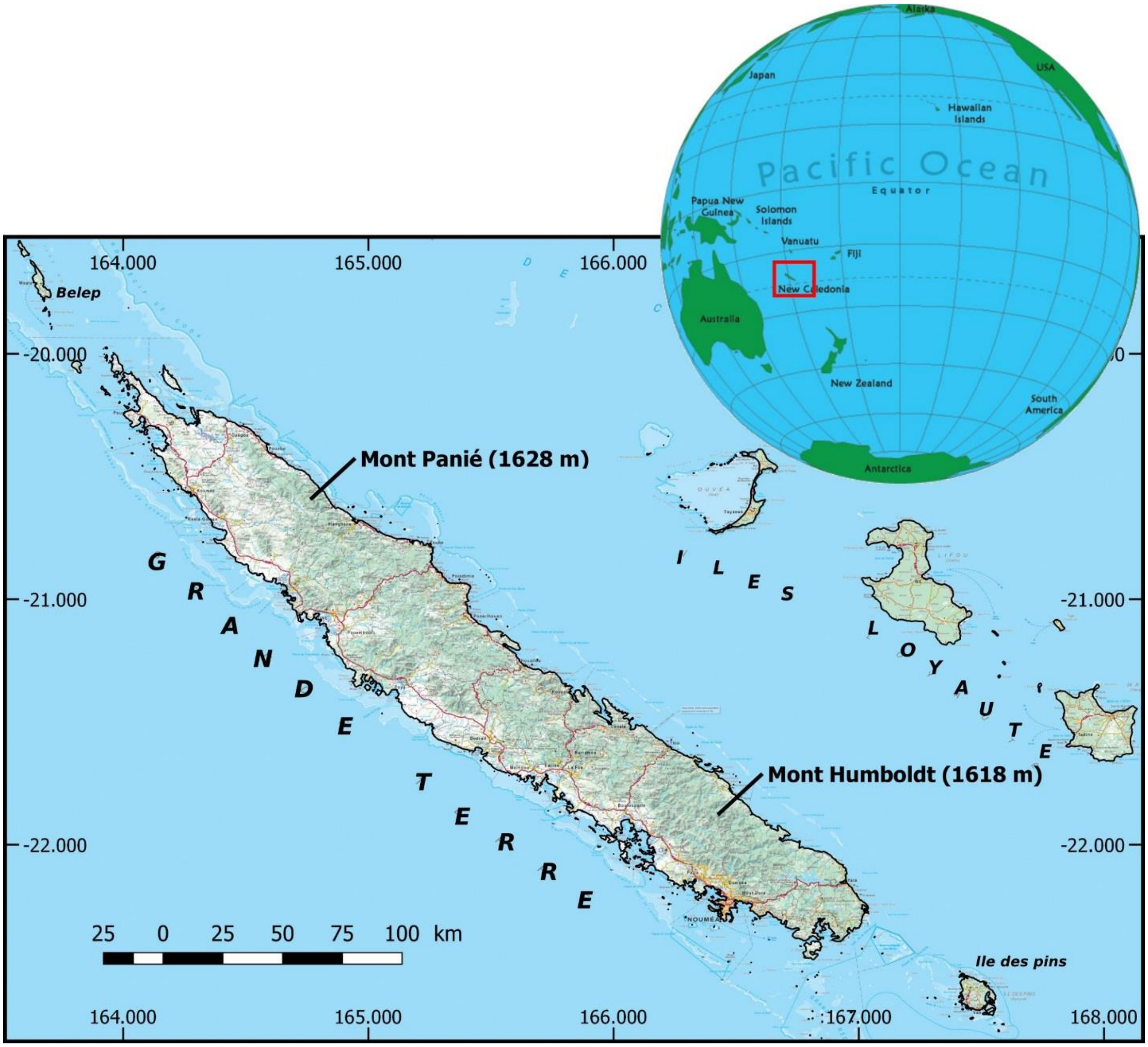


FIGURE 2.1 – Topographical map of New Caledonia (modified from *georep.nc*) and location in the South-West Pacific (modified from *geographicguide.com*).

Maitrepierre, 2012; Menkes, 2012).

Three main geological substrates are distinguished in New Caledonia (Paris, 1981; Jaffré, 1993) (Figure 2.2-A). (i) Ultramafic substrate covers ca. 1/3 of *Grande Terre*, mainly in the southeast of *Grande Terre* and on the northwest mountain massifs. Soils derived from ultramafic substrate are generally poor in plant-essential nutrients (P, Ca, K) and rich in elements which are normally toxic for plants (Ni, Co, Mn, Cr) (Jaffré, 1976, 1980; Isnard et al., 2016). (ii) Volcano-sedimentary substrates cover ca. 2/3 of *Grande Terre* and are highly diverse in origin and composition (Fritsch, 2012). They comprise mainly micaschists, glaucophtanites and phtanites in the North of *Grande Terre,* whereas the central metamorphic mountain groups are formed of greywacks (Paris, 1981; Jaffré, 1993). (iii) Calcareous substrate is much less common covering less than 20% of the archipelago (Paris, 1981; Morat et al., 2001) almost exclusively found in the Loyalty Islands and the *Ile des Pins* (raised coral formations), but also occurs in small areas on *Grande Terre* (basalt calcareous rocks) (Paris, 1981; Morat et al., 2001).

2.1.2 Geological and Paleoclimatic history

New Caledonia’s main island (along with *Belep* and the *Ile des Pins*) is a part of the New Caledonian ridge that split and spread from the eastern margin of the Gondwanan supercontinent during the Cretaceous (ca. -120 to -80 Myr) (Picard, 1999; Cluzel et al., 2001; Pelletier, 2006; Cluzel et al., 2012). The presence of numerous endemic relictual lineages on the island led some authors to think that this piece of Gondwana remained emerged from the rifting event until today (e.g. Raven and Axelrod, 1972). However geological insights have shown that New Caledonia was submerged from the Paleocene to the Eocene (ca. -62 to -50 Myr) at which time it was obducted under the Pacific plate and covered by oceanic crust (Picard, 1999; Cluzel et al., 2001; Pelletier, 2006; Cluzel et al., 2012), leading to the formation of metamorphic rocks and to the atypical ultramafic substrate. New Caledonia reemerged during the Eocene (-50 to -35 Myr, and probably ca. -37 Myr) after which the ultramafic layer progressively weathered to the present day resulting in the partial exposure of subjacent volcano-sedimentary substrates. This scenario is coherent with the evolutionary history of several New Caledonian lineages which suggests that local radiations are younger than 37 Myr (Murienne et al., 2005; Grandcolas et al., 2008; Pillon, 2012). The Loyalty Islands emerged more recently (Pliocene, ca. -2 Myr) through an uplifting of the Loyalty ridge (Picard, 1999; Pelletier, 2006).

Paleoclimatic data indicate that the Southwest Pacific has experienced a general cooling since early Neogene (ca. -23 Myr), leading to an increase in aridity (Gallagher et al., 2001; Zachos et al., 2001; Dodson and Macphail, 2004). This trend was punctuated by several more or less pronounced oscillations such as the drastic increase in both temperature and precipitation in the Miocene (ca. -15 to -17 Myr, Zachos et al., 2001; Böhme, 2003) coupled with intense cooling (Gallagher et al., 2003; Dodson and Macphail, 2004). This overall climate aridification had important consequences on vegetation, especially a decline of rainforest areas, which probably disappeared in some regions such as Australia (Gallagher et al., 2003; Crisp et al., 2004; Dodson and Macphail, 2004; Byrne et al., 2008; Byrne et al., 2011). For New Caledonia, paleoclimatic data are scarce but its small size and isolated position in the Pacific are thought to have buffered the effects of general aridification (Barrabé, 2013). Nevertheless, the archipelago is likely to have experienced several glacial episodes during the Neogene (ca. -6.5 Myr) and Quaternary (ca. -2.5 Myr) (Chevillotte et al., 2006; Karas et al., 2011) and also more recently (-22000 and -12000 yr, Tournebize et al., 2017). Despite these glacial episodes, rainforests seem to have continuously persisted in New Caledonia for quite a long period (Hope and Pask, 1998; Stevenson and Hope, 2005; Tournebize et al., 2017), contrary to adjacent regions (Kemp, 1978; Gallagher et al., 2003;

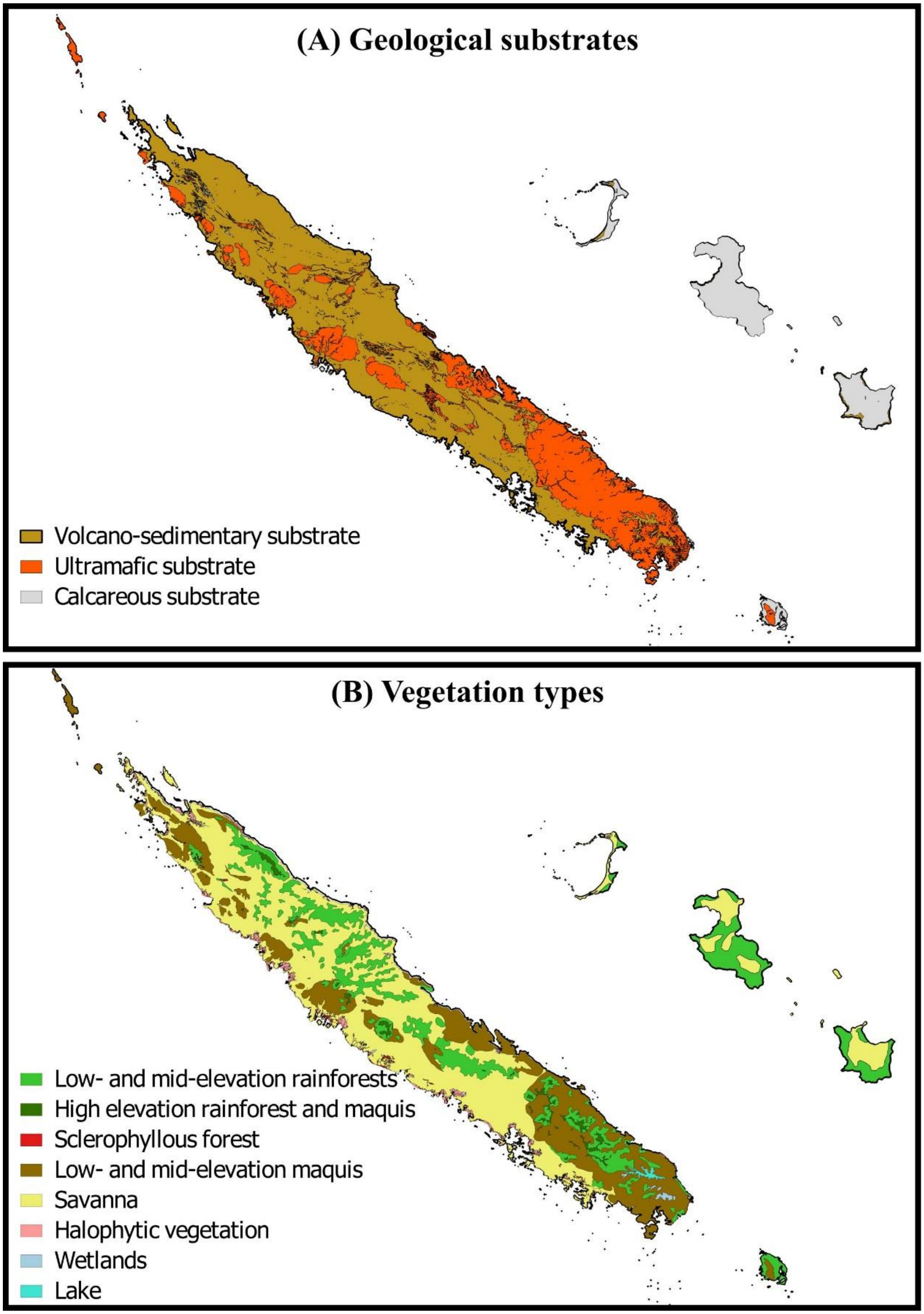


FIGURE 2.2 – Main environmental characteristics of New Caledonia. **(A)** Distribution of the three main geological substrate (from DIMENC/SGNC-BRGM and Morat et al. 2001). **(B)** Distribution of the seven main vegetation types (from Jaffré et al. 2012).

Crisp et al., 2004; Dodson and Macphail, 2004; Byrne et al., 2008; Byrne et al., 2011). In investigating the evolutionary history of rainforest lineages, Pillon (2012) argued that this vegetation type is likely to have persisted in New Caledonia since at least 6.9 Myr.

2.1.3 Flora and vegetation

The New Caledonian flora is known worldwide for its exceptional levels of diversity and endemism. The flora comprises ca. 3400 species of vascular plants, of which ca. 2500 (75%) are endemic (Morat et al., 2012; Munzinger et al., 2016). This high level of endemism is also seen at supra-specific levels as the flora includes between 62 and 91 endemic genera (ca. 13%, Pillon et al., 2017) and 3 endemic families (Amborellaceae, Oncothecaceae, and Phellinaceae). The taxonomic composition of New Caledonia's flora is highly disharmonic compared to adjacent regions, some lineages being over-represented (e.g. Gymnosperm, Cunoniaceae, Myrtaceae and Basal Angiosperms) while others are under-represented (e.g. Asteraceae, Ericaceae and Lamiaceae) (Morat et al., 1994; Jaffré, 1995; Pillon et al., 2010; Trueba, 2016). This disharmony also involves functional groups, for example a high proportion of metal hyper-accumulators (Jaffré et al., 2013; van der Ent et al., 2015; Jaffré et al., 2018) and dioecious species (Carpenter et al., 2003; Schlessman et al., 2014), as well as a low richness of lianas (Bruy et al., 2018). Several unusual biological forms are also known, such as the world's only parasitic or mycotrophic gymnosperm (De Laubenfels, 1959; Feild and Brodribb, 2005; Heide-Jørgensen, 2008), a monocarpic and branched large tree (Veillon, 1971; Read et al., 2008), and an aquatic fern that can live completely submerged (Veillon, 1981).

This astonishing flora is also of conservation importance because it is highly threatened (Jaffré et al., 1998; Lowry, 1998). The system of protected areas appears to be inadequate, particularly for the highly fragmented rainforest and ultramafic substrate (Jaffré, 2005; Jaffré et al., 2010; Wulff et al., 2013; Ibanez et al., 2017a; Ibanez et al., 2018b). These threats, along with the New Caledonia's outstanding diversity, led scientists to recognize the archipelago as one of the 10 original "Biodiversity Hotspots" (Myers, 1988). Today, the archipelago remains the smallest of the 34 recognized Hotspots (Mittermeier et al., 2004). Recently, the risk of extinction of New Caledonian plant species started to be extensively evaluated using the IUCN Red List criteria (IUCN, 2012). Among the 833 species evaluated to date, 43% appeared to be threatened and one species was considered as extinct (RLA-NC Flora, unpublished data). The principal threats are bushfires (ca. 64% of species concerned), mining activities (ca. 40%) and introduced herbivores such as deer (28%).

Several vegetation types have been recognized in New Caledonia, the most general classification used being that of Jaffré et al. (2012). Based on climatic, structural and floristic features, this classification includes seven main types: (i) low- and mid-elevation rainforest, (ii) high elevation rainforest and maquis, (iii) sclerophyllous forest, (iv) low- and mid-elevation maquis, (v) savanna (essentially non-native), (vi) halophytic vegetation, and (vii) wetlands (Figure 2.2-B). Among the native vegetation types, maquis, whose occurrence is related to the fire regime (Jaffré, 1980; Isnard et al., 2016), is the most extensive (covering 4600 km²). Rainforests (covering ca. 3,800 km²) contain by far the greatest diversity (more than 2000 native species against ca. 1200 in maquis) (Jaffré et al., 2009; Birnbaum et al., 2015a; Birnbaum et al., 2015b) and is one of the most threatened formations (Jaffré, 2005; Jaffré et al., 2010; Ibanez et al., 2017a), along with dry forests (Bouchet et al., 1995; Lowry, 1998). New Caledonian rainforests are characterized by high beta diversity, very high stem density coupled with small stem diameter (inferior to 10 cm DBH), and low canopy height (about 15-25 m) (Jaffré and Veillon, 1990; Jaffré and Veillon, 1995; Ibanez et al., 2014; Blanchard et al., 2016; Ibanez et al., 2017b).

The floristic and structural distinctiveness of the New Caledonian biota is the result of several factors, of which ultramafic substrate, rainforest refugia and cyclones are considered as the most important. As suggested by New Caledonia's geological history (see above), its flora is the result of post-emergence colonization (mainly from Australia, Morat, 1993; Swenson et al., 2014; Thomas et al., 2014) either through long-distance dispersal or shorter-distance dispersal from now submerged intermediate islands (Pelletier, 2006). Species establishment was largely filtered by the constraining ultramafic substrate, which is considered as the main driver of taxonomic disharmony (Jaffré et al., 1987; Pillon et al., 2010; Isnard et al., 2016). Another important driver is the long-term persistence of rainforests in the archipelago (see above), which are thought to have served as refugia for drought-sensitive lineages such as basal Angiosperms or palms (Pintaud et al., 2001; Poncet et al., 2013; Pouteau et al., 2015; Tournebize et al., 2017) that disappeared from dryer regions in the western Pacific (Bowler et al., 1976; Byrne et al., 2011). Post-glaciation periods provided several ecological opportunities for occurring lineages to diversify and are suspected to have driven the recent diversification of the flora (Pillon, 2012). Forest structural characteristics (e.g. high stem density) and composition are believed to have been largely shaped by strong climatic forces (cyclones, see above) that recurrently impact vegetation (Read and Jaffré, 2013; Ibanez et al., 2017b; Ibanez et al., 2018a).

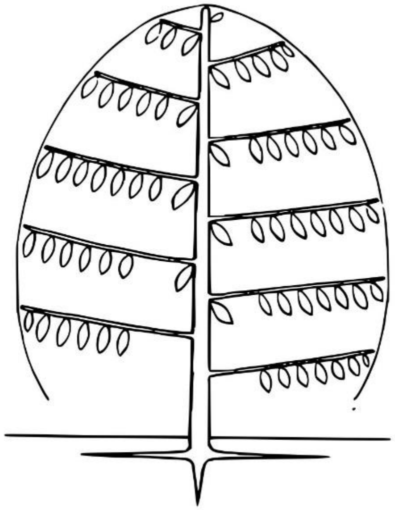
2.2 Plant architecture

Plant architecture is a domain of plant science that concerns the nature and organization of plant parts and their evolution during ontogeny. It emerged with the fundamental works of Hallé et al. (Hallé and Oldeman, 1970; Hallé et al., 1978) in which fundamental principles of plant morphology (growth patterns, branching modalities, axis differentiation, and the position of reproductive functions) were combined into a comprehensive and dynamic approach to define 23 architectural models. These models illustrate both the general architecture of a plant and the way it was constructed (Hallé and Oldeman, 1970; Hallé et al., 1978; Barthélémy et al., 1989; Nicolini, 1997) (Figure 2.3-A). While compelling for the recognition of common overall species forms, architectural models appeared too general to understand fines aspects of complex plant construction (Edelin, 1977; Barthélémy and Caraglio, 2007).

A deeper characterization of plant architecture came with the development of notions of axis category and architectural units (Edelin, 1977, 1984; Barthélémy et al., 1989; Barthélémy et al., 1991). Individuals of each species are made of a limited number of axis categories (1-6), each characterized by a non-limitative combination of morphological, anatomical and functional traits (Figure 2.3-B). The number of axis categories, their characteristics and their spatial arrangement determine the so-called architectural unit, i.e. the species-specific expression of an architectural model (Barthélémy and Caraglio, 2007). The higher an axis category (i.e. situated at the periphery of the plant), the more functionally specialized it is (Barthélémy and Caraglio, 2007). For example, in most of tree and treelet species, trunks (axis category 1 = C1) have the general functions of support and storage. The more the axis number increases (C2, C3…), the more specialized the axis is in exploration, photosynthesis and reproductive functions. Extreme examples of axis specialization are provided by some inflorescences for reproduction function (Van Steenis, 1963; Hallé et al., 1978) or by phyllomorphic branches for photosynthesis (Corner, 1949; Hallé, 1967; Hallé et al., 1978).

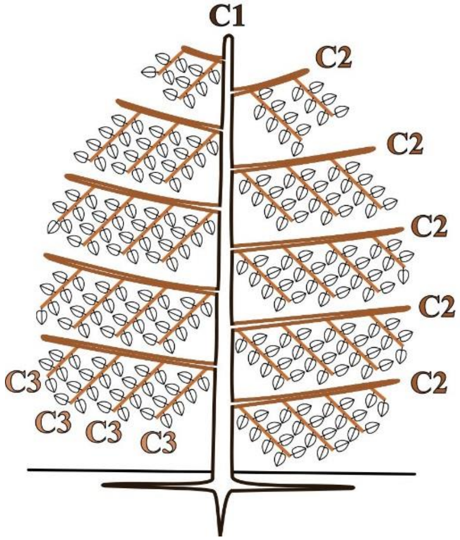
In most cases, a well-defined architectural unit is modified through the morphogenetic process of reiteration. Reiteration is a special branching process by which a plant duplicates its architectural unit (Oldeman, 1974; Hallé et al., 1978; Barthélémy and Caraglio, 2007). The process of reiteration is complex and not necessarily well understood. Different modalities of reiteration

(A) Architectural model



Roux model	
Growth pattern	Indeterminate
Growth direction of trunk	Orthotropic
Growth direction of branches	Plagiotropic
Reproduction	Lateral
Branching position	Continuous

(B) Architectural unit



	C1	C2	C3
Growth pattern	Indeterminate	Indeterminate	Determinate
Growth periodicity	Continuous	Continuous	Continuous
Branching pattern	Monopodial	Monopodial	*Not applicable*
Growth direction	Orthotropic	Plagiotropic	Plagiotropic
Reproduction	Absent	Absent	Lateral
Branching position	Continuous	Continuous	*Not applicable*
Symmetry	Radial	Bilateral	Bilateral
Leaf type	Cataphyll	Assimilative	Assimilative
...	...	...	...

FIGURE 2.3 – Illustration of **(A)** architectural model (from Hallé et al. 1978) and **(B)** architectural unit for *Phyllanthus caudatus* var. *caudatus* (Phyllanthaceae).

have been recognized according to whether (i) the complete architectural unit is duplicated (total reiteration) or only a part of it (partial reiteration), (ii) the reiterate is produced by the development of a dormant bud (delayed reiteration) or by the transformation of an already growing meristem (immediate reiteration), and (iii) the reiteration process is included in the developmental sequence of the species (sequential reiteration) or is due to either plant damage (traumatic opportunistic reiteration) or to an increase in resource levels (adaptive opportunistic reiteration). All combinations of reiteration modalities are theoretically possible (Figure 2.4) but all of them have never been observed in a single species, each taxon having instead its own reiterative strategy (Edelin, 1986; Barthélémy, 1991).

2.3 Toward a new definition of monocauly: between structure and function

Plant architecture has taught us that plant form is due to the genetically controlled association of several structuro-functionnal entities (phytomers, growth units, axis categories, reiterates…) whose arrangement and differentiation change with age and are shaped by the environment. This integrative approach revealed objective criteria that could be powerful for defining growth habit (Millan, 2016). For instance, among the few attempts to define the monocaulous habit (see Chapter 3), that of Hallé et al. (1978) is probably the most successful. These authors made the distinction between the structural definition (“trees with a single axis” = monoaxial) and the physiognomic definition (“trees with a single trunk or visible stem of the plant” = monocaulous). The latter, referring to the general appearance of the plant rather than its structural construction, seems more appropriate for an ecological study since it is directly linked with the space exploration strategy of species. To pursue this functional aspect of growth habit further, monocauls could be defined as “self-supporting woody plants whose cardinal functions rely on a single visible stem”. This functional definition, better suited to studying the adaptive aspects of

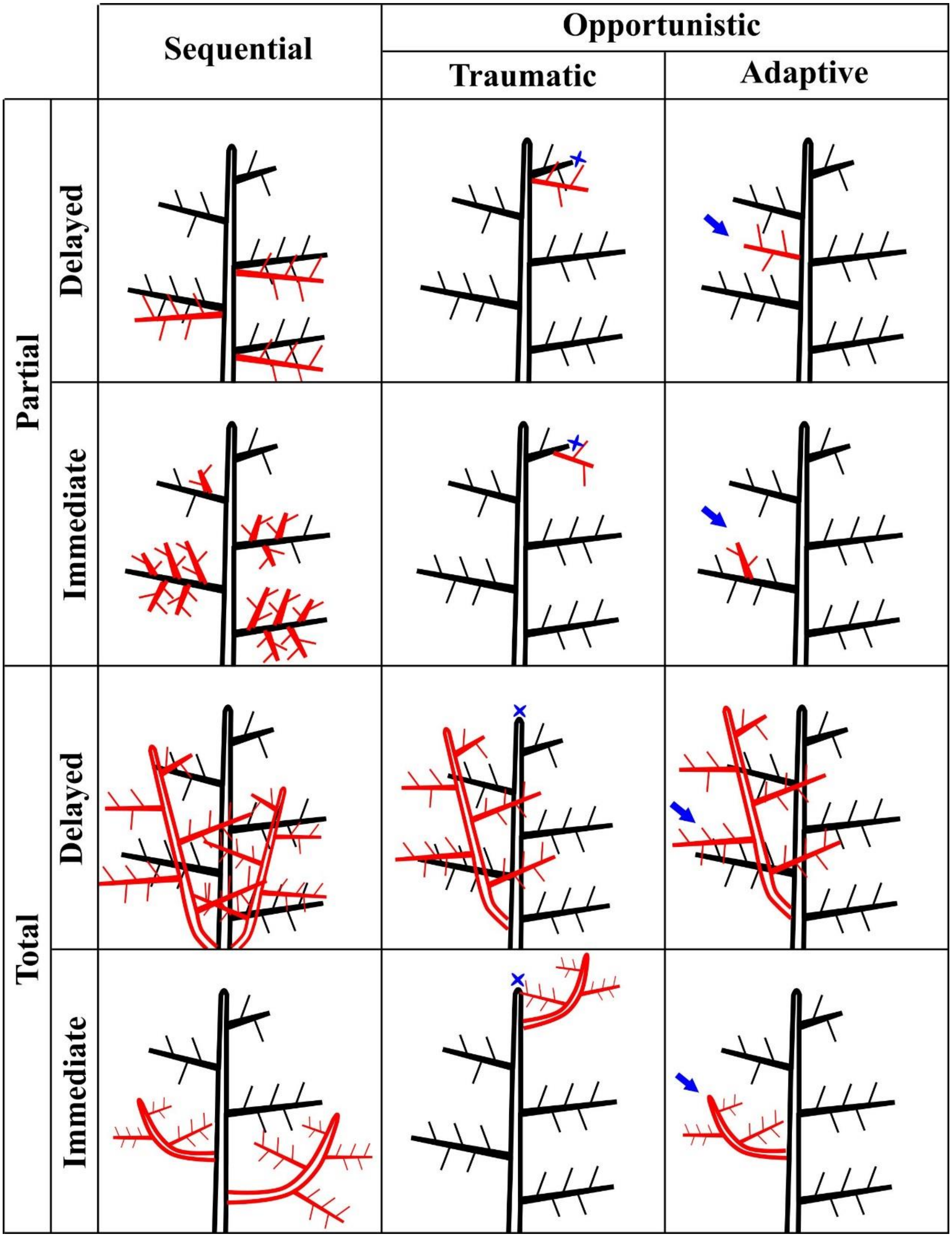


FIGURE 2.4 – Illustration of the twelve theoretically possible reiteration types for *Phyllanthus caudatus* var. *caudatus* combining the three described reiteration modalities. Red entities represent reiterated complexes. Blue cross represent traumatic apices death. Blue arrows represent environmental stimuli (here light). Note that for *P. caudatus* var. *caudatus*, only five of the theoretical combination were observed in nature.

growth habit, is the one we will use here. Beyond giving a clear physiognomic definition of monocauly, the architectural approach of Hallé et al. (Hallé and Oldeman, 1970; Hallé et al., 1978) was the first to provide clear discriminating morphological criteria. The classification of a species in the monocaulous class relies on the selection of structural types fitting the given definition of monocauly. In the work of Hallé et al. (Hallé and Oldeman, 1970; Hallé et al., 1978), structural types corresponded to architectural models. This classification, while providing a fundamental basis for plant architecture, nevertheless appeared to be too general to understand the precise architecture of plants and more integrative concepts such as architectural units and reiteration were later developed (see section 2.2). The work of Hallé et al. (Hallé and Oldeman, 1970; Hallé et al., 1978) aimed to present the known diversity of developmental plans observed in tropical trees. Our aim is different, since our interest is to segregate plants for which vegetative functions are assumed by one visible stem, from other plants (i.e. branched). For all these reasons, we will not strictly refer to architectural models to define our structural types of monocauly but our classification will, in essence, largely overlap that of Hallé et al. (1978). Our definition of monocauly, focusing on function rather than structure, includes true woody plants with a single orthotropic entity functioning as a trunk and determined plagiotropic structures functioning as leaves. The only other aboveground structures are those specialized in reproduction (i.e. inflorescences) or are due to exogenous stimuli (i.e. opportunistic reiterates).

Trunk entity – As argued by Hallé et al. (1978), a single trunk could be constructed in two different ways. (i) In most cases (and quite apart from traumatisms), single trunks are produced by one single meristem functioning throughout the plant’s lifespan (Figure 2.5-A). In this case, the trunk is monoaxial and the meristem might stop functioning following flowering (monocarpic plant) or natural senescence (polycarpic plant). (ii) In some cases, a single trunk could be

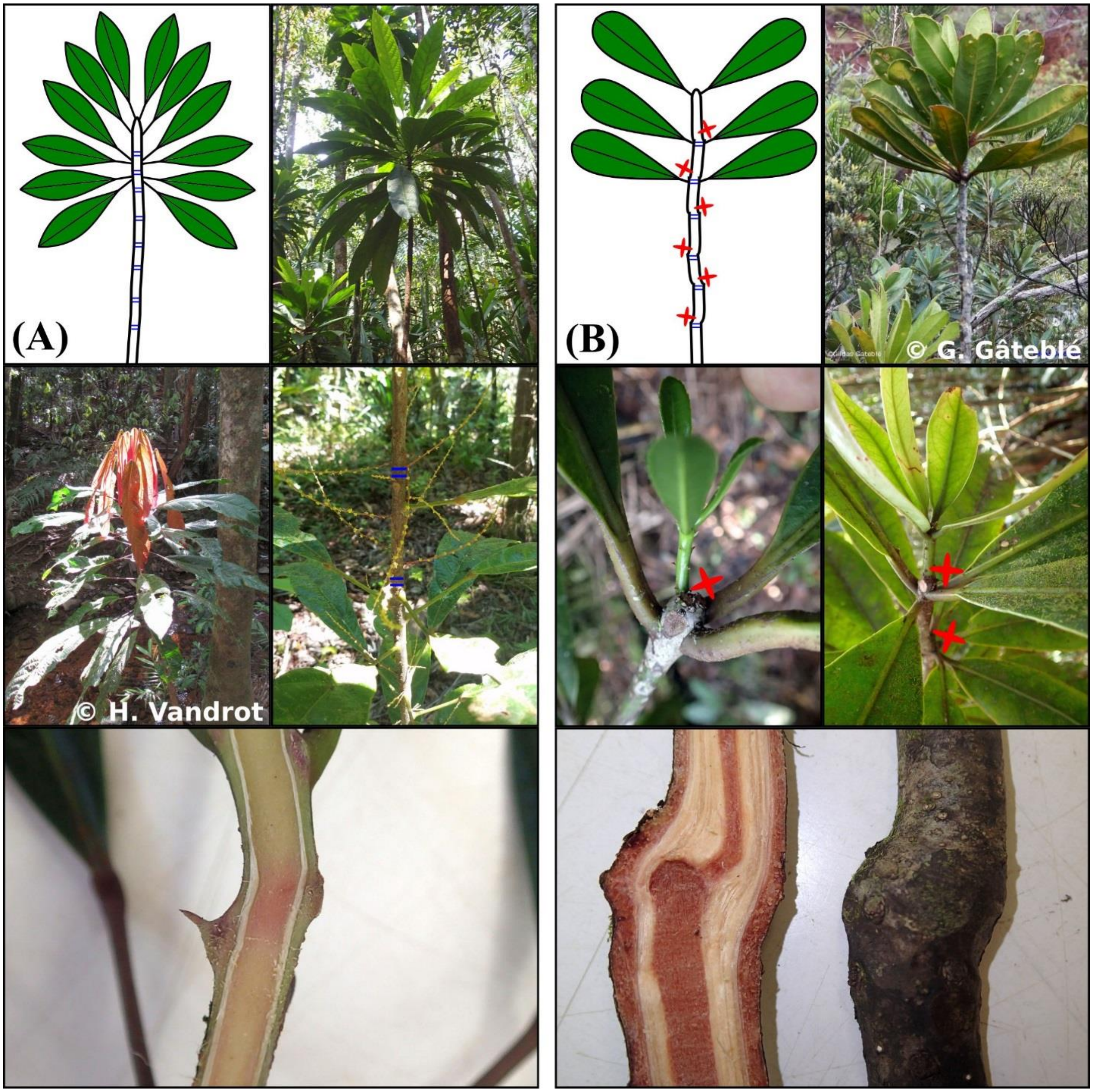


FIGURE 2.5 – Representation of the two possible modes of trunk construction for monocaulous plants. Pairs of blue segments represent growth rest sites, red crosses represent apex deaths. **(A)** *Bocquillonia* species (Euphorbiaceae) exhibit a monoaxial trunk and rhythmic growth, each growth-unit being produced by the same meristem. Growth-rest sites are not sharply bent and only anatomically characterized by slightly narrower and red pith (no pith rupture). **(B)** *Balanops pancheri* (Balanopaceae) exhibits a pluriaxial trunk and rhythmic growth, each growth-unit (i.e. module in this case) being produced by a sub-apical axillary meristem of the previous module (sympodial branching). Growth-rest sites are sharply bent and anatomically characterized by pith rupture.

constructed by several meristems, each producing a module, that stack up to form a linear sympodium (Figure 2.5-B). In this case, the trunk is polyaxial and meristems of each module might stop functioning by flowering (hapaxanthic module) but not necessarily (see Cremers and Edelin, 1995).

Photosynthetic entity **–** The classical photosynthetic organ is the leaf, an often determinate bilateral organ highly specialized in photosynthesis (Harris and Harris, 2001) (Figure 2.6-A). However, functional differences between leaves and stems may in some cases be vague and some authors have argued that the transition from branch function toward leaf function is continuous (see Sattler, 1984, 1988; Sattler and Jeune, 1992; Sattler, 1996). For example, in several species, classical leaf functional characteristics are supported by highly specialized stems (e.g. cladodes, Cooney-Sovetts and Sattler, 1987; Bell, 1991) (Figure 2.6-B). To rigorously consider function and not structure, such stems must be considered as the functional photosynthetic entities of plants. As such, in the present study, photosynthetic entities are defined as "determinate growth structures highly specialized in photosynthesis and with an abscission point" (see Hallé et al., 1978). This definition is largely fitted by phyllomorphic branches, as introduced by Corner (1949) and defined by Hallé (1967), which are plagiotropic stems functionally considered as compound leaves (Hallé et al., 1978) (Figure 2.6-D). Similarly, leaves with indeterminate growth, as described for example in Meliaceae (Corner, 1964; Steingraeber and Fisher, 1986), will not be considered as photosynthetic entities but rather as additional exploration structures (but no such leaves are known in New Caledonia).

Reproductive entity **–** In morphological terms, inflorescences are stems highly specialized in the reproduction function. Accordingly, strictly monoaxial plants do not exist or are very rare (Hallé and Oldeman, 1970). Once again, the demarcation between inflorescences and vegetative

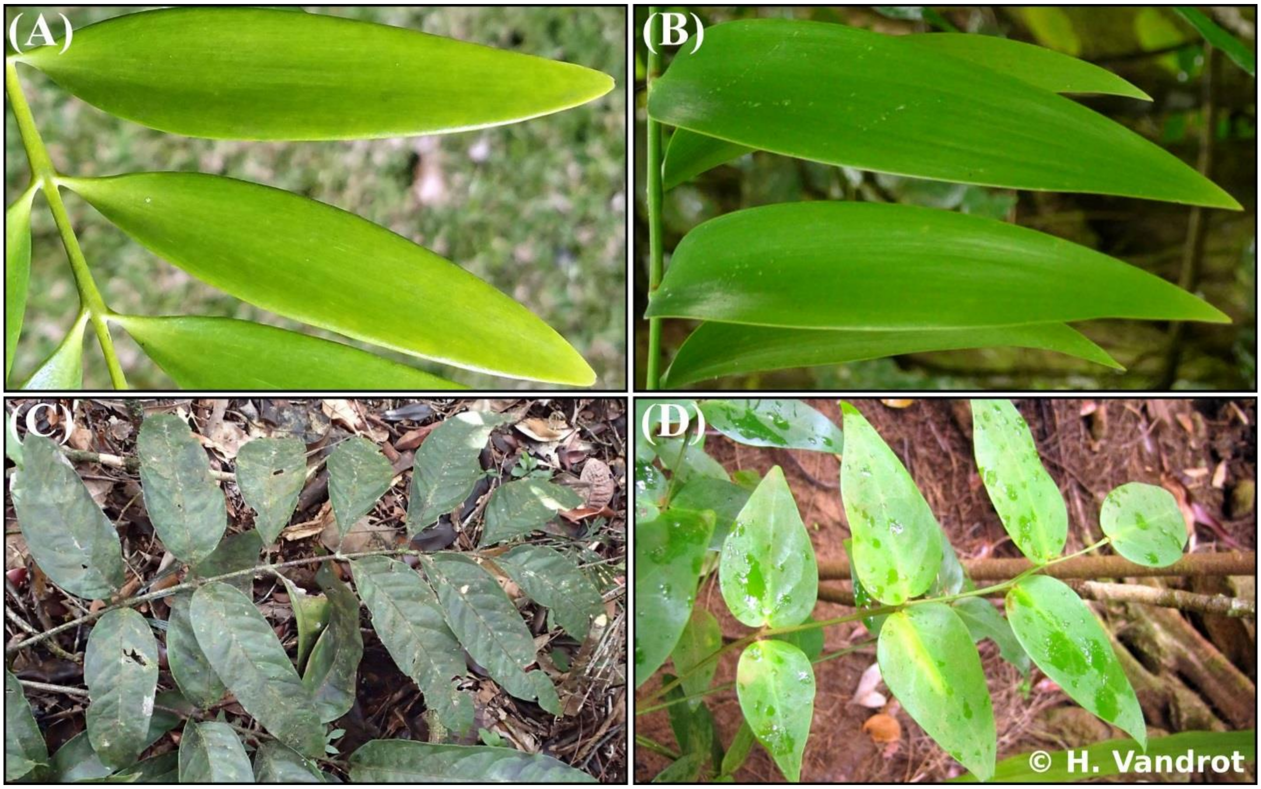


FIGURE 2.6 – Example of similar functions carried out by different organs (leaf and twig). **(A)** Leaf of *Agathis lanceolata* (Araucariaceae). **(B)** Cladode (i.e. modified stem) of *Semele* sp. (Asparagaceae). **(C)** Compound leaf of *Cupaniopsis oedipoda* (Sapindaceae). **(D)** Phyllomorphic branch of *Phyllanthus bupleuroides* var. *ngoyensis* (Phyllanthaceae).

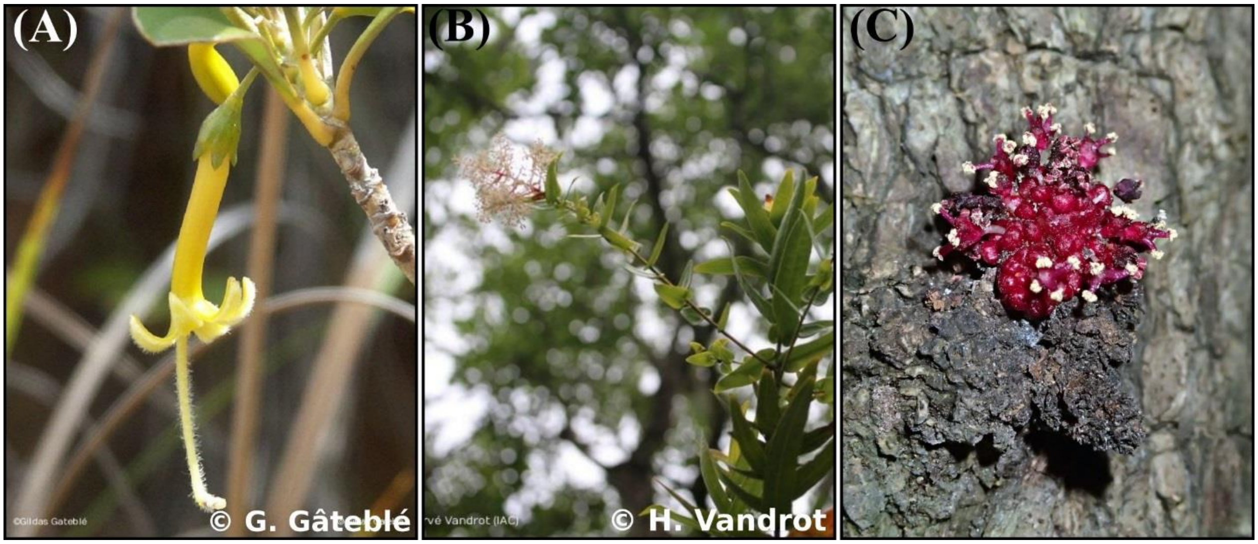


FIGURE 2.7 – Illustration of the variation in inflorescence complexity. **(A)** *Scaevola coccinea* (Goodeniaceae): inflorescence is reduced to a single axillary flower. **(B)** *Tapeinosperma ateouense* (Primulaceae): determinate inflorescence supports several small assimilative leaves. **(C)** *Bocquillonia corneri* (Euphorbiaceae): annual flowering occurs on contracted axis complexes whose growth is indeterminate.

branches could be confusing and they appear to be two extremes of a continuum (Van Steenis, 1963; Hallé et al., 1978). For example, while some inflorescences comprise only a single lateral flower (Figure 2.7-A), others are quite long and bear numerous assimilative leaves (Figure 2.7-B) or comprise a densely branched complex of axes functioning during the entirety of the plant's lifespan ("bud complex" leading to cauliflory, Figure 2.7-C). Our main purpose here is to identify discriminating criteria to classify axes under the inflorescence or branch classes. Van Steenis (1963) proposed that inflorescences "post-anthesis do not participate in the vegetative extension of the individual". In the present study, we extend this finding by considering inflorescences as "axes or complex of axes highly specialized in reproduction and whose contribution to whole plant vegetative exploration and photosynthesis is negligible". Consequently, species with additional axes that do not fit this definition will be considered as branched.

***Reiterates* –** For a given species, it is common to find individuals exhibiting an architecture that differs from the architectural unit that characterizes the taxon. Similarly, almost all of the species previously described as monocaulous (e.g. Hallé et al., 1978; Hallé, 2004) can occasionally be seen in nature with several axes (except for most monocotyledons). In this case, all supernumerary stems are morphologically and functionally identical to each other and to the primary trunk: that is, they are reiterates (see section 2.2). It is consequently crucial to distinguish a reiteration that results from a developmental sequence (i.e. sequential reiteration) from one triggered by exogenous factors (i.e. opportunistic reiteration). In the first case, a species will be considered as branched and in the second as monocaulous. If the theoretical differentiation between opportunistic and sequential reiteration seems obvious (Barthélémy and Caraglio, 2007), there are no clear morphological characters to differentiate easily the two processes in the field, particularly for delayed reiteration. In the present study, if reiteration of a species is predictable in space and

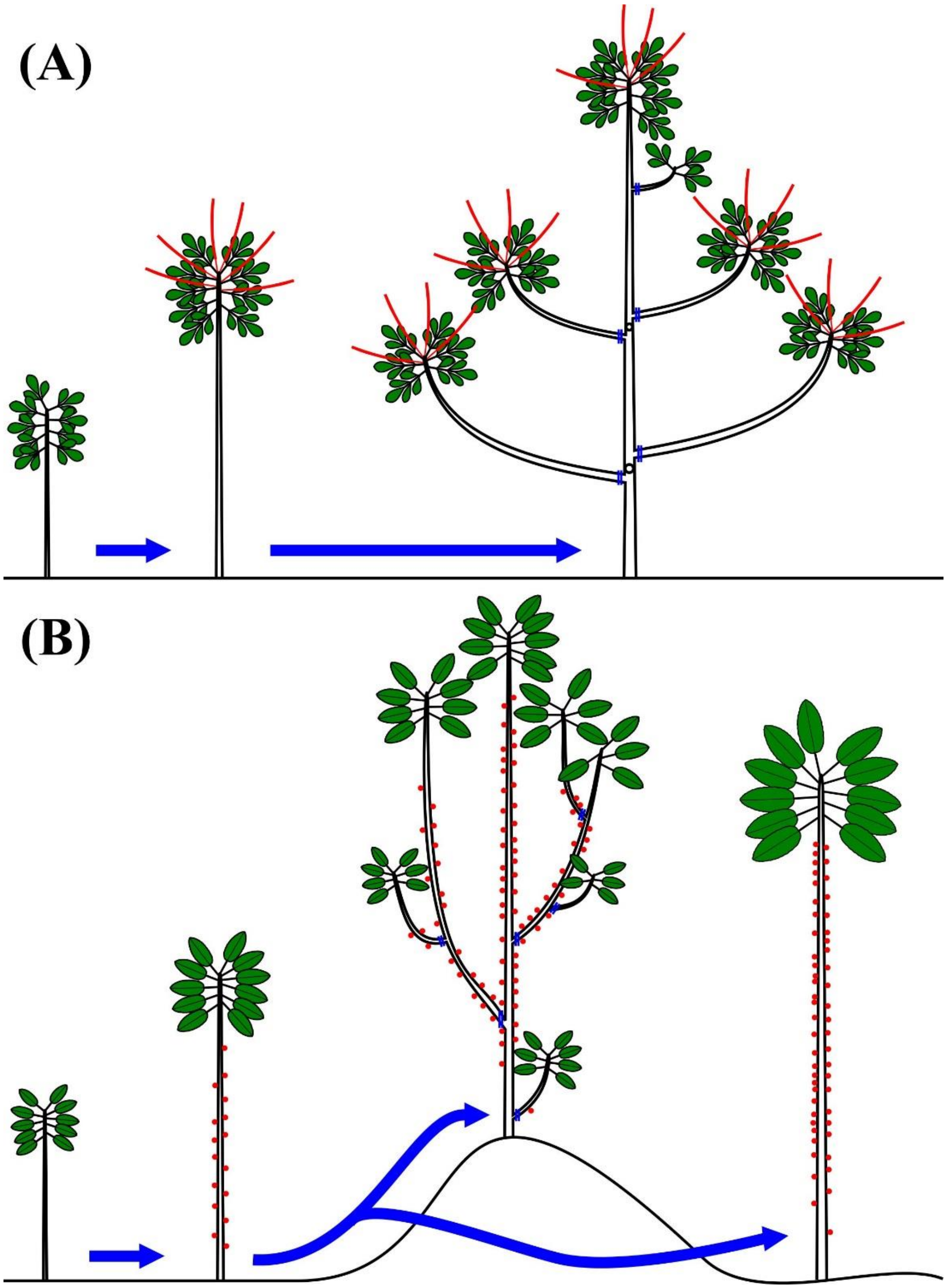


FIGURE 2.8 – Illustration of sequential reiteration (branched species) and opportunistic reiteration (monocaulous species). Pairs of blue traits illustrate the differed character of reiterates, red circles or segments represent inflorescences. **(A)** *Soulamea muelleri* (Simaroubaceae): Reiterates appear on all individuals of the species and are regularly clustered on the primary trunk. **(B)** *Bocquillonia sessiliflora* (Euphorbiaceae): Reiterates appear very early on some individuals and never on others, their positions on the primary trunk are not predictable.

time, it is considered as sequential and the species is therefore classified as branched (Figure 2.8).

To summarize, in the present study we consider as monocaulous all self-supporting woody species whose cardinal functions rely on a single visible stem, i.e. which are made of (i) a trunk (either monoaxial or pluriaxial), (ii) determinate growth structures highly specialized in photosynthesis and with an abscission point, (iii) axes or complex of axes highly specialized in reproduction and whose contribution to whole plant vegetative exploration and photosynthesis is negligible, and possibly (iv) opportunistic reiterates. This definition encompasses the two monoaxial models of Hallé et al. (1978): the Holttum's model for terminal flowering species and the Corner's model for lateral flowering taxa (Figure 2.9-A). Our definition also includes Chamberlain's model except that we consider both hapaxanthic (terminally flowering) and non-hapaxanthic (lateral flowering) modules (Figure 2.9-B), while the initial definition of Hallé et al. (Hallé and Oldeman, 1970; Hallé et al., 1978) only includes linear sympodia made of terminally flowering modules. The definition of monocauly adopted here also includes the Cook's architectural model in its extreme expression (i.e. with short-living determinate phyllomorphic branches, Figure 2.9-C). Hallé (2004) suggested that the Cook's model should be merged into the Roux's model, their differences being mainly quantitative. In our opinion, differences between classical long shoots (Roux's model) and phyllomorphic branches as considered here (the Cook's model) are more than just quantitative given the fundamental difference in the growth pattern (indeterminate vs. determinate, respectively). Finally, our definition also corresponds to the Tomlinson's model as initially described by Hallé et al. (Hallé and Oldeman, 1970; Hallé et al., 1978) as the basal repetition of two of our above-described monocaulous models (the Holttum's and the Corner's models). Cremers and Edelin (1995) challenged the validity of this architectural model by showing that basal repetition occurs at least in seven other architectural models, including

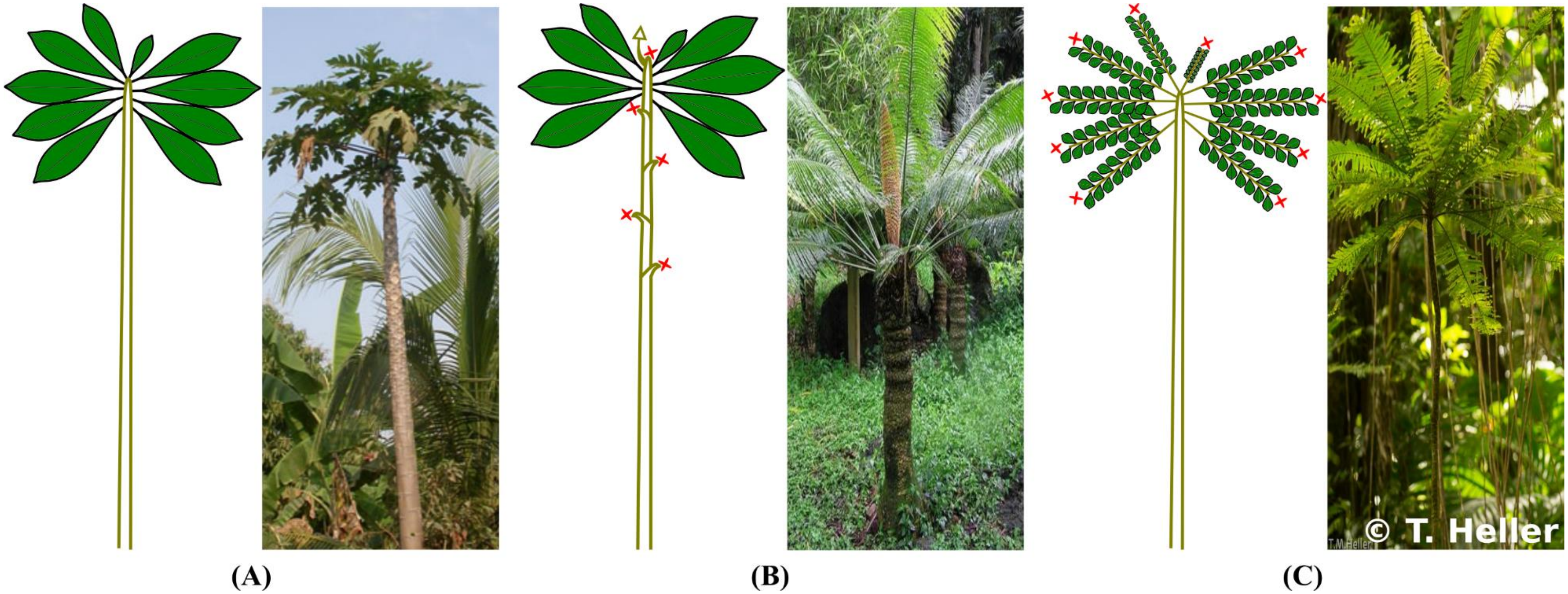


FIGURE 2.9 – Illustration of the three main structural types conforming to the definition of monocauly used in the PhD study. Only vegetative architecture is represented here. **(A)** Monoaxial architecture exemplified by papaya (*Carica papaya*, Caricaceae). **(B)** Sympodial architecture exemplified by several male Cycas (here *Cycas seemannii*, Cycadaceae). **(C)** Phyllomorphic-branches architecture exemplified by the "fougère bâtarde" (*Phyllanthus mimosoides*, Phyllanthaceae).

the monocaulous Chamberlain’s model. These authors proposed that such repetitions are reiterations occurring basally (Cremers and Edelin, 1995), the process sometimes being predictable in space and time (i.e. sequential reiteration) and sometimes not (i.e. opportunistic reiteration). Consequently, some plants initially described under the Tomlinson’s architectural model will be considered as monocaulous in the present study since they match the definition presented above. Other theoretical structural types fit our definition of monocauly, such as those constituted by a sympodial trunk and phyllomorphic branches, but that does not conform to any of the described architectural models because they remain unobserved in nature.

2.4 List of monocaulous species

To assess the evolutionary history of monocaulous plants in New Caledonia, an exhaustive list of monocaulous species native to New Caledonia has been established. As our definition of monocauly applies to woody plants, the list is limited to the non-monocot flora, which is by far the most diverse group (Munzinger et al., 2016). Monocotyledons were not considered because they represent a highly different monocaulous condition since aerial branching is developmentally constrained by shoot growth and the absence of wood (Tomlinson and Zimmermann, 1969; Tomlinson and Esler, 1973; Haushahn et al., 2012).

A preliminary list of New Caledonian monocaulous species was compiled based on an extraction of the NOU Herbarium database using appropriate keywords (“monocaul”, “peu ramif”, “pachycaul”, “non ramif”, “unbranch”). The list was supplemented through expert opinion and extensive bibliographic analysis, particularly in the series *Flore de la Nouvelle-Calédonie (et Dépendances)* (Aubréville et al., 1967-1992; Morat and MacKee, 1992-2004; Hopkins et al., 2014) and taxonomic publications. The resulting initial list of taxa was cross-checked with the Florical taxonomic reference (Munzinger et al., 2016) to ensure that only valid names of species were used.

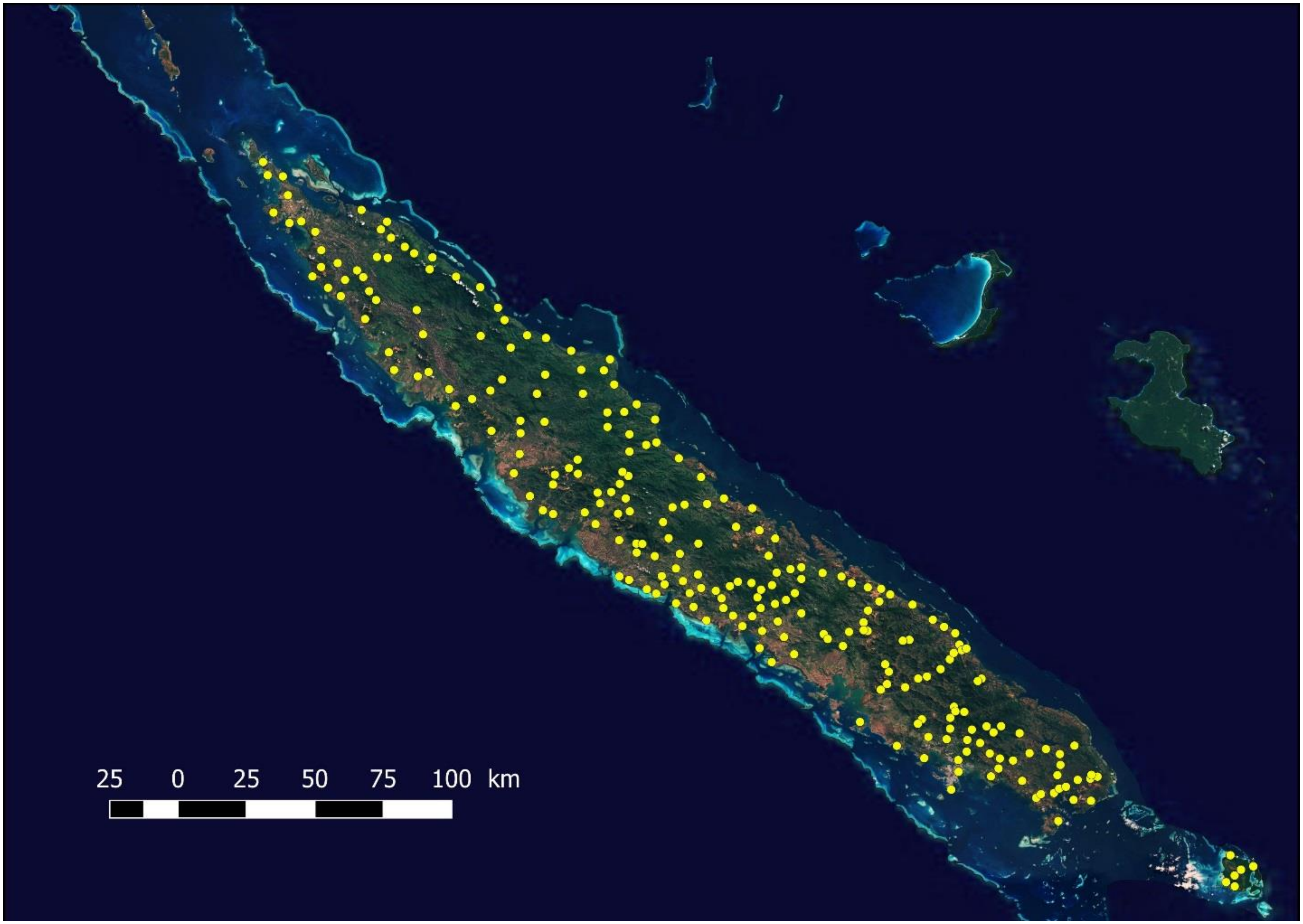


FIGURE 2.10 – Satellite map of New Caledonia (from *georep.nc*) and investigated sites during the thesis (yellow dots).

When possible, the architecture of each taxon on this list was studied through extensive field work on *Grande Terre* (documented by more than 1200 herbarium collections, Figure 2.10) to verify whether each species fit our definition of monocauly. Species were studied using as many individuals and ontogenetic stages as possible. For most widespread species, an attempt was made to investigate several populations. However, these precautions were sometimes not applicable due to time limitation, access or population-size constraints. In such cases, field observations were supplemented with observations of some photographs (UMR AMAP-IAC database and Endemia website). Photographs led to the exclusion of some species from the monocaulous list, but did not permit the validation of whether they had a monocaulous architecture. As such, some species require further investigation to confirm or refute their monocaulous habit. This concerns less than 10 species for which distinction between sequential and opportunistic reiteration was equivocal (belonging to the genera *Bocquillonia*, *Sloanea*, *Dysoxylum* and *Pycnandra*). Only one species was never observed (*Symplocos paniensis*) and was therefore coded as NA.

The final list of monocaulous species (Appendix 1) was used in the following chapters to investigate the diversity, ecology and evolution of monocaulous plants in New Caledonia. For this purpose, we used several approaches combining taxonomy, architectural analysis, functional ecology and phylogenies (Figure 2.11). More details about the methods relating to phylogenies and functional traits are provided in the corresponding chapters.

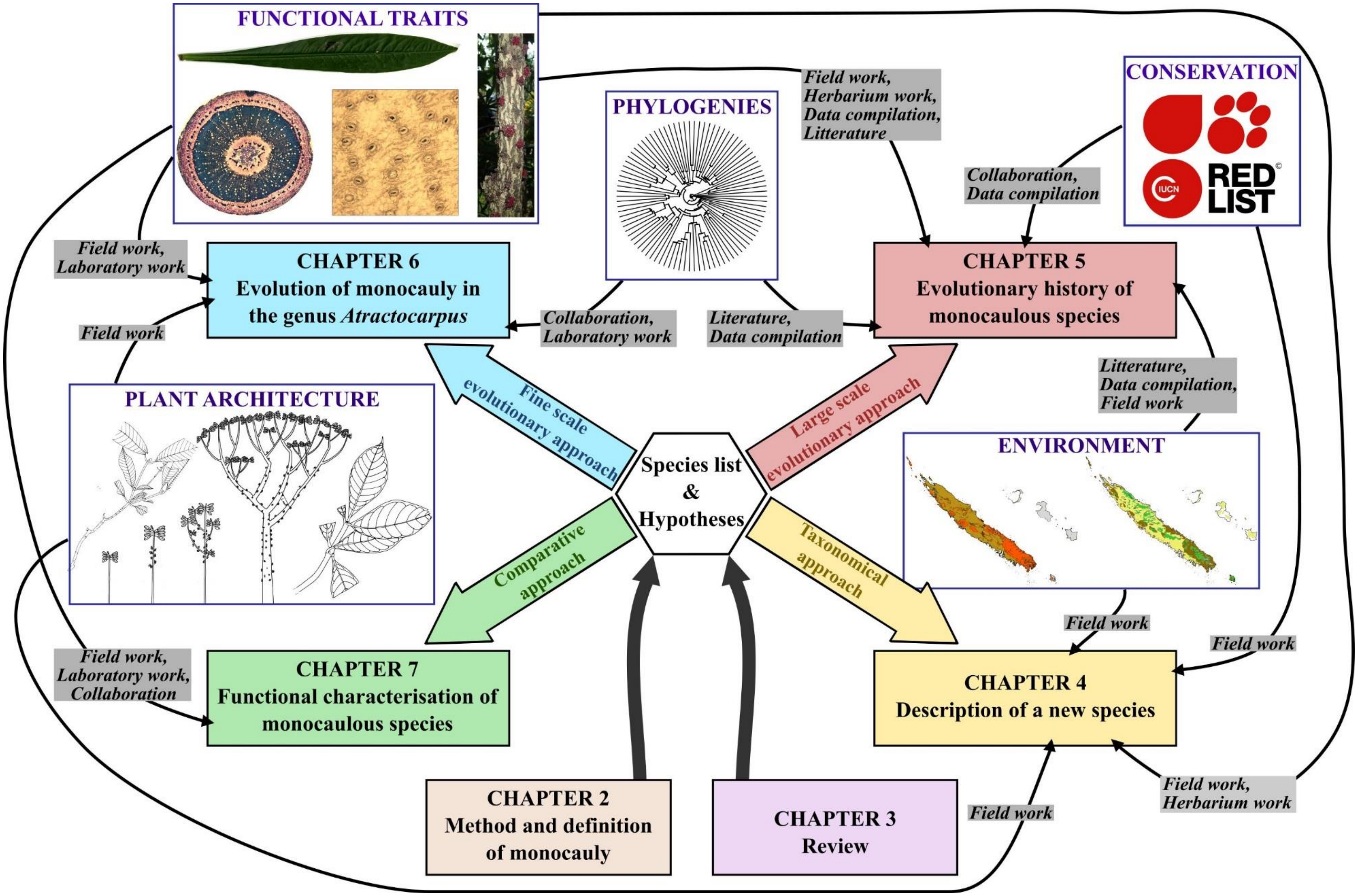


FIGURE 2.11 – General method and tools used in each chapter of the PhD study.

Chapter 3 — The monocaulous growth habit: a review

3.1 History and definitions

The term *monocauly*, derived from the Latin *monocaulis* (*mono* = one, *caulis* = stem), has been used since at least the 17th century (see Mentzelius, 1682) to characterize plants or parts of plants (curiously including roots, e.g. Clementi, 1855). As far as we know, this Latin term was anglicized for the first time by E.J.H. Corner (*monocauly*, *monocauls*, *monocaulous species*) to illustrate his Durian theory about the origin of the modern tree (Corner, 1949). While the Latin term was mainly applied to herbaceous species, the tropical approach of Corner restricted the English term to whole woody plants (“trees”). In this fundamental work (Corner, 1949), monocauls are considered as an extreme of *pachycauls* (few branches, thick stems and large leaves) in their total absence of branching. Since then, the term *monocauly* has been used by a variety of authors to characterize the growth habit of some sparsely-branched plants, the definitions being more or less accurate depending on the study. The vast majority are taxonomic studies in which new species of monocauls are described (e.g. Morat, 1988; Tange, 1997; Sonké et al., 2009; Jebb and Prance, 2011; Taylor et al., 2011; Yu and van Welzen, 2018). In this case, monocauls are sometimes considered under a broad physiognomical definition, i.e. sparsely-branched plants with large leaves clustered in distal part of the stem. Such a general definition better matches Corner’s pachycauly (Corner, 1949) than his more restricted monocauly and fits with several other botanical terms used at different times and in different languages: *palmenforms* or *bananenform* (Von Humboldt, 1808), *rosettentrager* (Reiter, 1885), *tuft-trees* (Warming, 1909), *rosette-trees* (Du Rietz, 1931), *megaphytes* (Cotton, 1944), *cabbage-trees* (Irvine, 1961), *columnar-trees* (Zimmermann and

Brown, 1971), *palmoid* (D'Arcy, 1973), *caulescent-trees* (Halloy, 1990), *giant rosette plant* (Hedberg and Hedberg, 1979), *Schopfbaume* (Zona and Christenhusz, 2015), *scapose-trees* (D'Arcy, 1973). Each of these terms is highly figurative but was often used without an unambiguous definition, making them largely subjective. Hallé et al. (1978) made the distinction between the structural definition (“trees with a single axis” = monoaxial) and the physiognomic one (“trees with a single trunk or visible stem of the plant” = monocaulous). These two approaches to monocauly were reinforced by the designation of a set of architectural models corresponding to each definition (i.e. the Holttum’s and the Corner’s in the first case and the Holttum’s, the Corner’s and the Chamberlain’s in the second). In the course of this thesis, monocauly was regarded from a functional perspective, and a preferred definition has been adopted: “self-supporting woody plants whose cardinal functions rely on a single visible stem”, i.e. plants (i) made of a trunk (either monoaxial or pluriaxial) and with, (ii) determinate growth structures highly specialized in photosynthesis and with an abscission point, (iii) an axis or complex of axis highly specialized in reproduction and whose contribution to whole plant vegetative exploration and photosynthesis is negligible, and possibly (iv) opportunistic reiterates (see Chapter 2).

3.2 Evolution of the monocaulous habit

The oldest known plant macrofossils, dated from ca. 430 Ma (Silurian), were probably isodichotomously branched, producing two daughter branches of similar size (e.g. *Cooksonia*) with terminal sporangia (Meyer-Berthaud and Decombeix, 2009). They presented a mixture of prostrate and erect axes. This simple morphology is suggested to have been dominant up to the Early Devonian (ca. -400 Myr). Devonian is also the period during which pseudomonopodial branching became widespread. In this mode of branching, daughter branches are different in size and orientation, leading to the appearance of a vertical growth and side branches. This mode of branching is suggested to have played an important role in the evolution toward arborescence (Meyer-Berthaud and Decombeix, 2009; Chomicki et al., 2017). These fossil plants were, however, of small size. The tree growth habit evolved in several lineages via convergent evolution (Niklas, 1997), with the earliest known modern tree dating from the Middle Devonian (-390 Myr) (Stein et al., 2007). In the Earth's "oldest forest", these tree-fern-like plants (Cladoxylopsida) had a trunk bearing large branches that probably abscised (cladoptosis or branch shedding), as a "frond-like module" (Stein et al., 2007). The architecture of these fossil plants corresponds to Berry's model (Chomicki et al., 2017). *Archaeopteris*, another modern tree from the late Devonian, was shown to form excurrent deciduous branches (Type A, in Meyer-Berthaud's model, Meyer-Berthaud et al., 1999; Chomicki et al., 2017). Thus, large fossil trees seem to be dominated by non-perennial photosynthetic or lateral structures. Among tree-ferns, an advance level of organization of branching has also been described (Galtier and Hueber, 2001), but most fossil tree-ferns known since the Carboniferous had a monocaulous trunk supporting large compound leaves, comparable to extant tree-ferns of Cyatheaceae and Dicksoniaceae. Plants expressing Corner's architectural model are known from the early Devonian (ca. -400 Myr) and the Holttum's model dates back to at least the Late Devonian (ca. -355 Myr), i.e. before the appearance of most extant and extinct architectural models (Chomicki et al., 2017). While these first unbranched plants probably do not fit with our definition of true woody monocauly (vascular cambium of extant species appearing in the late Triassic (-220 Myr, Savidge, 2008), they show that unbranched architectures were clearly more represented in the past. It was particularly abundant from the Carboniferous (ca. -350 Myr) to the early Cretaceous (ca. -110 Myr), representing between ca. 20% and 40% of the total fossil record for which information is available (Chomicki et al., 2017). From the early Cretaceous, the proportion of taxa with an unbranched architecture gradually decreased in favor of architectures expressing axillary branching. This is in agreement with the rise of small-leafed and highly branched angiosperms, which have progressively replaced the often large-leafed monocaulous habit of ferns and progymnosperms (Coiffard et al., 2012). Today, the monocaulous habit is estimated to represent only ca. 2% of the total known architectures (Chomicki et al., 2017).

The abundance and diversity of monocaulous forms in the floras of the Paleozoic and Mesozoic has often led scientists to consider it as primitive for seed plants (Galtier, 1999) or Angiosperms (Hallier, 1912 in Meeuse, 1967). In his Durian theory on the origin of the modern tree, Corner (1949) suggested that “the more remote ancestors [=of Angiosperms] appear to have been monocarpic and monocaulous, with the Cycad-habit”. This idea was supported by early classifications in which *Cycas* was placed as sister to Gymnosperms and Angiosperms. Such a primitive form was thought to have gradually evolved toward branched forms (with smaller and simpler leaves, flowers, seeds and fruits) to colonize drier and colder habitats, leading in the extant Angiosperm architectural diversity. Corner (1949) argued that extant monocaulous species, occurring in several tropical families, are “relicts” of this ancestral form. Other authors have suggested that the occurrence of monocauly in numerous unrelated families is instead evidence of recent convergent evolution (Richards, 1966; D'Arcy, 1973), the simplicity of monocaulous forms no being synonymous with “antiquity” (Mabberley, 1974b; Hallé et al., 1978). Recently, the rise of molecular phylogenies has largely supported this second view and – while the ancestral growth habit of Angiosperms is still under debate (Doyle, 2012) – Corner’s hypotheses about the evolution of monocauly have been discredited. In extant angiosperms, the monocaulous habit appears to be derived in Senecioneae (Asteraceae, Knox and Palmer, 1995), Lobeliads (Campanulaceae, Givnish, 2010) and the genera *Espeletia* (Asteraceae, Rauscher, 2002), *Oxera* (Lamiaceae, Barrabé et al., 2018) and *Aeonium* (Crassulaceae, Mort et al., 2007). Using a phylogenetic tree including more than 20,000 species of vascular plants, Chomicki et al. (2017) found 118 independent origins of monocauly, strongly suggesting that this habit is not (or not only) relictual in the extant flora.

For several monocaulous species occurring in islands or island-like environments (tropical mountains), evolution of this habit from herbaceous ancestors was suggested early on. Darwin (1859) proposed that herbaceous species, more likely to reach islands than woody taxa, evolved to be taller to outcompete other herbaceous species, ultimately leading to bushes and/or trees (Figure 3.1-A). This hypothesis of so-called secondary woodiness (Carlquist, 1974; Nattier et al., 2013) was first supported by data from comparative anatomy (e.g. Carlquist, 1962; Carlquist, 1969) and later confirmed by molecular phylogenies (Knox and Palmer, 1995; Rauscher, 2002; Givnish, 2010). Why these secondary woody plants are often monocaulous or sparsely branched has not yet been investigated, but it probably involves the conservation of an ancestral herbaceous architecture or of tissue too soft to allow branching (i.e. developmental constraints). Such an herbaceous evolutionary pathway involves heterochronic evolution through peramorphosis ("proportionate giantism") since size and lifespan increase in descendants (Gould, 1977; Alberch et al., 1979; Smith, 2001) (Figure 3.1-A). However, if such a process appears to be nearly certain in some groups, a meta-analysis showed that out of 118 independent evolutions of monocauly, only 34% involved herbaceous ancestors (Chomicki et al., 2017). Based on the observation that several tropical forest tree species have a long understory monocaulous phase (Carlquist, 1965; Richards, 1966), D'Arcy (1973) suggested that monocauls could arise from such trees "which have found it unnecessary to reach the forest canopy". This hypothesis is in accordance with Barthelemy's ideas (Barthélémy, 1988) and suggests heterochronic evolution through paedomorphosis (Barthélémy, 1988) since the descendants (monocauls) evolved to have a smaller size and a simpler form through a truncation of the developmental sequence of their ancestor (which were branched trees). In this case, the paedomorphic processes would be neoteny (decreased growth rate) and possibly

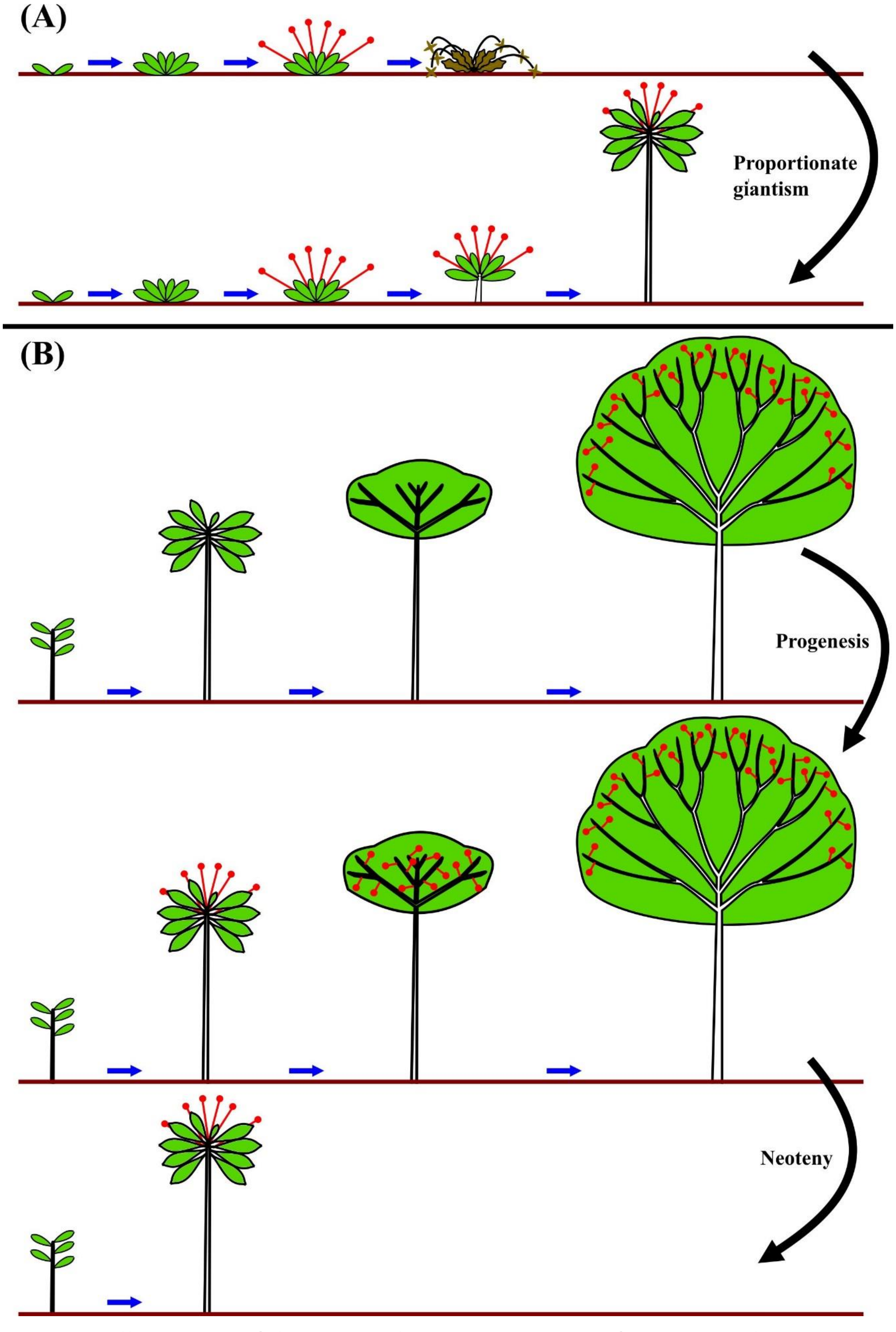


FIGURE 3.1 – Illustration of the two evolutionary scenarios for monocauly as suggested in literature. **(A)** Evolution from an herbaceous ancestor through hypermorphosis. **(B)** Evolution from a branched canopy tree through neoteny (and possibly progenesis).

progenesis (earlier offset of the vegetative phase) if branching appeared before flowering in the ancestral developmental sequence (Figure 3.1-B). This kind of heterochronic evolution was proposed for fossil lycopsids, where *Chaloneria* (Isoetales), a small unbranched shrub, is thought to have evolved from *Sigillaria* (Lepidodendrales), a 15 meter branched tree (Bateman, 1994). Without phylogenies, however these idea will remain hypothetical. Examples of heterochronic evolution in plants mainly involve fragments of plants (e.g. wood, stem, leaves or flowers) while the importance of such processes in the evolution of growth habit remains largely unknown (reviewed in Li and Johnston, 2000).

3.3 Life history and environmental traits associated with monocauly

Like all growth habits (see section 1.3), monocauly is not only characterised by an unbranched stem but also by a large set of morpho-physiological traits. The most striking feature, inherent in most terms used to describe monocauls (see section 3.1), is the presence of large leaves. This relationship between branching intensity and leaf size is an element of Corner's rules (Corner, 1949, 1953-1954). These rules concern two fundamental statements: (i) *Axial conformity*, stipulating that "the stouter, or more massive, the axis in a given species, the larger and more complicated its appendages" and (ii) *Diminution on ramification*, stipulating that "the greater the ramification, the smaller become the branches and their appendages" (Corner, 1949). By "appendages", Corner meant leaves, fruits, inflorescences and flowers. Consequently, monocauls are not only expected to have larger leaves but also a thicker stem, larger fruits and more complex inflorescences (Figure 1.2). The relation between leaf area and twig thickness, namely the worldwide leaf size – twig size spectrum (Westoby and Wright, 2003), and to a lesser extent the relation between leaf area and fruit size, has been extensively investigated (White, 1983b; Bond and Midgley, 1988; Brouat et al., 1998; Cornelissen, 1999; Brouat and McKey, 2001; Westoby et al., 2002; Preston and Ackerly, 2003; Westoby and Wright, 2003; Pickup et al., 2005; Sun et al., 2006; Normand et al., 2008). On the other hand, the relation with branching intensity (i.e. *Diminution on ramification*) received much less consideration. Few studies have shown a negative correlation between branching intensity and twig cross-sectional area or leaf size (White, 1983b; Ackerly and Donoghue, 1998; Westoby and Wright, 2003) or inflorescence length (Ackerly and Donoghue, 1998) but, as far as we are aware, never with fruit size. Moreover, none of these studies included monocaulous species and the measurement methods used to quantify branching intensity are highly variable in the literature. For example, some authors measured the number of active growing tips on whole plants (White, 1983b; Ackerly and Donoghue, 1998) while others measured the mean length between apices and the first branch (Westoby and Wright, 2003), the proportion of trunk nodes producing branches (Ackerly, 1996), or the number of non-branched nodes between two branched nodes (Thomasson, 1972). Such discrepancies call for the need for the definition of a standardized index measuring branching intensity in relation to plants architecture and function.

Consequently, our understanding of the relationships between monocauly and life history trait attributes largely comes from empirical observation and virtually never from attempts to quantify them. Such associations concern cauliflory (Hallé and Mabberley, 1976; Hallé et al., 1978; Barthélémy, 1988; Schmid, 1990), compound leaves (Corner, 1949; Hallé, 1967; Hallé and Mabberley, 1976; White, 1983a), short internodes (Corner, 1949; Chuah, 1977; Hallé et al., 1978; Sussex et al., 2010), dioecy (Hallé et al., 1978), rhythmic growth (Hallé et al., 1978), and high slenderness (D'Arcy, 1973). Their relationship with standard functional traits such as SLA (Specific Leaf Area) or related traits (see Wright et al., 2004) are difficult to estimate given that studies have never clearly included monocauls and that the relation with leaf area is unclear (Westoby and Wright, 2003). In terms of anatomy, studies suggest that pith area along with stem size and leaf area generally increase during ontogeny until the branching point and then progressively decrease (Eggert, 1961; Lauri, 1988). This in turn suggests a higher pith size in the distal part of the stem for monocaulous species than for branched taxa, as confirmed by several studies (Cotton, 1944; Carlquist, 1974; Mabberley, 1974a; Hallé et al., 1978; Meinzer and Goldstein, 1986). Research also suggests that monocauls have a large cortex (Cotton, 1944; Mabberley, 1974a; Hallé et al., 1978; Mosbrugger, 1990) and a thin wood layer composed of a high proportion of parenchyma (Cotton, 1944; Mabberley, 1974a; Aldridge, 1978). The relation between monocauly or pachycauly and vessel or fiber size has been investigated indirectly (Aldridge, 1978; Aldridge, 1981) but results are blurred by the variety of sampled environmental conditions. The life history and functional characteristics of monocaulous plants, as suggested by the published literature, are summarized in Figure 3.2.

Each of these morpho-anatomical attributes depends on particular genetic and physiological processes that are undoubtedly linked with the evolution of monocauly. Apical dominance, i.e. the control exerted by the growing apical meristem over the outgrowth of lateral buds (Cline, 1991), seems of prime importance. While genetics and physiology offer a promising way to understand the evolution of monocauly (see Doebley et al., 1997), they will not be considered in the present study, which instead focus on macro-ecological processes. The importance of hormonal pathways and gene expression on plant branching have been reviewed elsewhere (e.g. Cline, 1994; Sussex and Kerk, 2001; Chomicki et al., 2017).

Monocauls are almost restricted to tropical regions (Corner, 1949; Hallé et al., 1978), where they are known from areas with diverse environmental conditions, but mainly from rainforests. D'Arcy (1973), for instance, reviewed environmental occurrences of diverse monocaulous plants and concluded that “all are found in wet forests”. Such an ecological preference has actually been

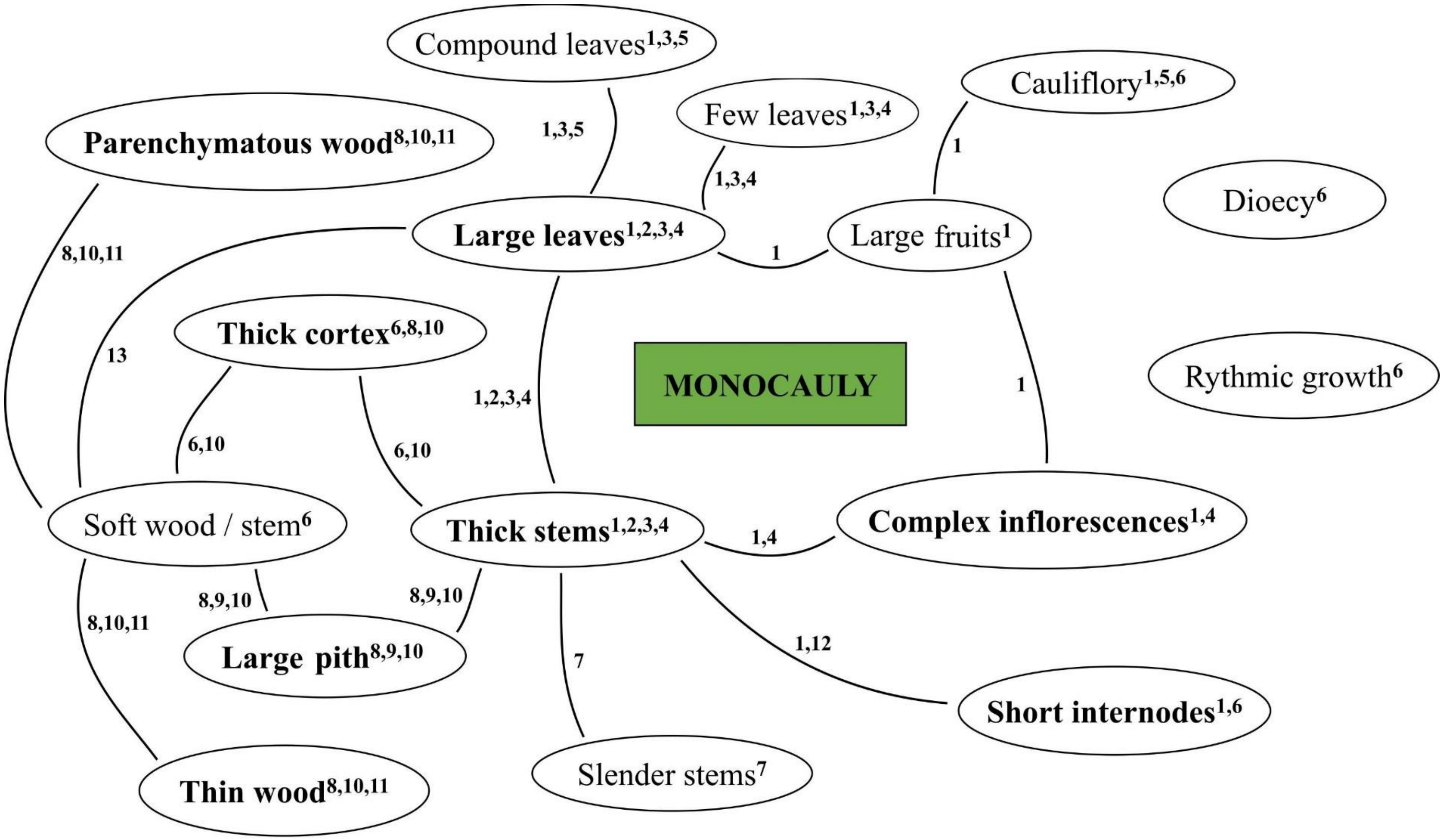


FIGURE 3.2 – Synthesis of life history trait attributes suggested to be related with monocauly in literature. Numbers point on references in which trait associations were suggested. Bold text represents trait attributes for which association with branching intensity was statistically showed. [1]Corner (1949), [2]Westoby & Wright (2003), [3]White (1983a), [4]Ackerly & Donoghue (1998), [5]Hallé & Mabberley (1976), [6]Hallé et al. (1978), [7]D'Arcy (1973), [8]Cotton (1944), [9]Carlquist (1974), [10]Mabberley (1974a), [11]Aldridge (1978), [12]Chuah (1977).

suggested for each monocaulous architectural model independently (Hallé and Mabberley, 1976; Hallé et al., 1978) and in more general terms, for monocaulous plants as well (Corner, 1949; Hallé, 1974; Schmid, 1981). In rainforests, some insights suggest that pioneer trees, well suited for sunny environments, are less branched than non-pioneer species (White, 1983a; Ackerly, 1996). This could particularly pertain to compound-leaved trees, for which large dissected leaves are less costly than branches (Givnish, 1984, 1995). Even though monocauly and compound leaves have often been associated in the literature (Corner, 1949; Hallé, 1967; Hallé and Mabberley, 1976), no data show whether these pioneer features apply to monocauls. Richards (1966) argues that monocauls are “fitted only for a permanently favorable environment”, which he considers to include tropical rainforests and some tropical islands. However, while monocauls are obviously present on islands (Carlquist, 1974), recent studies suggest that the evolution of woodiness in these species is associated with greater drought tolerance suited for open habitat (Mort et al., 2007; Lens et al., 2013) and Cotton (1944) even argues that their evolution on islands is linked with high insolation. Finally, an important part of the literature on monocauly discusses tropical mountain species. This growth habit seems very well adapted to such sunny and cold environments (Hedberg and Hedberg, 1979; Meinzer and Goldstein, 1986; Givnish, 2016). A detailed morpho-anatomical study of monocaulous plants growing preferentially in rainforest understory conditions might shed light on adaptations and evolutionary constraints related with this more widespread model of monocauly.

Chapter 4 — *Novitates neocaledonicae VII*: A new monocaulous species of *Bocquillonia* (Euphorbiaceae) from New Caledonia

Published article

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Abstract:

A new species of Euphorbiaceae, *Bocquillonia corneri*, narrowly endemic to the extreme north-east of New Caledonia's main island, is here highlighted, described and illustrated, based on original morphological and architectural characteristics. This new species differs notably by its unique monocaulous tree habit, while other *Bocquillonia* species are ramified shrubs, small monocaulous shrubs or well reiterated trees. A previous identification key to *Bocquillonia* species is expanded to include this new species. *Bocquillonia corneri* is located in a very confined gully forest at low-elevation on volcano-sedimentary substrate. A preliminary IUCN conservation status of Critically Endangered (CR) is proposed.

Keywords: Acalyphoideae, plant architecture, taxonomy

4.1 Introduction

The genus *Bocquillonia* Baillon (1862: 225) (Euphorbiaceae) was initially described with two species. Additional species or varieties were subsequently described by Müller Argoviensis (1865), Baillon (1873), Guillaumin & Beauvisage (1913 publ. 1914) and Airy Shaw (1972, 1974, 1978a, 1978b, 1980, 1981). The nomenclature and taxonomy of the genus were finally entirely studied in a global revision (McPherson & Tirel, 1987), adding one new species and putting two species and three varieties in synonymy. The genus is currently composed of fourteen species all endemic to New Caledonia (McPherson & Tirel 1987; Govaerts *et al.* 2000; Munzinger *et al.* 2016). *Bocquillonia* can easily be distinguished from other New Caledonian Euphorbiaceae by a combination of morphological characters: limb with abaxial laminar glands; plants dioecious or rarely monoecious; glomerulose to narrowly racemiform inflorescences; flowers without corolla; calyx 2–3 lobed in male flowers, calyx shorter than gynoecium in female flowers (McPherson & Tirel 1987). Moreover, recent observations show that *Bocquillonia* species present internal phloem, i.e. a supernumerary phloem tissue in the stem between pith and wood (Bruy pers. obs.). The only phylogenetic study including *Bocquillonia* species (Wurdack *et al.* 2005) shows that the genus belongs to the tribe Alchorneeae (Acalyphoideae) and suggests its inclusion in the pantropical genus *Alchornea* Swartz (1788: 98). However, this study includes too few species (one *Bocquillonia* and two *Alchornea*) to invalidate the genus (Pillon *et al.* 2017).

Bocquillonia exhibits a great diversity of architectures and is therefore included in an ongoing PhD study conducted by David Bruy concerning the diversity, ecology, and evolution of monocaulous New Caledonian species. Some *Bocquillonia* species such as *B. rhomboidea* (Schltr.) Airy Shaw (1974: 320) are ramified (e.g. close to the Koriba's architectural model, Hallé *et al.* 1978, Figure 4.1-A) while others such as *B. castaneifolia* Guillaumin (in Guillaumin & Beauvisage

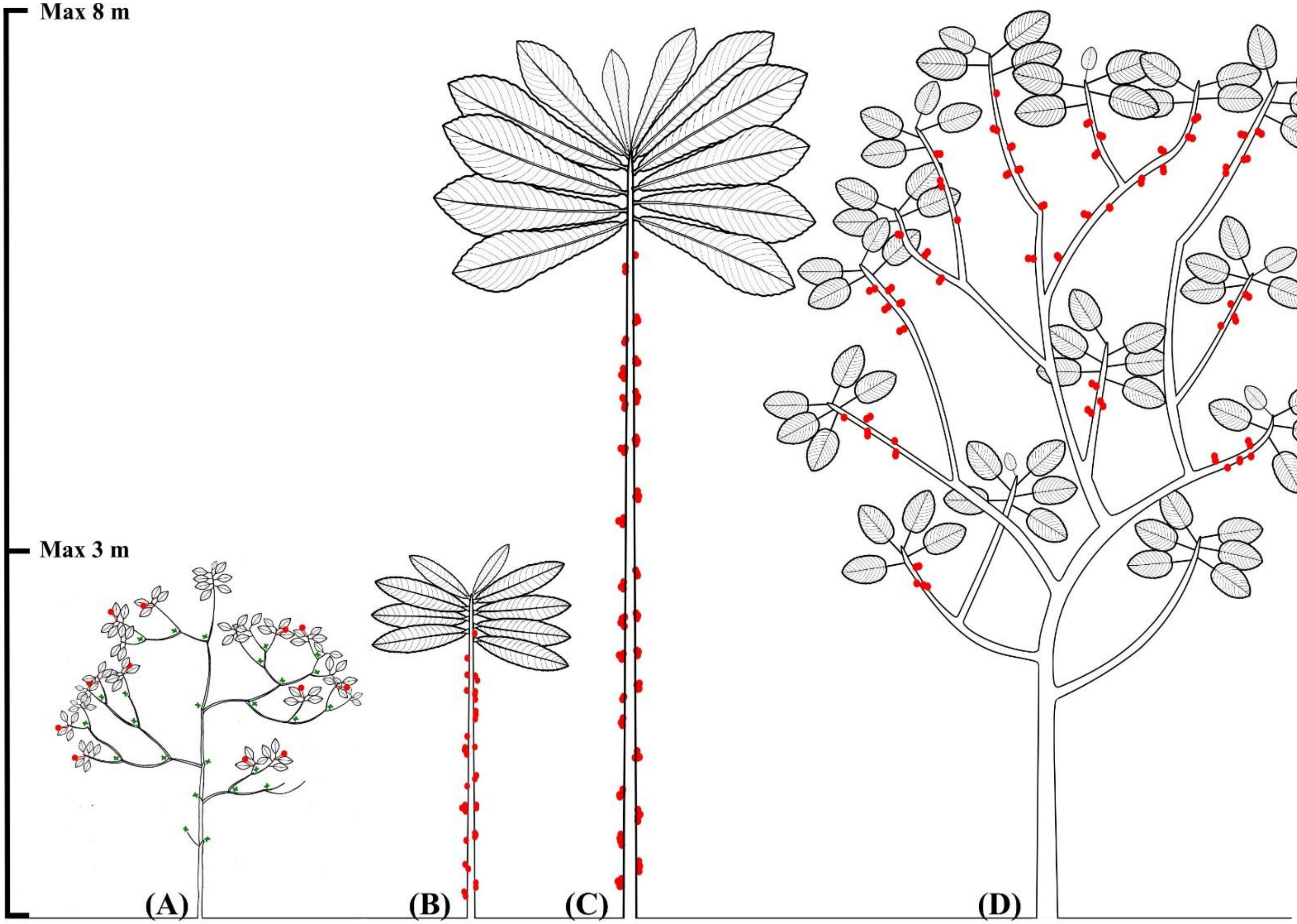

FIGURE 4.1 – Diagram of the different growth habits known for *Bocquillonia* species at full maturity. **(A)** Shrub whose architecture is close to the Koriba's architectural model (exemplified by *B. rhomboidea*). **(B)** Almost not reiterated shrub conforming to the Corner's architectural model (exemplified by *B. castaneifolia*). **(C)** Almost not reiterated tree conforming to the Corner's architectural model (exemplified by *B. corneri*). **(D)** Well reiterated tree conforming to the Corner's architectural model (exemplified by *B. grandidens*). Green cross represents sequential apical death and red points represent inflorescences.

1913 publ. 1914: 110) are monocaulous (i.e. with a single stem carrying out all essential functions; Corner's model, Figure 4.1-B,C). Other species such as *B. grandidens* Baillon (1873: 128), can be monocaulous in early maturity but become very ramified when older (Figure 4.1-D). In this case, the process of ramification is called 'opportunistic reiteration' (Barthelemy & Caraglio, 2007), which corresponds to the production of a new stem morphologically and functionally identical to the initial stem as a response to stress or increase in resource levels. All of the currently described monocaulous species are small treelets with few reiterations or very reiterated trees. However an unusual population of monocaulous *Bocquillonia* observed in the extreme northeast of New Caledonia's main island (Grande Terre) differs notably from the other monocaulous species since it is very tall (8 m) and almost not reiterated. Morphological herbarium investigations and field observations confirmed clearly that this population represents a distinct taxon from all other *Bocquillonia* species. This giant monocaulous taxon is consequently described and illustrated here, and a preliminary IUCN status is proposed. A modification of the *Bocquillonia* identification key of McPherson & Tirel (1987) is proposed to include this new species.

4.2 Material and Methods

Measurements, shapes and colours of the different organs are based on the examination of herbarium material and several field observations. All herbarium specimens of *Bocquillonia* present at NOU, P and MPU were examined (Herbarium acronyms follow Thiers 2017). All available virtual collections of K were also studied online (http://apps.kew.org/herbcat/). Terminology used for description follows Harris & Harris (2001). Small morphological organs were observed using a Leica M165C binocular microscope mounted with a Leica EC3 camera for photography, and measurements were performed using pictures edited in the imageJ software (Schneider *et al.* 2012). Field pictures were taken with an Olympus Stylus TG-2 camera. The risk of extinction assessment was conducted using the IUCN Red List Criteria (IUCN 2012); Area Of Occupancy (AOO, using a 2 × 2 km grid) and Extent Of Occurrence (EOO) values were calculated using the online “geocat” software (Bachman *et al.* 2011); the number of individuals was established after a half-day of botanical prospection along the single creek where the species is known.

4.3 Taxonomy

Bocquillonia corneri Bruy, Barrabé & Munzinger *sp. nov.* (Figures 4.2, 4.3)

Type:—NEW CALEDONIA. Province Nord. Commune de Ouégoa: Base du col d’Amoss, 105 m, 20°19’2.4”S, 164°25’22.8”E, 11 August 2017 (fl.), *Bruy, Barrabé & Hattermann 923* [♀] (Holotype P01156371!, Isotypes NOU088193!, MPU310860!, K!, MO!, BRI!).

Diagnosis – Vegetatively, *Bocquillonia corneri* resembles *B. castaneifolia* Guillaumin in its monocaulous architecture, its oblanceolate to obovate blade shape and in having very short petioles. *Bocquillonia corneri* differs most notably from the latter species by the dimensions of the stem (up to 8 cm DBH and 8 m height, vs. 3 cm and 2 m), petiole length (> 9.4 mm, vs. < 5 mm) and blade length (> 25 cm long, vs. < 24 cm) and in having caducous stipules (vs. persistent) and stigmas applied against the ovary in female flowers (vs. erect).

Based on reproductive organs, *Bocquillonia corneri* resembles *B. sessiliflora* Baillon (1862: 226), which has also condensed inflorescences and in which the stigmas are oval and applied against the ovary. *Bocquillonia corneri* differs most notably from the latter species by the strictly monocaulous architecture (vs. well reiterated treelet), the narrowly oblanceolate leaf blade (vs. ovate to oblong), the lack of an upper pulvinus on the petiole (vs. present) and the fushia calyx *in vivo* (vs. green).

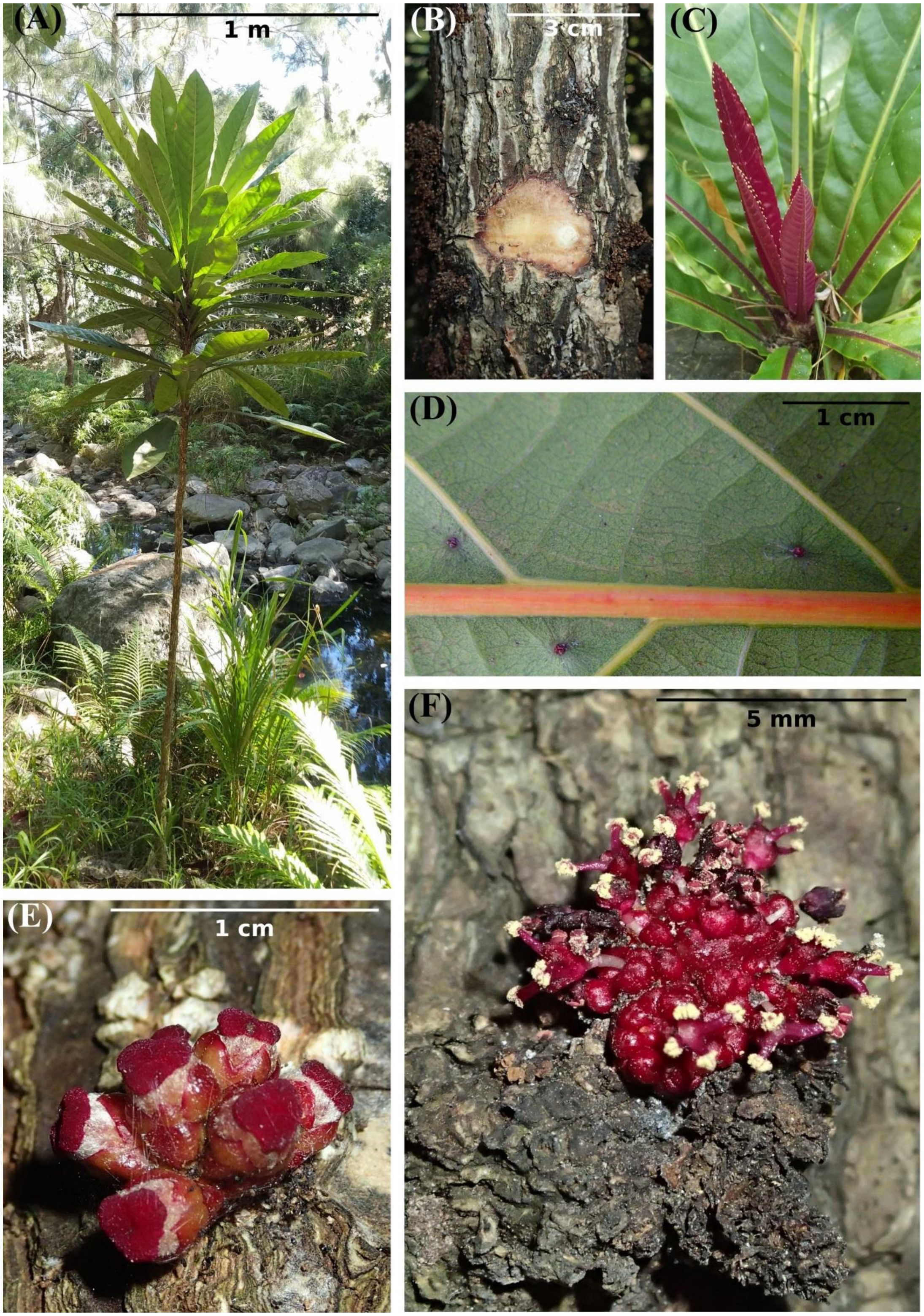

FIGURE 4.2 – Pictures of *Bocquillonia corneri*. **(A)** Early mature individual in its natural environment. **(B)** Bark and slash with old staminate inflorescences. **(C)** Apex and flushing young leaves. **(D)** Detail of nervation and glands of the abaxial surface. **(E)** Pistillate inflorescences; **(F)** Staminate inflorescences.

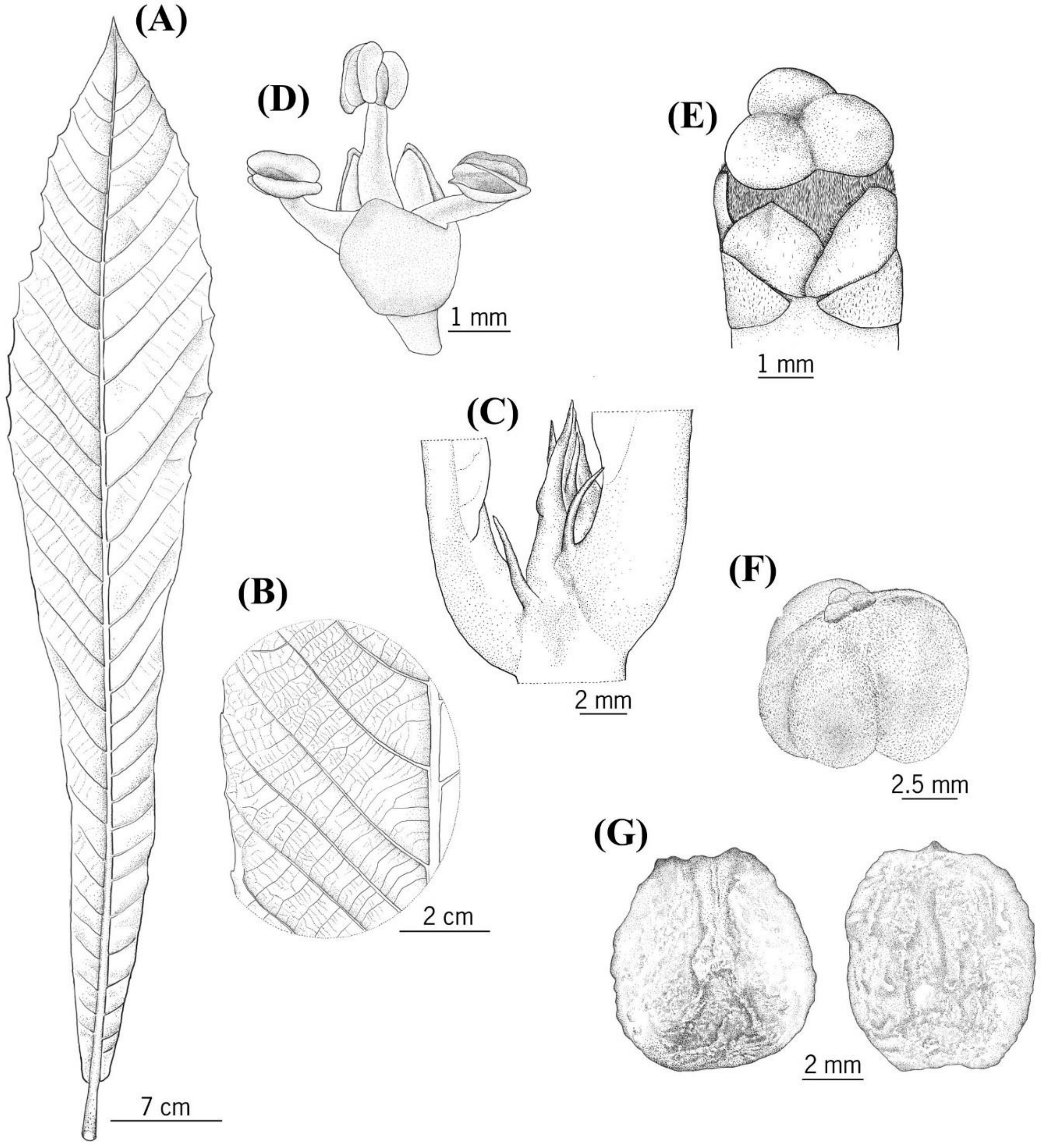

FIGURE 4.3 – Drawing of *Bocquillonia corneri*. **(A)** Mature leaf. **(B)** Detail of venation. **(C)** Stem apex with stipules. **(D)** Male flower. **(E)** Female flower. **(F)** Fruit. **(G)** Seed in ventral (left) and dorsal face (right). Illustrator: Ramon L..

Monocaulous treelet to monocaulous tree, 1.50 m to 8.00 m tall, sometimes with a few reiterations.

Stem glabrous, light grey to white, with brown longitudinal scars; young stems bearing alternatively cataphylls and pseudoverticillate assimilative leaves bundled at the proximal part of the stem.

Stipules caducous, subulate, 3–7 mm long, 0.5–1.2 mm wide, dark brown *in sicco*, glabrescent. Cataphyll: caducous, narrowly lanceolate, navicular, pectinate, 6–11 (–15) mm long, 0.8–2.1 mm wide, densely strigose with silvery trichomes *in sicco*. Assimilative leaf: blades narrowly oblanceolate, (24.6–) 36.1–72.5 × 6–16.5 cm, dark purple when young, then pinkish and green when mature, chartaceous to subcoriaceous, adaxial surface glabrous, abaxial surface nearly glabrous; base cuneate to rounded, sometimes asymmetrical; apex acuminate to acute, rarely rounded; margin dentate and minutely revolute; leaf teeth (13–) 21–27 on each side, white on young leaves, black on mature leaves; sunken laminar glands (6–) 13–34 (–49) on each side of the midrib, circular to elliptic, (0.3–) 0.5–1.3 (–1.5) mm in diameter, black *in sicco*, generally close to the midrib. Venation craspedodromous; midrib not or barely raised adaxially, prominent abaxially, pink to purple when young, green when mature, glabrous adaxially, sparsely and obscurely appressed-puberulent abaxially; secondary veins (16–) 24–30 on each side of the midrib below the acumen, raised adaxially, prominent abaxially, spaced from 8–38 mm, angle with midrib 48–92 °, glabrous; tertiary venation scalariform, not or barely raised on both surfaces, glabrous; quaternary venation obscure adaxially, minutely raised abaxially, glabrous. Petioles without an upper pulvinus, flat adaxially, subtriangular in cross-section, 9.4–34.4 mm long, 3.3–7.1 mm in diameter, pink to purple when young, green when mature, striate *in sicco*, sparsely and obscurely appressed-puberulent to glabrous.

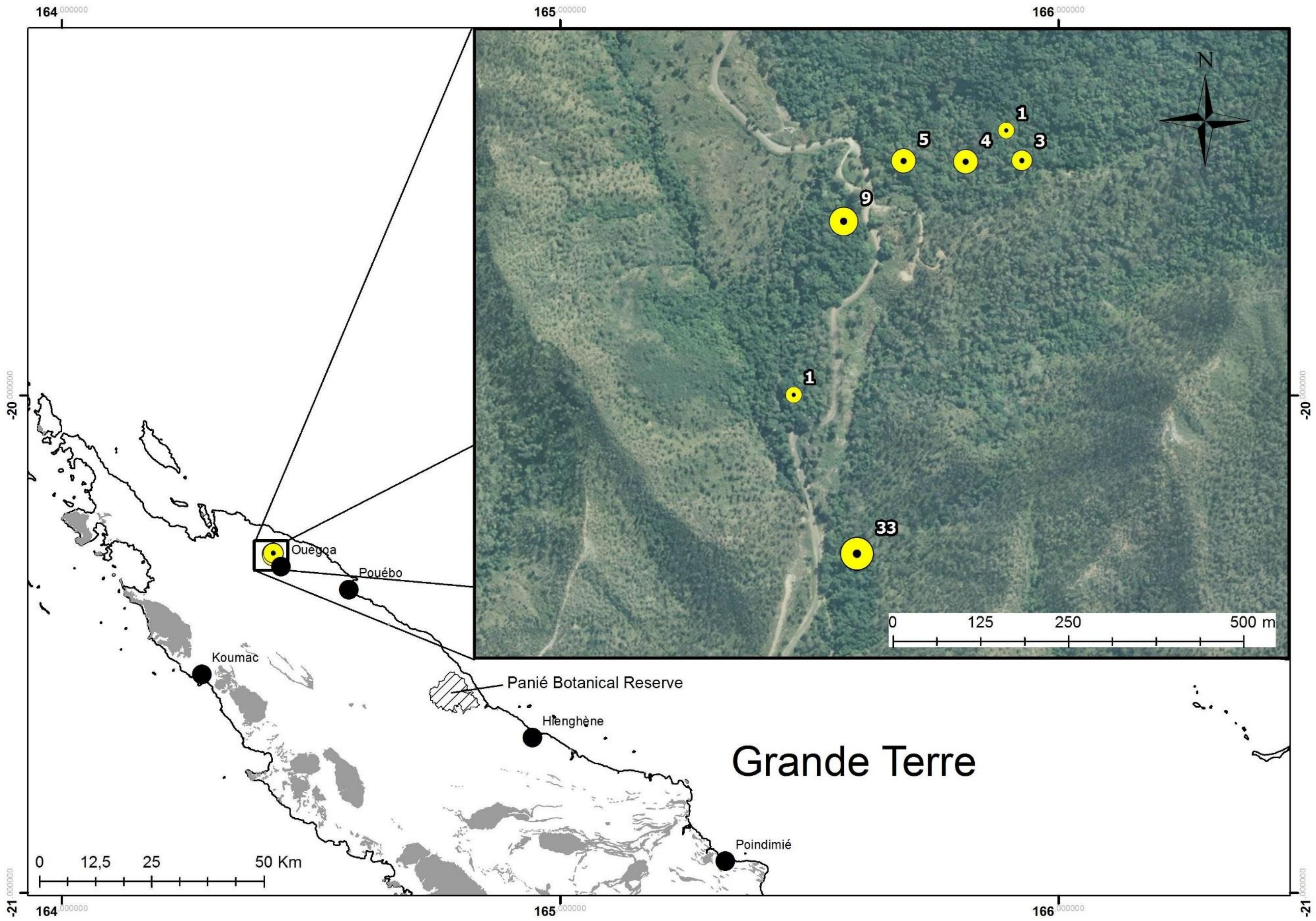

FIGURE 4.4 – Distribution map of *Bocquillonia corneri* in the North Province and detail of the distribution of known individuals along Indanou creek. Numbers near the yellow dots represent the number of individuals.

Plants dioecious, sometimes monoecious. Inflorescences reduced to cauliflorous glomerules sometimes axillary to oldest leaves, borne on short shoots; staminate inflorescences (3.5–) 4.4–7.8 mm long, 4.5–14.5 mm in diameter; bracts ovate, with an acuminate to rounded apex, reducing in size from outside to inside of the inflorescence, fushia, sparsely pubescent and ciliate. Staminate flowers glabrous, pedicel ca. 1.5–3.5 mm long, ca. 0.4–1 mm wide, white pinkish; calyx (2-) 3-lobed, fushia, lobes ovate, 0.8–3.1 mm long, 1.5–2.6 (–3) mm wide, with an obtuse to acute apex, with a turbinate tube 2.3–3.8 mm long, 1.8–2.9 mm wide; stamens 2–4, connate at the base, fushia, glabrous, anthers 0.8–1.9 × 1.0–2.0 mm, filaments 1.8–3.6 mm long above the connate section, 0.25–0.60 mm wide, pistillode lacking. Pistillate inflorescences 6.5–13.5 mm long, (7–) 9.9–16.7 (–18.5) mm in diameter, bracts ovate, 1.8–5.6 × 1.7–5.1 mm, with a rounded to acute apex, fushia, ciliate and pubescent, glands present. Pistillate flowers fushia, sessile; sepals 4–5, ovate, 2.2–5.6 mm long, 1.8–4.4 mm wide, with an acuminate apex, ciliate, pubescent to sparsely pubescent; stigmas (2–) 3 (–4), oval, slightly domed, papillate, applied against the ovary; ovary spherical, 2.7–4.6 mm in diameter, densely hirsute. Fruit 3-lobed, ca. 9 mm long, 9–11 mm in diameter, exocarp rugulose, ochre *in sicco*, sparsely strigose with silvery trichomes; placental column 5.5 mm long; seeds 6–7 × 4.5–5.5 mm, covered with low, blister-like swellings, dark grey *in sicco*.

Phenology – Flowers of *Bocquillonia corneri* have been observed in March, August and November, and mature fruits have been collected in April and August.

Distribution and Ecology – This new species is only known from the *Indanou creek*, at the base of Col d’Amoss in the northeastern part of Grande Terre, in Province Nord, near Ouégoa village (Figure 4.4), where it occurs in thalweg (gully) forest on volcano-sedimentary substrate, more specifically on micaschists, at around 60–150 meters elevation. Only 56 adult individuals are known but intensive field prospection in the area could potentially locate other individuals.

Etymology – The plant is named in honour of E.J.H. Corner who provided interesting insights about monocaulous plants and whose theories inspired generations of botanists. In addition, the architecture of this plant conforms perfectly to the Corner's architectural model (Hallé *et al.* 1978).

Species recognition – *Bocquillonia corneri* is easily recognizable in the field because it is the only species of the genus that is a very few times reiterated monocaulous tree. It is also the only species to combine condensed inflorescences, pistillate flowers with a fuchsia calyx and oval stigmas applied against the ovary.

Conservation status – *Bocquillonia corneri* is only known from a single population, critically threatened by fire, human activity and invasive species, in particular the deer *Rusa timorensis* de Blainville (1822: 267). The population corresponds to one unique location *sensu* IUCN since all individuals could be affected by a single threatening event. Only 56 mature individuals are known, with approximately 25 female individuals. Even though individuals not seen by the authors may be present in the region, it is very probable that the population is smaller than 250 mature individuals. The EOO calculated is 0.092 km² and the AOO is 4 km². We assign consequently a preliminary conservation status of Critically Endangered to *B. corneri* (CR) B1 ab(iii,v)+2ab(iii,v) using the IUCN Red List criteria (IUCN 2012).

Additional specimens examined (Paratypes) – NEW CALEDONIA. Ouégoa. Route Koumac–Ouégoa, peu avant le Col d'Amoss, 28 November 2008 (fl.), *Barrabé & Létocart 788* [♂] (NOU033871); Ouégoa: Base du col d'Amoss, 100 m, 20°19'40.6"S, 164°25'34"E, 11 August 2017 (fl.), *Bruy, Barrabé & Hattermann 921* [♂] (BRI, K, MO, MPU310861, NOU088196, P01156372); Païta: Chez D. et I. Létocart, 1 June 2017 (fl.) [Cultivated plant], *Bruy, Barrabé &*

Létocart 807 [♂] (NOU088195); Nouméa: Val Plaisance, Chez J.M. Veillon, 16 June 2017 (fl.) [Cultivated plant], *Bruy, Barrabé & Veillon 879* [♀] (NOU088194); Ouégoa: Indanou (Amoss), 41 m, 20°19’18.947”S, 164°25’23.058”E, 10 March 2016 (bd.), *Fleurot 224* [♂] (NOU085638); Ouégoa: Indanou (Amoss), 41 m, 20°19’19.722”S, 164°25’23.380”E, 27 April 2018 (fr.), *Fleurot 433* [♀] (NOU088719); Ouégoa: Col d’Amoss, 200–300 m, 19 October 1956 (fr.), *MacKee 5479* [♀] (L0449021, P00160238); Ouégoa: Bas du col d’Amoss, côté Ouégoa, 10–20 m, 27 August 2006 (fr.), *Munzinger 3544 (Leg. D. et I. Létocart)* [♀] (NOU013877).

4.4 Identification key of McPherson & Tirel (1987), modified to include *B. corneri*.

1. Inflorescences elongated, typically more than 5 cm long; inflorescences ♀ with spaced flowers; inflorescences ♂ composed of several glomerules, generally distinct 2

-. Inflorescences shorter, up to 4 cm long, sessile (rarely inflorescences ♀ slightly elongated) with flowers solitary or clustered in a single glomerule hiding the axis..11

2. Blades 5–10.5 cm long, elliptic; stigmas mostly spreading..***B. rhomboidea***

-. Blades > 10 cm long (rarely blades smaller, in this case blades obovate and stigmas erect) 3

3. Branches with persistent pubescence; stigmas spreading, with margin minutely laciniate; species from North-East (Aoupinié, Tonine, Panié)..***B. phenacostigma***

-. Branches quickly glabrescent; stigmas erect or spreading, with margin entire or ± lobed................4

4. Blades narrowly obovate, with cordate to obtuse bases; petioles < 2.5 cm..5

-. Blades elliptic, ovate or obovate, generally with acute bases (if bases obtuse, longest petioles > 3 cm long) 6

5. Stigmas ca. 5 mm long; blades generally coriaceous, generally with strongly marked teeth..........

………***B. codonostylis***

-. Stigmas ca. 1 mm long; blades generally chartaceous, with ± marked teeth……………………***B. brevipes***

6. Axils of secondary veins often with domatia (tufts of trichomes); male glomerules often tightly clustered; tree 9–15 m tall; species from *Ile des Pins*……………………………………………………***B. arborea***

-. Axils of secondary veins without domatia (trichome tufts); male glomerules spaced; treelet or tree 0.5–8 m tall; species from *Grande-Terre*……………………………………………………………………7

7. Apical pulvinus of petiole smaller than the basal one……………………………………………***B. goniorrachis***

-. Apical pulvinus as large as the basal one……………………………………………………………………8

8. Stigmas > 6 mm long, erect; mature male flower-buds > 1 mm in diameter, ovoid or cylindrical; blades often glossy on both faces……………………………………………………………………***B. lucidula***

-. Stigma ± spreading, ca. 1 mm long; mature male flower-buds 0.5–1 mm in diameter, spherical; abaxial blade faces dull……………………………………………………………………………………9

9. Blades 4 times longer than wide, abaxial faces generally glaucous; petiole slightly flattened above; species from peridotitic mountains of South, West and North-West…………………………***B. spicata***

-. Blades 2–3 times longer than wide, abaxial faces green; petioles generally cylindrical………………10

10. Petioles < 11 cm long; blades 3 times longer than wide, up to 13 cm wide; species from North-East on schists……………………………………………………………………………………***B. nervosa***

-. Petioles (10–) 14–28 cm long; blades 2 times longer than wide, the wider ones > 13 cm wide; species from peridotitic mountains of North-West………………………………………………………***B. longipes***

11. Petioles absent or without pulvini……………………………………………………………………12

-. Leaves clearly petiolate and with pulvini…………………………………………………………………13

12. Petioles < 7 mm long and < 3 mm wide; blades < 24 cm long; monocaulous shrub up to 2 m height; stipules persistent; stigmas erect; species from peridotitic massif of extreme North-West...***B. castaneifolia***

-. Petioles > 7 mm long and > 3 mm wide; blades > 24 cm long; monocaulous shrubs or trees up to 8 m height; stipules caducous; stigmas applied against the ovary; species from micaschists of extreme North-East...***B. corneri*, sp. nov.**

13. Longer petioles < 18 mm; shrub up to 3 m height, sequentially well ramified; stipules filiform...***B. brachypoda***

-. Longer petioles > 18 mm; shrubs or trees up to 7 m height, well ramified by reiteration; stipules with enlarged bases...14

14. Blades 1.7–2.5 times longer than wide, 10–23 cm wide; petioles 4–16 cm long; stipules shortly triangular; inflorescence generally elongated up to 3.5 cm; stigmas laciniate................***B. grandidens***

-. Blades (2.7–) 3–5 times longer than wide, 2–11 cm wide; petioles 1.8–10 cm; stipules subulate; inflorescence generally spherical, sometimes slightly elongated (up to 2 cm); stigmas not laciniate...***B. sessiliflora***

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Chapter 5 — A remarkable case of evolutionary convergence: correlated evolution and environmental contingencies of monocauly in the flora of New Caledonia

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Submitted article

Annals of Botany

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Abstract:

Background and Aims Convergent evolution is recognized as a key driver of biological diversity. While tropical islands host the most remarkable cases of convergence, this phenomena has never been described in the New Caledonian biodiversity hotspot, known for the exceptional distinctiveness and richness of its biota. In this study, we document a new case of convergence by illustrating the evolutionary history of monocauly in the woody flora.

Methods Using herbarium data, extensive field work and literature compilation, we listed New Caledonian monocaulous species and scored six life history and two environmental traits for 2114 New Caledonian woody self-supporting species. We constructed a phylogenetic supertree for New Caledonian woody genera to investigate the minimum number of evolutionary events, phylogenetic signal, and evolutionary correlates of monocauly in the island. IUCN risk of extinction status and threats for New Caledonian flora was used to evaluate major threats on monocaulous species.

Key Results We recorded 182 monocaulous species belonging to 41 genera, 30 families and 15 orders. We found at least 31 independent evolutionary events leading to monocauly. The habit showed a non-random distribution over the supertree that suggests some prerequisites facilitating its evolution. Monocauly evolved preferentially in rainforest and on ultramafic substrate, and triggered the evolution of both cauliflory and marked rhythmic growth. However, no preadaptation was identified in this study although architectural prerequisites appear to be a promising trait for further investigation. Monocaulous species appeared more threatened (IUCN risk of extinction status) than the branched taxa, with a particularly high impact of introduced herbivores.

Conclusions The evolution of monocauly in New Caledonia is comparable to the most famous cases of convergence on islands. Evolutionary hypotheses explaining this remarkable convergence involve rainforest features and history, ultramafic substrate and long-term absence of browsers.

Keywords: Biodiversity hotspot, Cauliflory, Convergence, Correlated evolution, Disharmony, Growth habit, Islands, IUCN redlist, New Caledonia, Plant architecture, Rainforest, Ultramafic substrate

5.1 Introduction

The isolation and environmental heterogeneity of New Caledonia, an archipelago in the Southwest Pacific, and the multiple colonizations from different geographical areas that have taken place since over ~37 Ma have resulted in a flora that harbours many peculiarities. The New Caledonian flora is well known for its exceptional level of richness and endemism (Morat et al., 2012; Munzinger et al., 2016), the high incidence of relictual lineages (Pillon, 2012; Pouteau et al., 2015; Pillon et al., 2017), a great diversity of conifers (Jaffré, 1995), and some unusual biological forms such as the world's only parasitic Gymnosperm (*Parasitaxus usta*, De Laubenfels, 1959; Feild and Brodribb, 2005) and a monocarpic large tree (*Cerberiopsis candelabra*, Veillon, 1971). This astonishing flora is of important conservation concern (Jaffré et al., 1998), recognized by Myers (1988) as one of the 10 original "Biodiversity Hotspots" and the smallest among the 36 currently recognized hotspots (Mittermeier et al., 2004).

An important feature of insular biota, considered as major evidence of long-distance dispersal, is their taxonomic disharmony, i.e. the unbalanced representation of plant groups (Carlquist, 1965, 1974; Pillon et al., 2010). The presence of novel biotic and abiotic conditions encountered following colonization have, in many instances, triggered functional shifts (Patiño et al., 2017) that can lead to losses in functional diversity (Boyer and Jetz, 2014) and uneven representation of functional groups, i.e. functional disharmony. In New Caledonia, several examples of functional and taxonomic disharmony have been described recently, including the high incidence of dioecy (Carpenter et al., 2003; Schlessman et al., 2014), the over-representation of relict angiosperms (Morley, 2001; Pouteau et al., 2015; Trueba, 2016), the diversity of metal hyper-accumulator species (Jaffré et al., 2013; van der Ent et al., 2015), and the low richness in liana (Bruy et al., 2018). The cause of disharmony in the New Caledonian flora is often attributed to the high incidence of ultramafic substrates, covering about a third of the main island, *Grande Terre*, (Pillon et al., 2010; Isnard et al., 2016) and to the persistence of rainforests through periods of paleoclimatic fluctuation (Pintaud et al., 2001; Poncet et al., 2013; Pouteau et al., 2015; Tournebize et al., 2017), while adjacent regions experienced intense extinction events (Kemp, 1978; Crisp et al., 2004; Dodson and Macphail, 2004; Byrne et al., 2008; Byrne et al., 2011).

Another evolutionary mechanism that has long fascinated biologists in island systems is convergence in plant form and function (Elmer and Meyer, 2011; Whittaker et al., 2017). Convergent evolution, i.e. the rise of similar trait attributes among distantly related lineages subjected to similar selection pressures, is a key driver of biological diversity (Givnish, 2016). In many islands, cases of evolutionary convergence have been well documented such as divaricating plants in New Zealand (Greenwood and Atkinson, 1977; Tomlinson, 1978; Howell et al., 2002) and giant rosette shrubs in Hawaii (Carlquist, 1974; Givnish et al., 2009; Givnish, 2010) and Macaronesia (Shmida and Werger, 1992; Mes and Hart, 1996). One of the most famous cases of convergence in island floras is the high proportion of woody species that evolved from herbaceous ancestor, a phenomenon referred to as “insular woodiness” (Carlquist, 1974, 2013; Lens et al., 2013). A high incidence of insular woodiness, as well as other evolutionary convergence, has, however, not been observed in New Caledonia (Carlquist, 1974; Pillon et al., 2017).

Here we report a previously uninvestigated case of convergence occurring in the New Caledonian flora: the presence of numerous monocaulous (i.e. unbranched) plants in multiple lineages. This phenomenon has been repeatedly described by botanists who have studied the New Caledonian flora and have mentioned its presence in many distinct lineages (Veillon, 1976; Schmid, 1979, 1990). Monocaulous plants, characterized by a thick unbranched trunk and large leaves clustered in the distal part of the stem, have long fascinated naturalists (Von Humboldt, 1806; Corner, 1949; Hallé et al., 1978). Beyond being a botanical curiosity, monocauly has been widely discussed in ecological and evolutionary contexts, and was central to the development of a major biological theory (Corner, 1949). The monocaulous habit was long considered as primitive in Angiosperms (Corner, 1949, 1953-1954) until recent phylogenetic work showed a recent origin of this growth habit in many lineages (Givnish, 2010; Chomicki et al., 2017; Barrabé et al., 2018; Chapter 6). Several monocaulous species, sometime corresponding to rosette trees, evolved from herbaceous ancestors (Carlquist, 1974; Hallé et al., 1978; Chomicki et al., 2017), particularly on islands (Carlquist, 1969; Böhle et al., 1996; Lens et al., 2013). However, in the New Caledonian flora, the few phylogenetic reconstructions available for groups containing monocaulous species rather suggest that they evolved from woody ancestors (Barrabé et al., 2018; Chapter 6). The breadth of this pattern remains to be confirmed through the study of other clades. Monocauly has also largely been associated with diverse life history trait attributes such as cauliflory (Hallé and Mabberley, 1976; Hallé et al., 1978; Barthélémy, 1988; Schmid, 1990), dioecy (Hallé et al., 1978), and the presence of compound leaves (Corner, 1949; Hallé, 1967; Hallé and Mabberley, 1976; White, 1983b). From an ecological and evolutionary perspective, some authors have addressed the question of the selective advantage of monocauly (Richards, 1966). This growth habit appears to be almost exclusively tropical (Corner, 1949; D'Arcy, 1973; Hallé et al., 1978). In some giant rosette trees the packing of leaves around terminal buds has been suggested to be adaptation to nightly frosts or short-duration fires (Givnish, 2016). In New Caledonia, as in other tropical regions, monocaulous plants are, however, preferentially found in rainforest (Corner, 1949; D'Arcy, 1973; Hallé, 1974; Hallé and Mabberley, 1976; Hallé et al., 1978; Schmid, 1990; Chapter 6), suggesting other selective pressures. Their single growing apical meristem make them particularly sensitive to environmental damage (Costes et al., 2013; Charles-Dominique et al., 2017), implying adaptive growth pattern that would prevent or reduce apical damages (Givnish, 1994).

To examine the evolution of the monocaulous habit in the New Caledonian flora, we compiled a dataset combining architectural, morphological, taxonomic, phylogenetic, and ecological information on monocaulous species. We used this dataset to investigate the evolutionary history of monocaulous plants in New Caledonia. Using a phylogenetic supertree of New Caledonian woody genera, we quantified the phylogenetic signal and estimated the minimum number of independent evolutionary events leading to monocauly in the archipelago. We investigated the relation between the presence of monocaulous species in a genus and species richness in that genus. We then tested for correlated evolution between monocauly and trait attributes related to growth (marked growth rhythms), leaf shape (compound leaves), reproduction (cauliflory, dioecy, plain flower, fleshy fruits) and environment (rainforest, ultramafic substrate). We also analysed risk of extinction and threats to monocaulous species according to the IUCN Red List criteria. Finally, we explored evolutionary contingencies and selective advantages that could explain the observed convergence of monocauly in the New Caledonian flora.

5.2 Materials & methods

5.2.1 Definition of monocauly

The monocaulous habit has long been recognized by numerous authors who have adopted various definitions (e.g. Warming, 1909; Du Rietz, 1931; Cotton, 1944; D'Arcy, 1973; Hallé et al., 1978; Hedberg and Hedberg, 1979). In most of cases, these only concerned woody plant since cambial activity has a considerable incidence on plant morphology and development. As such, monocotyledons represent a highly different monocaulous condition given that aerial branching is developmentally constrained by shoot growth and the absence of wood (Tomlinson and

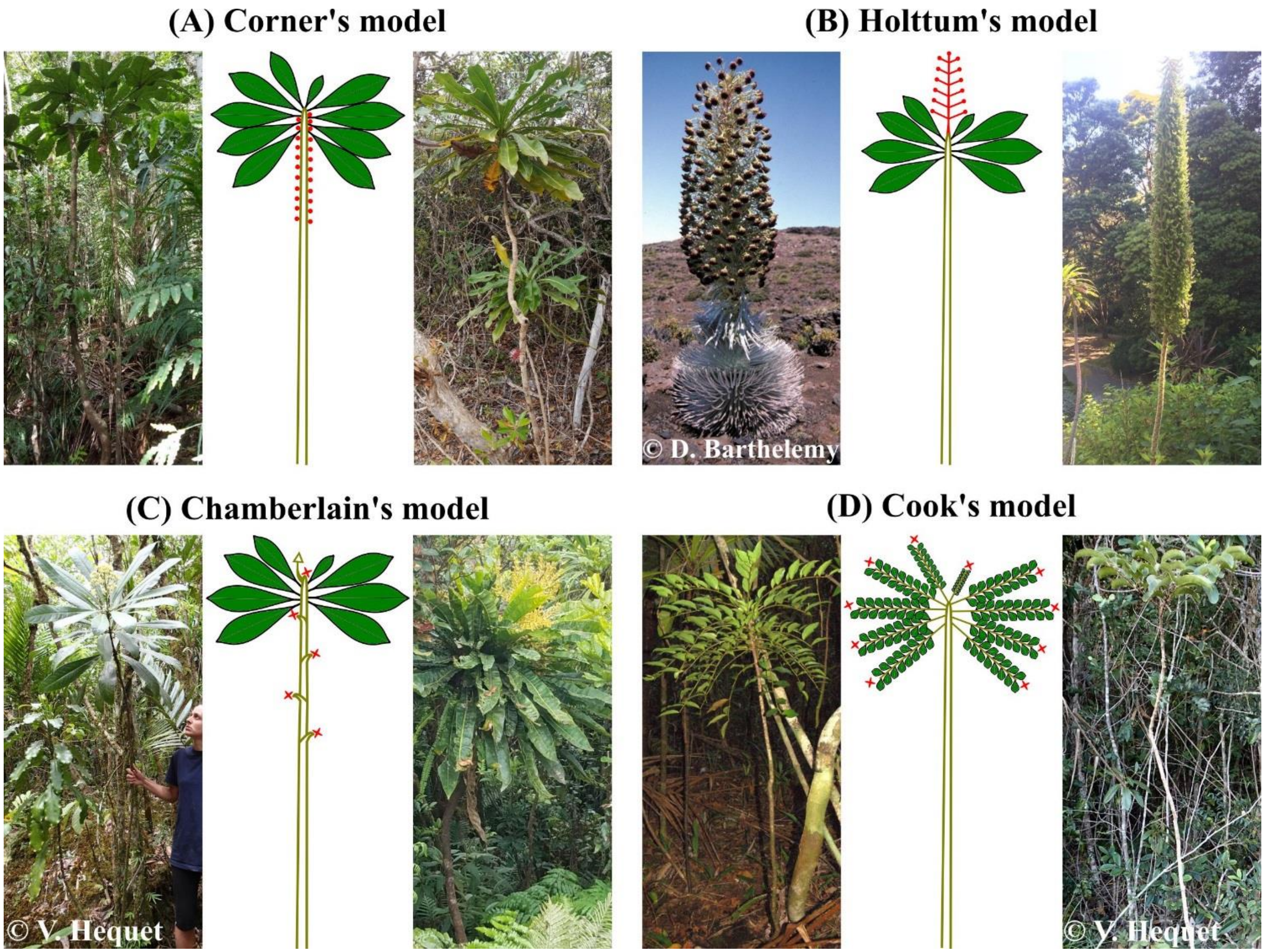


FIGURE 5.1 – Illustration of the fourth monocaulous architectural models. Plain circles represent inflorescences and cross represent apex death. Illustrated taxa (from left to right and top to down): *Acropogon* aff. *austrocaledonicus* (Malvaceae); *Virotia angustifolia* (Proteaceae); *Argyroxiphium sandwicense* (Asteraceae); *Echium pininana* (Boraginaceae); *Pittosporum paniculatum* (Pittosporaceae); *Meryta balansae* (Araliaceae); *Phyllanthus francii* (Phyllanthaceae); *Casearia silvana* (Salicaceae). **(A)**, **(C)** and **(D)** from New Caledonia; **(B)**, from Hawaii and California respectively.

Zimmermann, 1969; Tomlinson, 1973; Haushahn et al., 2012). In a recent work linking architecture and function, Bruy et al. (Chapter 6) proposed the following definition for monocauly: “self-supporting woody plants whose cardinal functions rely on one single apparent stem”. Following this definition, the structural types corresponding to four architectural models conform to monocaulous plants: Corner’s, Holttum’s, Chamberlain’s and Cook’s models (Hallé and Oldeman, 1970; Hallé et al., 1978). Architectural models describe both the overall architecture of a plant and the developmental growth process generating it (Hallé and Oldeman, 1970; Hallé et al., 1978). While they are too restrictive to understand the precise architecture of complex plants (Barthélémy and Caraglio, 2007; Chapter 6), they have proved to be well suited for characterizing simple forms (Hallé et al., 1978; Chapter 6). The Corner’s and the Holttum’s architectural models correspond to monoaxial systems (i.e. a single axis built up by a single apical meristem) with lateral (Figure 5.1-A) or terminal (Figure 5.1-B) reproductive structures respectively. Chamberlain’s model is characterized by a single trunk build up by several successive determinate modules (sympodial branching, Figure 5.1-C). Finally, the Cook’s model is based on a monoaxial trunk supporting lateral branches that are functionally equivalent to compound leaves (“phyllomorphic branches”, which are structure highly specialised in photosynthesis, with determinate growth and an abscission point, Corner, 1949; Hallé, 1967; Hallé et al., 1978) (Figure 5.1-D).

During the life of a plant, a structure that corresponds to one of these well-defined architectural models is often modified by the morphogenetic process of reiteration, corresponding to a repetition of the architectural units (Oldeman, 1974; Hallé et al., 1978). This process can be sequential, i.e. genetically determined, or opportunistic, i.e. driven by exogenous factors such as an injury or an increase in available resources (Barthélémy and Caraglio, 2007). Consequently, if the process of reiteration is inherent to a plant’s development (i.e. sequential), it is not considered

TABLE 5.1 – List of phylogenetic studies used to build the genus supertree.

Family	References
Acanthaceae	McDade et al. (2008)
Anacardiaceae	Wannan (2006)
Annonaceae	Chatrou et al. (2012)
Apocynaceae	Potgieter and Albert (2001); Meve and Liede (2004); Wanntorp et al. (2006); Endress et al. (2007); Livshultz et al. (2007); Simões et al. (2007); Liede-Schumann et al. (2012); Surveswaran et al. (2014)
Araliaceae	Plunkett et al. (2005); Nicolas and Plunkett (2009)
Bignoniaceae	Olmstead et al. (2009)
Celastraceae	Simmons et al. (2012a); Simmons et al. (2012b)
Cunoniaceae	Bradford and Barnes (2001); Pillon (2008); Pillon, 'pers. comm.'
Elaeocarpaceae	Crayn et al. (2006)
Ericaceae	Kron et al. (2002); Quinn et al. (2005); Wagstaff et al. (2010)
Euphorbiaceae	Wurdack et al. (2005); Tokuoka (2007); Horn et al. (2012); Costion et al. (2016)
Fabaceae	Bruneau et al. (2001); Wojciechowski (2003); Wojciechowski et al. (2004); Stefanović et al. (2009); Brown et al. (2012); Manzanilla and Bruneau (2012); Gagnon et al. (2013); Egan et al. (2016); Jabbour et al. (2018);
Gesneriaceae	Woo et al. (2011)
Lamiaceae	Bendiksby et al. (2011); Drew and Sytsma (2011)
Lauraceae	Chanderbali et al. (2001)

Loganiaceae	Gibbons et al. (2012)
Malvaceae	Alverson et al. (1999); Whitlock et al. (2001)
Meliaceae	Koenen et al. (2015)
Monimiaceae	Renner and Chanderbali (2000)
Moraceae	Datwyler and Weiblen (2004)
Myodocarpaceae	Nicolas and Plunkett (2009)
Myrtaceae	Lucas et al. (2007); Snow et al. (2011); Thornhill et al. (2015); Vasconcelos, ‘pers. comm.’
Oleaceae	Costion (2011); Guo et al. (2011); Hong-Wa and Besnard (2013)
Paracryphiaceae	Tank and Donoghue (2010); Soltis et al. (2011); APG IV (2016)
Phyllanthaceae	Wurdack et al. (2004)
Picrodendraceae	Tokuoka and Tobe (2006)
Primulaceae	Anderberg et al. (2002); CEC Gemmill, Waikato University, New Zealand, unpubl. res.
Proteaceae	Sauquet et al. (2008); Reyes et al. (2015)
Rhamnaceae	Richardson et al. (2000); Hopkins et al. (2015)
Rhizophoraceae	Setoguchi et al. (1999)
Rubiaceae	Achille et al. (2006); Razafimandimbison et al. (2008); Bremer and Eriksson (2009); Rydin et al. (2009); Manns and Bremer (2010); Barrabé et al. (2011); Kainulainen et al. (2013); Wikström et al. (2013); Mouly et al. (2014); Neupane et al. (2015); Wikström et al. (2015)

Rutaceae	Appelhans et al. (2012); Bayly et al. (2013); Appelhans et al. (2014)
Salicaceae	Alford (2006); Tokuoka and Tobe (2006)
Santalaceae	Su et al. (2015)
Sapindaceae	Buerki et al. (2011); Buerki et al. (2012)
Sapotaceae	Swenson and Anderberg (2005); Swenson et al. (2013)
Solanaceae	Olmstead et al. (2008)
Thymeleaceae	Beaumont et al. (2009)
Urticaceae	Wu et al. (2013); Kim et al. (2015)

as monocaulous; opportunistic reiteration is, however, compatible with the definition of monocauly.

5.2.2 Species list and phylogenetic trees

A comprehensive list of non-monocot species occurring in New Caledonia was extracted from the most recent update taxonomic reference for the island’s flora (Munzinger et al., 2016) supplemented by some unpublished species. Species that are strictly herbaceous or climbing (Bruy et al. unpublished data) were removed from the list. Taxonomy was pruned to species level meaning that infraspecific taxa were not considered. This yielded a final list of 2114 species belonging to 316 genera and 90 families.

Several phylogenetic trees of these woody New Caledonian genera and species were computed using supertree methods (Gordon, 1986; Sanderson et al., 1998; Bininda-Emonds, 2004). R software (v. 3.4.3) was used through the following packages: *ape* (Paradis et al., 2004), *adephylo* (Jombart and Dray, 2008), *ade4* (Dray and Dufour, 2007), *apTreeshape* (Bortolussi et al., 2018), *phytools* (Revell, 2012), *picante* (Kembel et al., 2010), *MonoPhy* (Schwery and O'Meara, 2016) and *geiger* (Luke et al., 2008). The phylogenetic tree of angiosperm families produced by Magallon and Sanderson (2001) was initially used, from which all but one of the 90 New Caledonian families were extracted. The missing family, Metteniusaceae, was added in position of Garryaceae and Eucommiaceae, its two closest relatives (APG IV, 2016), which are not represented in New Caledonia. For each family, generic relationships were resolved using published molecular phylogenies (Table 5.1) or taxonomic studies for a few genera that have not been studied using sequence data (Table 5.2). *Cupaniopsis* and *Arytera* have been shown to be polyphyletic (Buerki et al., 2012) with its members forming three groups: *Cupaniopsis sensu stricto* and two unpublished genera (*Arytera* 1 and *Cupaniopsis* 2, Munzinger et al., unpublished data). Estimates of intergeneric

TABLE 5.2 – List of taxonomic studies used to build genus supertree for genera that have never been sequenced.

Genus	References
Dutailliopsis	Hartley (1997)
Dallachya	Geer et al. (2010)
Longetia	Webster (1994)
Alphandia	McPherson and Tirel (1987); Webster (1994)
Myricanthe	Webster (1994)

and intrageneric branching times were randomised 100 times to produce a hundred species phylogenetic trees. Given the lack of a robust phylogeny for most New Caledonian genera, these hundred trees were unresolved at the species level, resulting in polytomies.

5.2.3 Character coding

An initial list of New Caledonian monocaulous species was built using an extraction from the NOU Herbarium database. This was then refined through extensive bibliographic analysis, particularly of the series *Flore de la Nouvelle-Calédonie* (Aubréville et al., 1967-1992; Morat and MacKee 1992-2004; Hopkins et al., 2014) and taxonomic publications. From this expanded list, the architecture of each taxon was studied in the field to determine whether it fit the definition of monocauly (i.e. whether it conforms to the Corner's, the Holttum's, the Chamberlain's and the Cook's architectural models). When field observations were impossible, architecture was checked by examining photographs (UMR AMAP-IAC database and Endemia website, *continuously updated*). Some monocaulous species were added to the list based on field observation. Of the 2114 species in the final dataset, only one could not be coded for architecture (*Symplocos paniensis*).

To test evolutionary correlates of monocauly, both life history and environmental traits were scored for each of the 2114 species when possible (Table 5.3). Data on sexual system, fruit type, and flower attraction were extracted from the dataset of Schlessman et al. (2014). Data on endemism and vegetation were extracted from the *Florical* database (Munzinger et al., 2016) and substrate information was obtained from the dataset of Isnard et al. (2016). For environmental traits, a binary approach was used for considering the main drivers of floristic richness and disharmony in New Caledonia: (i) ultramafic (covering 1/3 of the territory) versus non-ultramafic substrate (Jaffré, 1993; Pillon et al., 2010; Isnard et al., 2016) and rainforest versus non-rainforest vegetation (Jaffré, 1993; Poncet et al., 2013; Birnbaum et al., 2015a; Pouteau et al., 2015). Each of

TABLE 5.3 – List of characters scored on the 2114 New Caledonian woody species and associated analyses.

Treatment	Trait	Nb of na	States	Definition
Correlated evolution for binary traits (Pagel's method) within the specific supertree	Growth habit	1	Monocaulous	Cardinal functions assumed by a single apparent stem
			Branched	Cardinal functions assumed by more than one stem
	Sexual system	2	Dioecious	Each individual single sexed
			Not dioecious	At least some individuals with both sex
	Fruit type	0	Fleshy	Fruit with fleshy pericarp
			Dry	Fruit with dry pericarp
	Flower attraction	0	Plain	Petals < 10 mm and white, green, or greenish white
			Showy	Petals > 10 mm or brightly colored
	Leaf type	0	Simple	Leaf composed of an unique limb
			Compound	Leaf composed of several limbs separated by portion of rachis
	Position of sexuality	21	Cauliflorous	Flowers could appear under the older assimilative leaf
			Not cauliflorous	Flowers appear only apically or on the leafy stem portion

	Growth rhythms	3	Marked	Growth rhythm marked with long portion of cataphylls-boring stem alternating with portion of assimilative leaves-boring stem
			Not marked	Growth rhythm not marked by an important portion of cataphylls-boring stem
	Vegetation	10	Rainforest	Species only found in rainforest
			Not rainforest	Species not only found in rainforest
	Substrate	40	Ultramafic	Species only found on ultramafic substrate
			Not ultramafic	Species not only found on ultramafic substrate
Permutation test	Species endemism	0	Endemic	Species only found in New Caledonia
			Autochthonous	Species native of New Caledonia but occurring in other countries
	IUCN status	1390	Very threatened	Species evaluated as Extinct, Critically Endangered or Endangered following IUCN red list criteria
			Not very threatened	Species evaluated as Least Concerned, Near Threatened or Vulnerable following IUCN redlist criteria
			Data deficient	Species for which data has not been sufficient to permit an evaluation following IUCN red list criteria
			Bushfire	Species for which fire has been considered as threat by IUCN

	Threat	1390	Introduced herbivores	Species for which dear, pig or rats have been considered as threat by IUCN
			Mining activity	Species for which mining activity have been considered as threat by IUCN
Comparative analysis within the genera supertree	Genera richness	0	Integer	Total number of species in the considered genus
	Genera endemism	0	Binary	All species of the considered genus are endemic to New Caledonia

these datasets was thoroughly reviewed based on our own observations and herbarium material (NOU). IUCN conservation status and threats for each evaluated species (728 in total) were extracted from the IUCN Red List website (IUCN, 2017) and from the local Red List Authority dataset (RLA-NC Flora, unpublished data, on 24 April 2018). Finally, leaf type, position of reproductive structures and growth rhythm were compiled from field observations, herbarium material (NOU), and the literature. Missing values for other characters were also obtained when possible using this method.

5.2.4 Data analysis

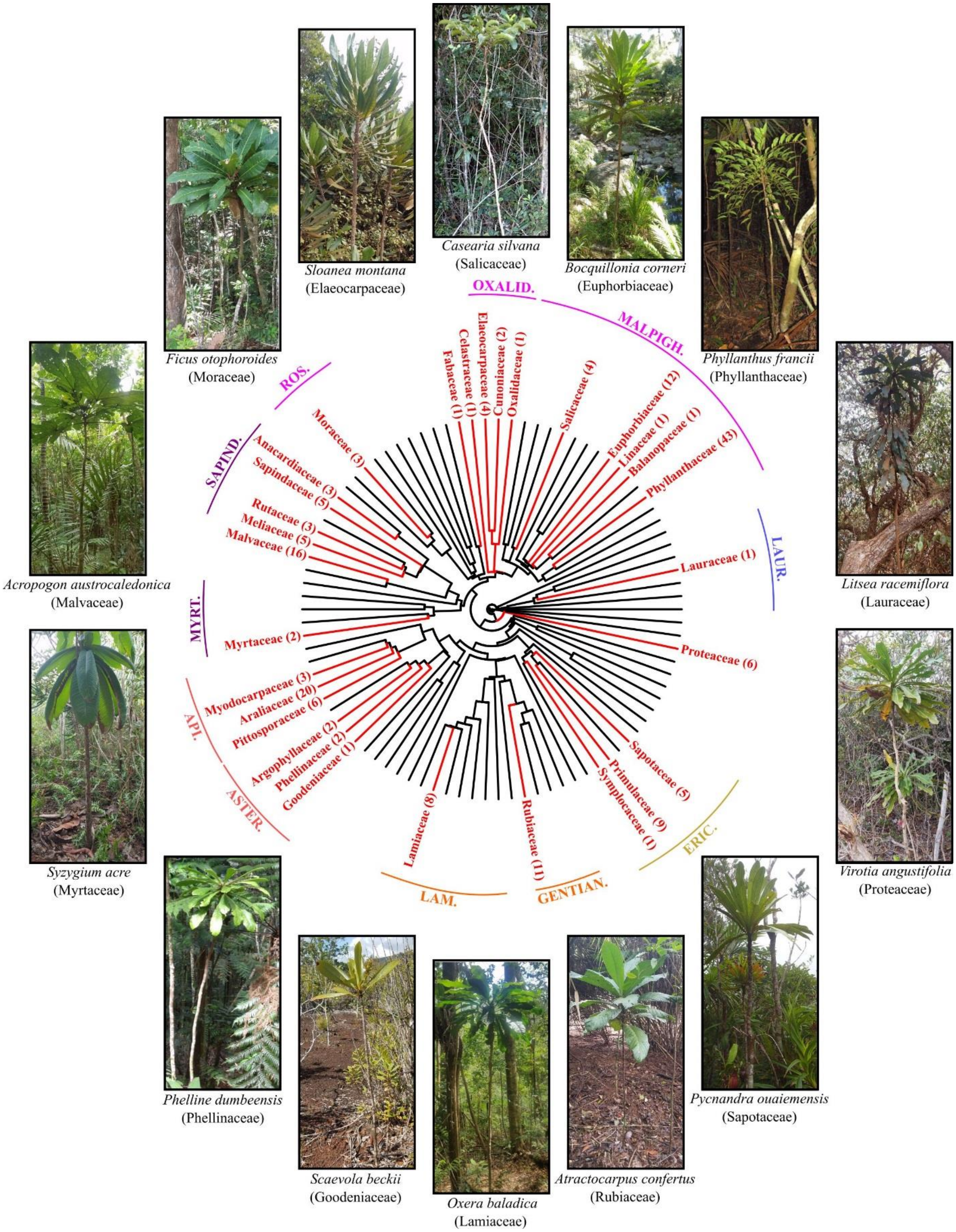
Richness in monocaulous species **–** To assess the relative richness of monocauly at the level of genus, we followed the method proposed by Boucher et al. (2016). Considering the proportion of monocaulous species in the whole woody flora (9%), null models were built for each genus containing monocaulous species with random binomial distributions. For each model (i.e. each genus), the number of observation equalled 1000, the number of trials equalled the total number of species in the genus, and the probability of success equalled 0.09. The observed number of monocaulous species in a given genus was then compared to the null distribution to estimate whether it is richer or poorer in monocaulous species than expected by chance, with a confidence limit of 5 %.

Origin, convergence and diversification **–** The minimum number of independent origins of monocauly in the New Caledonian flora was estimated using the 100 genus-level supertrees and the *phytools* package for R (Revell, 2012). Each genus was scored as 0 (no monocaulous species) or 1 (at least one monocaulous species) and ancestor character estimations on this variable were simulated with an Mk model in which transition rates are different (“SYM”). For each 100 genus supertree, 100 simulations were performed and the mean and range of number of the independent origins of monocauly (from state 0 to state 1) were counted. The same method was used independently for each monocaulous architectural model.

The degree of convergence of monocauly in the New Caledonian flora was estimated with the Phylogenetic D Statistic (Fritz and Purvis, 2010), a measure of phylogenetic signal for binary traits. Using the *Caper* R package (Orme et al., 2013) we tested the departure of the observed D statistic from the distribution (1000 permutation) of expected D statistic under (i) a phylogenetic randomness model (no phylogenetic signal, D ≈ 1) and (ii) a Brownian threshold model (strong phylogenetic signal, D ≈ 0). Each test was performed on the 100 species supertrees. The phylogenetic signal of each monocaulous architectural models was also calculated using the same method.

To investigate whether the appearance of monocauly could have promoted species diversification, the relation between presence of monocaulous species in a genus and its species richness was tested using phylogenetic regression for binary dependent variables (Ives and Garland, 2014). The model was fitted using the 100 genus supertrees with the *ape* R package (Paradis et al., 2004). The same method was used to test the relation between monocaulous genera and endemic genera (following Munzinger et al., 2016), i.e. whether monocauly is predominant in endemic genera.

Correlated evolution of traits with monocauly – At the specific level, correlated evolution between monocauly and life history or environmental trait attributes (Table 5.3) was tested using with the method of Pagel (1994) as implemented in the *phytools* R package (Revell, 2012). This method fits the Mk model for the dependent and independent evolution of two binary characters and test for significance of correlated evolution, comparing the log-likelihood of the two models. In the case of significant correlated evolution, transition rates from one character state to another



Ficus otophoroides
(Moraceae)

Sloanea montana
(Elaeocarpaceae)

Casearia silvana
(Salicaceae)

Bocquillonia corneri
(Euphorbiaceae)

Phyllanthus francii
(Phyllanthaceae)

Acropogon austrocaledonica
(Malvaceae)

Litsea racemiflora
(Lauraceae)

Syzygium acre
(Myrtaceae)

Virotia angustifolia
(Proteaceae)

Phelline dumbeensis
(Phellinaceae)

Pycnandra ouaiemensis
(Sapotaceae)

Scaevola beckii
(Goodeniaceae)

Atractocarpus confertus
(Rubiaceae)

Oxera baladica
(Lamiaceae)

FIGURE 5.2 – Phylogenetic supertree of New Caledonian woody families. Red branches represent families containing monocaulous species (number of monocaulous species in brackets).

were compared for the two traits in order to investigate which character was likely to appear first (monocauly or the other trait character).

***Species endemism, threats and conservation status* –** The association between monocauly and endemism, IUCN conservation status and principal threats was tested through permutation tests (Table 5.3). We focused on data deficient and highly threatened species (EX, CR or EN following the IUCN criteria) to test whether monocaulous species were less known or more threatened than expected by chance. Considered threats were bushfires, introduced herbivores (deer, pigs and rats) and mining activities, the three major threats to New Caledonian flora (IUCN, 2017, RLA-NC Flora, unpublished data). A phylogenetic framework was not considered for these analysis because such traits are unlikely to be inherited. For each trait, the attribute (e.g. "threatened") was permuted 10000 times and for each permutation, the proportion of monocaulous species presenting the attribute was calculated to build the null distribution. The observed proportion of monocaulous species presenting the attribute was then compared to the null distribution to test the departure from the null model (no association between monocauly and the considered attribute).

5.3 Results

5.3.1 Taxonomic and phylogenetic distribution of monocaulous plants

Of the 2114 woody self-supporting species present in New Caledonia, a total of 182 (8.6 %) were monocaulous, belonging to 41 genera and 30 families (Appendix 1). Monocaulous plants were widely distributed in the phylogeny and many families (12 of the 30) contained less than 3 monocaulous species. Some phylogenetic clustering was nevertheless observed, as much of the diversity occurred in a few clades (Figure 5.2). The orders Malpighiales and Apiales contained,

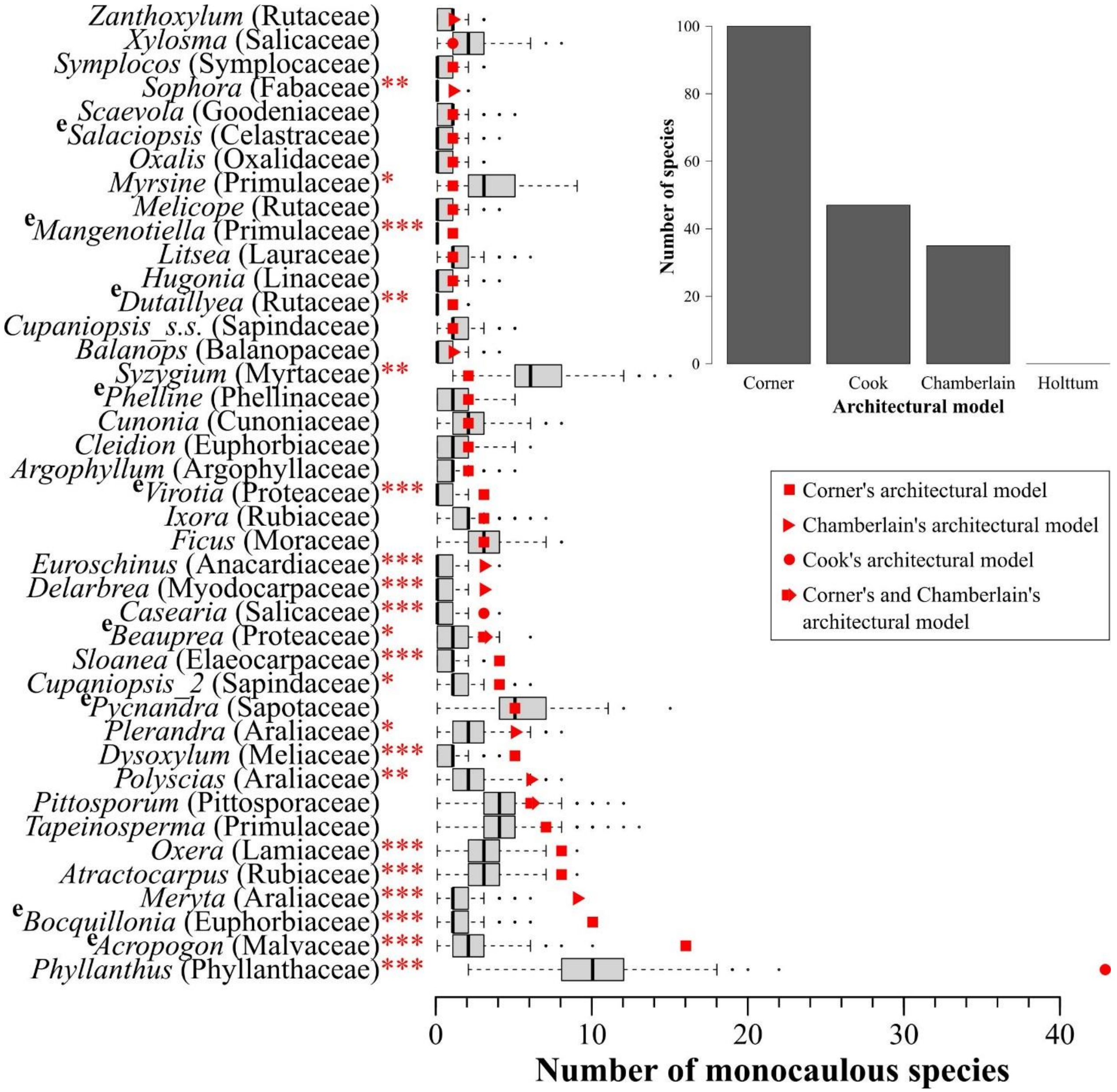


FIGURE 5.3 – Number of monocaulous species for the 41 monocaulous genera and per architectural models. Red forms indicate the observed number of monocaulous species in each genera and grey boxplots represent the expected distribution of number of monocaulous species following null model. Asterisks show the significance of over- or under-representation of monocaulous species in each genera (*** P < 0.001; ** P < 0.01; * P < 0.05). $^{\mathbf{e}}$, endemic genera.

respectively, about 34% and 16% of all monocaulous species, followed by Malvales, Sapindales and Ericales, each accounting for ca. 9% of monocaulous species. By contrast, the basally branched lineages of the phylogeny (e.g. Magnoliids) contained very few monocaulous species (ca. 1 %). At shallower phylogenetic level, monocauly was clustered in several families and genera, and was achieved through various architectural models (Figure 5.2, 5.3). The richest family was by far Phyllanthaceae, with 43 species of *Phyllanthus* expressing the Cook's architectural model, followed by Araliaceae, with 3 genera and 20 species (Chamberlain's model) and Malvaceae, with 16 species restricted to the endemic genus *Acropogon* (Corner's model). Most families contained only one genus with monocaulous species, with the exception of Euphorbiaceae, Rubiaceae, Sapindaceae, Proteaceae, Salicaceae, which contained two each, and Araliaceae, Primulaceae and Rutaceae, which contained three each. The six richest genera, *Phyllanthus*, *Acropogon*, *Bocquilllonia*, *Meryta*, *Atractocarpus* and *Oxera*, together contained 52% of all monocaulous species, and had significantly more monocauls than expected under the null model (Figure 5.3). More generally, many genera (19 out of 41) had significantly more monocaulous species than expected under null model, despite many of them (49%) containing only 1 or 2 monocaulous species (Figure 5.3). Only *Myrsine* and *Syzygium* had significantly fewer monocaulous species than expected under a null model, even though the latter is the third richest genus in the New Caledonian flora (Munzinger et al., 2016). *Phyllanthus*, the most species-rich genus in New Caledonia, had significantly more species than expected under the null model, while *Pycnandra*, the fourth richest genus and largest endemic genus, had the same number of monocaulous species as expected under the null model. In general, only a few genera contained a high proportion of monocaulous species. Those comprising more than ten species, of which at least half were monocaulous, were *Acropogon*, *Bocquillonia*, *Meryta* and *Dysoxylum* (Figure 5.3).

The most frequent architectural model observed among monocaulous species was the Corner's model (100 species in 30 genus, Figure 5.3) followed by the Cook's model (47 species in only 3 genera) and the Chamberlain's model (35 species in 10 genera). The Holttum's model does not appear to be represented in the woody flora of New Caledonia. Only *Pittosporum* and *Beauprea* expressed monocauly by two different architectural models (Corner's and Chamberlain's models) (Figure 5.3).

5.3.2 Genus diversity and endemism

The presence of monocaulous species in a genus was significantly and positively associated with species richness (phylogenetic regression, pvalue < 0.001) implying that species-rich genera were more likely to have evolved monocauly or that the evolution of monocauly favored genera diversification. The proportion of endemic species in the monocaulous flora (98.9%) was significantly higher than expected by chance (permutation test, pvalue < 0.001). Only two monocaulous species (ca. 1%) were not New Caledonian endemics (*Delarbrea paradoxa* and *Oxera baladica*) compared to 9 % for the branched woody flora. By contrast, endemism at the generic level was low (21.9% vs. 22.9% for the branched flora) and unrelated to the occurrence of monocauly (phylogenetic regression, pvalue = 0.75 ± 0.01). Only 9 of the 72 endemic genera in our list (sensu Munzinger et al., 2016) contained monocauls (*Acropogon*, *Beauprea*, *Bocquillonia*, *Dutaillyea*, *Mangenotiella*, *Phelline*, *Pycnandra*, *Salaciopsis*, and *Virotia*, Figure 5.3).

5.3.3 Evolution of monocauly and phylogenetic signals

Monocauly appeared independently on average 38.3 times across the genus trees, the number of shifts ranging from 31 to 49 over the 10,000 simulations. Reversion toward a branched habit occurred much less frequently, 7.9 times on average (ranging from 0 to 25 events). The

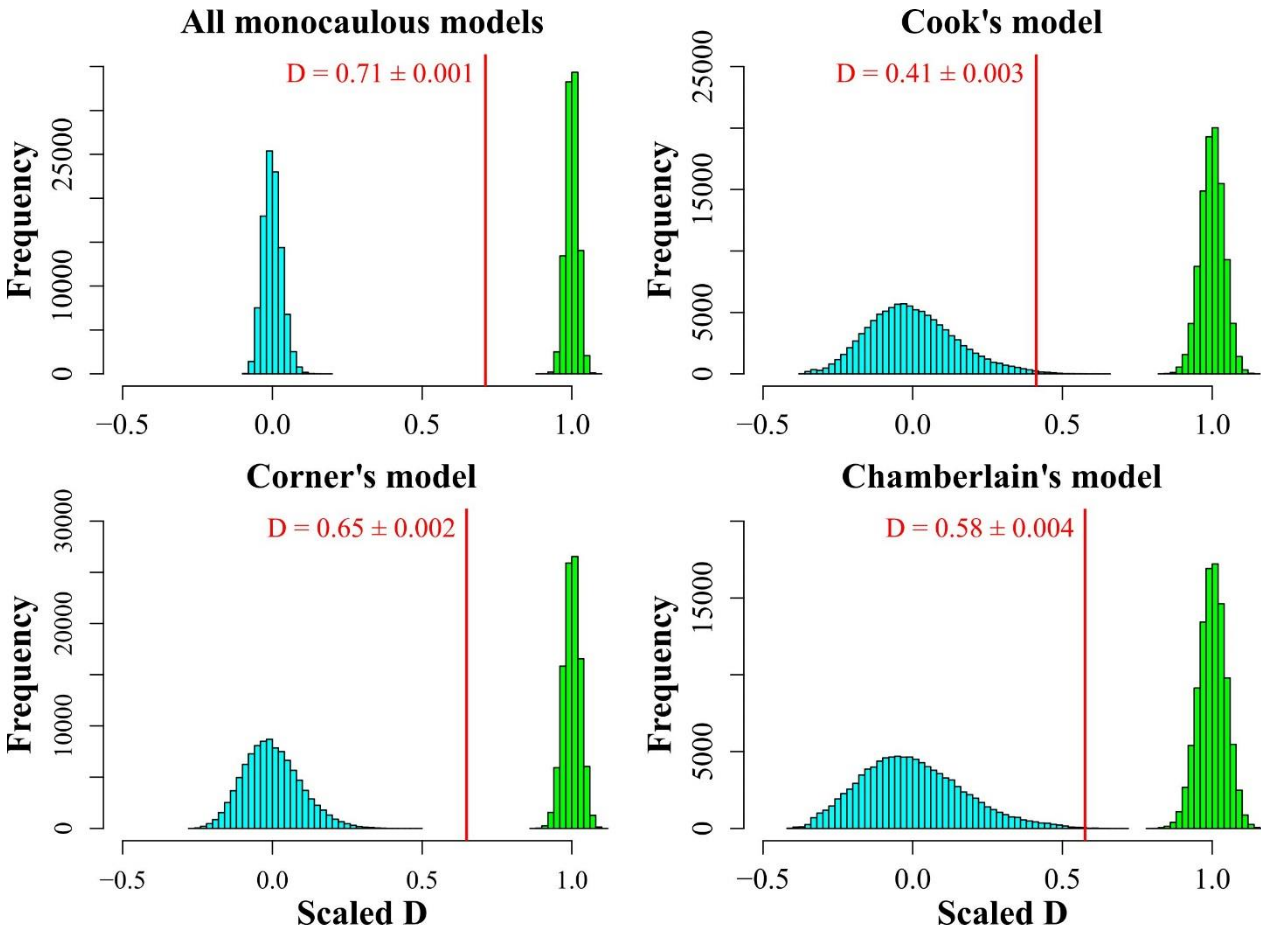


FIGURE 5.4 – Phylogenetic signals for monocauly and the three architectural models across the phylogeny of New Caledonian woody species. Blue histogram (left) represents the expected distribution of D under a Brownian threshold model (strong phylogenetic signal, 1000 permutation in 100 trees). Green histogram (right) represents the expected distribution of D under a phylogenetic randomness model (low phylogenetic signal, 1000 permutation in 100 trees). Red line represents the observed phylogenetic D statistic.

monocaulous architectural model with the highest minimum number of shift was the Corner's model (ranging from 24 to 36, with a mean of 28.1), followed by the Chamberlain's model (6 to 12 times, with a mean of 7.1) and finally the Cook's architectural model (2 to 5 times, with a mean of 3.0).

Monocauly showed a low phylogenetic signal in the woody flora of New Caledonia. The Phylogenetic D Statistic was 0.71 ± 0.001, which is close from a random distribution ($D \approx 1$), although significantly different from both 0 and 1 (Figure 5.4). The phylogenetic signal of each architectural model was also significantly different from 0 and 1. The Cook's model appeared to be more conserved across the phylogeny than Chamberlain's model and, *a fortiori*, Corner's model (Figure 5.4).

5.3.4 Contingent and correlated evolution

The evolution of monocauly was significantly correlated with both ultramafic substrate and rainforest (Pagel's model for correlated evolution, pvalue 0.029 and < 0.001 respectively, Table 5.4). Transition rates indicated a higher frequency of shift from branched toward monocauly on ultramafic substrate and in rainforest, meaning that monocauly evolved from branched species preferentially on ultramafics and in rainforest. The environmental preference was strongly marked for rainforest, where 65% of monocaulous species are restricted (Figure 5.5-B) whereas only 11% have never been observed in this habitat (not shown). The proportion of species occurring on ultramafic substrate was, however, similar between branched and monocaulous species (44% vs. 47% respectively).

The evolution of both cauliflory and marked rhythmic growth was strongly correlated with monocauly (Pagel's model for correlated evolution, pvalue < 0.001, Table 5.4). This result was corroborated by the proportions of cauliflorous species and those exhibiting rhythmic growth,

TABLE 5.4 – Results of correlated evolution for binary traits (Pagel's method) between monocauly and other trait atributes. P.values in bold indicate trait atributes for which significant correlated evolution is detected. Transition rates in bold indicate the higher transition rates when correlated evolution is significant (A+: Monocaulous, A-: Branched, B+: Presence of the second trait attribute, B-: Absence of the second trait attribute).

		Growth on UM	Growth in rainforest	Cauliflory	Marked rhythmic growth	Dioecy	Flower plain	Fruit fleshy	Compound leaf
p.values		**0.029 ± 0.002**	<< **0.001**	<< **0.001**	<< **0.001**	0.15 ± 0.01	0.916 ± 0.023	0.26 ±0.02	0.131 ± 0.298
Transition rates	A+:B- → A+:B+	0.11 ± 0.002	0.10 ± 0.001	**0.23 ± 0.001**	**0.36 ± 0.006**	0.15 ± 0.001	0.11 ± 0.001	0.14 ± 0.002	0.30 ± 0.030
	A-:B+ → A+:B+	**1.62 ± 0.013**	**1.95 ± 0.006**	0.01 ± 0.001	0.04 ± 0.044	0.00 ± 0.00	0.06 ± 0.003	0.01 ± 0.02	0.10 ± 0.058

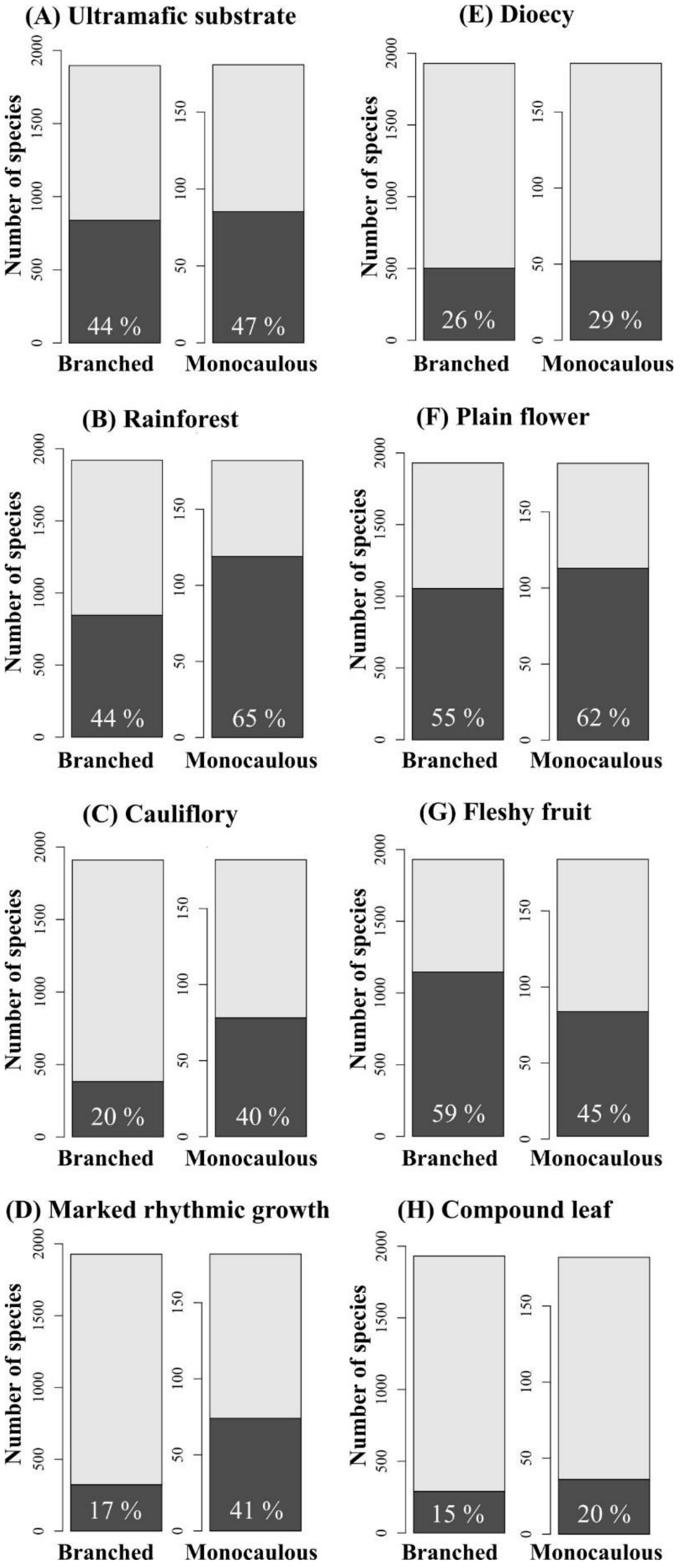


FIGURE 5.5 – Proportion of monocaulous and branched woody species for eight life history and environmental traits.

which were about twice as frequent in the monocaulous flora compared to the branched flora (Figure 5.5-C, D). In both case, transition rates were significantly higher for the evolution of cauliflory and rhythmic growth within monocaulous species. Compared to branched species, monocauls tended to have a slightly higher proportion of species with a dioecious sexual system (29% vs. 26%, Figure 5.5-E), plain flower (62% vs. 55%, Figure 5.5-F), non-fleshy fruits (55% vs. 41%, Figure 5.5-G) and compound leaves (20% vs. 15%, Figure 5.5-H), but none of these trait attributes showed significant correlated evolution with monocauly (Table 5.4).

5.3.5 IUCN risk of extinction status and threats

To date, 728 species (34%) of the woody non-monocot flora of New Caledonia have been assessed according to the IUCN Red List conservation categories and criteria (IUCN, 2017, RLA-NC Flora, unpublished data). This includes 63 monocaulous species (35% of the monocaulous flora), of which 51% were threatened (CR, EN, VU), 33% unthreatened (LC, NT), and 16% insufficiently known to be evaluated (“Data Deficient”, Figure 5.6). The proportion of CR and EN species was higher for monocaulous species than branched ones (41% and 32%, respectively), the difference being marginally significant (permutation test, pvalue = 0.08). The number of monocaulous species in the “Data Deficient” class was also higher than expected by chance (permutation test, pvalue = 0.034). Bushfire and mining activities were significant threats for the monocaulous flora, affecting respectively 51% and 43% of species, but they were not more so for monocaulous than for branched species (permutation test, pvalue = 0.19 and 0.82 respectively). By contrast, introduced herbivores, affecting 33% of monocaulous species, were more threatening for monocaulous species than expected by chance (permutation test, pvalue = 0.008).

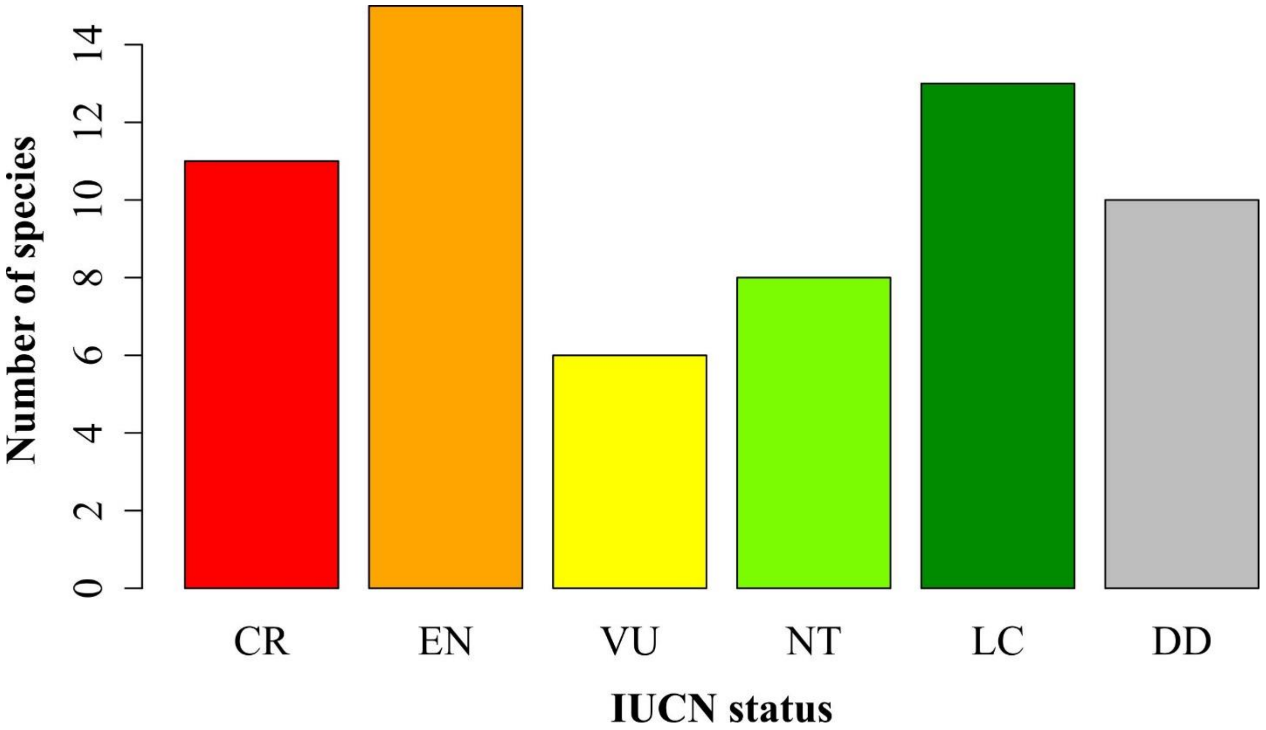


FIGURE 5.6 – IUCN extinction risk of evaluated monocaulous species (n = 63). CR = “Critically endangered”; EN = “Endangered”; VU = “Vulnerable”; NT = “Near Threatened”; LC = “Least Concerned”; DD = “Data Deficient”.

5.4 Discussion

5.4.1 A remarkable evolutionary convergence

Our study identified 182 monocaulous species representing 9% of the self-supporting woody flora and 5.5% of the New Caledonian flora as a whole. This proportion would have been even greater if monocotyledons, not considered in this study, had been included. The monocaulous habit is indeed frequent in monocotyledons (e.g. Arecaceae, Pandanaceae, Asparagaceae, Hallé et al., 1978), but represents a very different condition as aerial branching is developmentally constrained by shoot growth and the absence of wood in monocotyledons (Tomlinson and Zimmermann, 1969; Tomlinson, 1973; Haushahn et al., 2012). Monocaulous species belonged to 41 genera (13% of woody genus) and 30 families (33% of woody families), and was phylogenetically scattered, as illustrated by the low phylogenetic signal and multiple independent origins (at least 31, and as many as 49) of this growth habit. This result, based on a genus-level phylogeny, is conservative as monocauly could have evolved repeatedly within many genera. The only two studies we are aware of, involving two monocaul-rich genera (*Atractocarpus* and *Oxera*), indicated multiple independent origins of the monocaulous habit in New Caledonia (Barrabé et al., 2018; Chapter 6). Additionally, in two genera (*Pittosporum* and *Beauprea*), monocauly is expressed by different architectural models (Corner’s and Chamberlain’s models), also suggesting independent evolution of this habit. These observations are confirmed by molecular phylogenies in which monocaulous architectural models are seen in different clades (He et al., 2016, CEC Gemmill, Waikato University, New Zealand, unpubl. res.). Current knowledge on the phylogenetic relationships in the 41 monocaulous genera in New Caledonia (Table 5.1) indicates that only *Meryta* and *Plerandra*, two sister genera (Plunkett et al., 2005) with several monocaulous species, could potentially exemplify a common origin of monocauly.

The recurrent convergent evolution of this distinctive growth habit in New Caledonia is remarkable, and similar in its number of independent origins to most famous plant syndromes such as secondary woodiness in the Canary Island (38 origins, Lens et al., 2013). In terms of the proportion of the flora in which it is seen, monocauly in New Caledonia is similar to divaricating plants in New Zealand (10% of the woody flora, Greenwood and Atkinson, 1977).

5.4.2 Diversity and endemism of monocaulous lineages

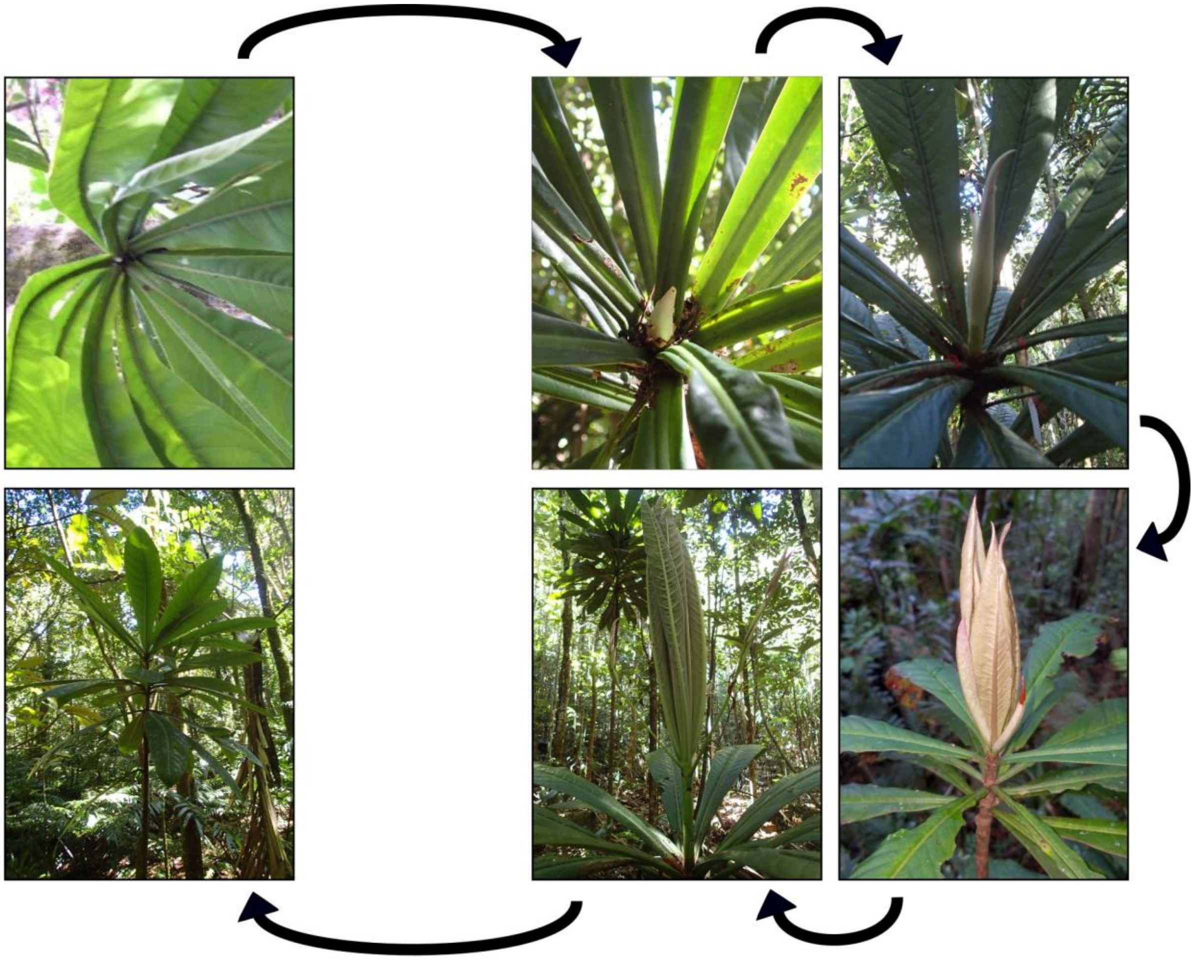
We found a significant positive relationship between the presence of monocauly and the total species richness in the genus, implying that monocauly is more likely to evolve in species-rich genera or that the evolution of monocauly promoted diversification, or both. This positive relationship most probably reflects the fact that six of the ten richest genera in New Caledonia contain monocaulous species. Among these is the archipelago's most speciose genus (*Phyllanthus*: 116 species, Munzinger et al., 2016), which also contains the highest number of monocaulous species. With the exception of some genera containing a large proportion of monocaulous species (e.g. *Acropogon*, *Bocquillonia* and *Meryta*), most (66%) had less than four monocaulous species, which account for a small proportion of their total richness. Globally, the diversity of monocaulous species appeared independent of the number of species within a genus or family (e.g. *Syzygium*, 71 species and only 2 monocauls), and cannot be considered as a key innovation leading to a large radiation. The evolution of monocauly might instead favour the diversification of ecological roles within lineages, especially related to the occupation of the forest understory. A previous study supported this idea and indicated that the evolution of monocauly on its own did not increase the diversification rates, but might contributed to niche partitioning in the understory of rainforest habitats (*Atractocarpus,* Chapter 6).

The high rate of endemism in the monocaulous flora (99%), much higher than expected by chance, suggests either an *in situ* evolution of monocauly in New Caledonia or extinction of monocaulous species in adjacent regions. Interestingly, very few close relatives of New Caledonian monocaulous genera occurring elsewhere (when known, see Table 5.1) contain monocaulous species (the exceptions being *Atractocarpus*, *Casearia*, *Dysoxylum, Meryta, Phyllanthus*, *Plerandra*, and *Tapeinosperma*). Conversely, we found no significant relationship between the level of endemism in a genera and presence of monocauls. Only 9 of the 62 to 91 endemic genera (sensu Pillon et al., 2017) contains monocauls, two of which, *Dutaillyea* and *Mangenotiella* should not be recognized (Appelhans et al., 2014; Gemmill, unpublished data), and *Bocquillonia*, *Virotia* and *Salaciopsis* are doubtful (reviewed in Pillon et al., 2017). The fact that most monocauls are endemic while they belong to non-endemic genera suggests a rather recent *in situ* evolution of monocauly in New Caledonia, as found for two genera: *Oxera*, with two evolution at ca. 2.4 and 1.3-0 Myr (Barrabé et al., 2018) and *Atractocarpus*, with at least two apparition at ca. 1.4 and 0.9-0.6 Myr (Chapter 6).

5.4.3 Life history correlates of monocauly

Despite a moderate phylogenetical signal, we found that most monocaulous species belong to few orders (e.g. Apiales, Malphigiales, Sapindales), which are major components of the New Caledonian flora (Munzinger et al., 2016). By contrast, monocauly is infrequent in basally branching Angiosperms and Myrtales. This pattern, supported by a D statistic significantly different from random distribution, suggests that there may be underlying morphological or physiological prerequisites (Boucher et al., 2016; Saslis-Lagoudakis et al., 2016). However, none of the morphological characters tested were found to be significantly involved in the evolution of monocauly. Some morphological characters (dioecy, plain flowers, fleshy fruits) were well represented in the monocaulous flora but were not correlated with the evolution of monocauly. As in other island floras, that of New Caledonia has a high incidence of dioecy (21% of the native angiosperm flora, Schlessman et al., 2014), suggested to have evolved on islands as a response to inbreeding depression in founding colonies (Carlquist, 1966; Böhle et al., 1996). In New Caledonia, plain flowers and fleshy fruits are considered as major ecological correlates of dioecy (Schlessman et al., 2014), and these traits are particularly pregnant in rainforest understory (Givnish, 1982) where most of monocaulous species occur. As such, the presence of these characters might rather considered as an insular syndrome that is well represented in the monocaulous flora. Similar results were found for compound leaves, which were not correlated with the evolution of monocauly but rather with colonization of open/arid habitats (Givnish, 1978). By contrast, the evolution of monocauly appears to have triggered the evolution of cauliflory and marked rhythmic growth.

***Cauliflory* –** Association between monocauly and cauliflory has long been noted (Hallé and Mabberley, 1976; Hallé et al., 1978; Barthélémy, 1988; Schmid, 1990) but we report for the first time a statistically supported correlated evolution. This result is largely influenced by species conforming to Corner's architectural model, which accounts for 70% of cauliflorous species (vs. 11% and 8% for the Chamberlain's and the Cook's models, respectively). Transitions rates showed that cauliflory appeared more frequently after the evolution of a monocaulous habit. Being single-stemmed, monocaulous plants have fewer leafy nodes than branched plants (White, 1983a; Ackerly and Donoghue, 1998; Chapter 6), constraining sexual reproduction to large axillary inflorescences (e.g. *Tapeinosperma*, *Atractocarpus*) or to areas below the leafy parts of the trunk (cauliflory). Cauliflory is often expressed by short shoots or secondary bud complexes (Hallé et al., 1978), which were observed in 22 of the 28 genera that are both monocaulous and cauliflorous (not shown), implying sites where flowers are borne in multiple years. Moreover, monocauls are known to have larger fruits than branched relatives (Corner, 1949; 1953-1954; Chapter 6). Cauliflory,



(A) Rest period: shoot apical meristem protected in the cluster of leaves (several month duration)

(B) Growth period: rapid set-up of the preformed growth unit (few days duration)

FIGURE 5.7 – Illustration of marked rhythmic growth in *Tapeinosperma gracile* (Primulaceae)

which involves the placement of fruits on woody, perennial stems rather than young, fleshy ones, seems more suited for supporting heavy and long-maturing fruits. These particular flowering and fruiting patterns in monocaulous plants may also be related to pollination and dispersion agents, and are probably also linked to growth in the intermediate strata of the forest understory (Yumoto, 1987; Appanah, 1991; Warren et al., 1997; Zjhra, 2008).

***Marked rhythmic growth* –** Correlated evolution between monocauly and marked rhythmic growth must be interpreted in the context of meristem protection. Transitions rates indicated that this character also appeared more frequently after the evolution of monocaulous habit. Except when reiteration takes place, a process that results in the production of new stems on some older plants (Oldeman, 1974; Hallé et al., 1978; Barthélémy and Caraglio, 2007), vertical exploration of monocaulous species is almost always accomplished by a single meristem. As such, traumatic apex death is particularly critical for unbranched plants. Several modes of meristem protection have been described, including the protection of apices by robust rosette of leaves (Potter, 1891; Groom, 1892). Hallé et al. (1978) noted that this mechanism concerned numerous monocaulous species and was often associated with rhythmic growth. However, while this mode of protection is efficient during periods of little or no growth, the meristem and young organs are dangerously exposed during phases of growth. It would therefore be advantageous for this "unprotected" phase to be short as possible, involving the rapid outgrowth of a preformed growth-unit comprising a long section of scale-like leaves and a distal cluster of large assimilative leaves. This marked rhythmic growth, common in monocaulous species, might take place in just a few days while the resting phase could last more than a year (Figure 5.7).

5.4.4 Evolution of plant architecture

Correlated evolution analysis failed to identify preadaptations facilitating the evolution of monocauly. A likely but uninvestigated preadaptation is the inherent architectural background. Monocauly in New Caledonia is expressed by three different architectural models, each presenting a low phylogenetic signal and numerous independent origins. Chomicki et al. (2017) showed that some transitions from one model to another are more frequent than others. In the flora of New Caledonia, at least 16 of the 30 genera exhibiting Corner's model also contain species with the Rauh's architectural model, and 7 out of 10 genera expressing Chamberlain's model contain species that conform to the Leeuwenberg's model. A detailed understanding of intra-generic relationships is needed to formulate any rigorous conclusions about the evolution from one model to another but these iterative associations suggest that there are some evolutionary links between the two pairs of models. The relation between the Chamberlain's and the Leeuwenberg's models is obvious given their morphological similarities (unichasial sympodium vs. plurichasial sympodium, respectively). Incidentally, the transition from the Chamberlain's toward the Leeuwenberg's model frequently occurs within an individual during ontogeny (Veillon, 1976; Hallé et al., 1978). The Rauh's model is one of the least differentiated branched models in that branches are morphologically identical to the trunk (Hallé et al., 1978). The Rauh's model could be seen as a sequential repetition of Corner's model or Corner's model as an expression of the Rauh's model in which branches were lost. In the first case, a probable evolutionary mechanism is the integration of an opportunistic reiteration process in the developmental sequence of the plant (see Millan, 2016). In the second case, a probable mechanism is the structural reduction through heterochronic developmental pathway (D'Arcy, 1973; Barthélémy, 1988; Chapter 6). Too few genera expressed the Cook's model and data on the architecture of related branched species are too lacunar to suggest whether one transition is more likely. Nevertheless, we noted that some species of *Phyllanthus* and *Casearia* expressed the Roux's model, which is morphologically close to the monocaulous Cook's model also seen in both genera (Hallé et al., 1978; Hallé, 2004).

Such associations between woody architectural models in monocaulous genera suggest a preferential evolution of this habit from woody ancestors, as shown in *Atractocarpus* (Chapter 6) and *Oxera* (Barrabé et al., 2018). However, the evolution of monocauly from herbaceous ancestors is common globally (Chomicki et al., 2017) and particularly on islands (Carlquist, 1969; Böhle et al., 1996; Lens et al., 2013). New Caledonia was noted to be particularly poor in secondary woody species (Carlquist, 1974; Pillon et al., 2017), known genus only in *Scaevola*, whose wood anatomy (Carlquist, 1969) and phylogeography (Howarth et al., 2003) indicate an evolution from herbaceous Australian ancestors toward woody Pacific-islands species. This genus includes one monocaulous species in New Caledonia (*S. beckii*) that is interestingly closely related with herbaceous to sub-woody Australian species (Howarth et al., 2003). Other potentially secondary woody species that are missing in the *Catalogue of Woody Herbs on Islands* (Carlquist, 1974) are found in *Oxalis*, represented by six species in New Caledonia (Munzinger et al., 2016) three of which are woody and one monocaulous (*O. balansae*). Given that the large majority of *Oxalis* worldwide are herbaceous (Cocucci, 2004), these species could highlight a new case of secondary woodiness, although anatomical and phylogenetic data will be needed to confirm this hypothesis (see Lens et al., 2013). As such, evolution of monocauly from herbaceous ancestors has probably occurred in both of these potential secondary woody New Caledonian genera, and the scarcity of this evolutionary pathway there seems further due to the general lack of secondary woodiness in the archipelago. This could also explain the surprising absence of plants exhibiting the Holttum's architectural model, which has principally been described from islands (Hallé et al., 1978). Most of the woody species conforming to this model belong to largely herbaceous families (e.g. Boraginaceae, Asteraceae, Geraniaceae, Gesneriaceae or Campanulaceae) and are therefore considered as secondarily woody taxa that have retained the ancestral Holttum's architectural model, the latter being frequent in herbaceous plants (Jeannoda-Robinson, 1977; Chomicki et al., 2018).

5.4.5 A threatened and poorly known growth habit

More than half (51%) of evaluated monocaulous species were threatened according to the IUCN Red List criteria. This proportion is probably to be moderated given that only 34% of the New Caledonian flora and 35% of monocaulous species have been evaluated to date, and the proportion of highly threatened species (EN and CR following IUCN conservation status) is higher among monocaulous species than in the branched taxa (41% vs. 32% respectively). The higher threat among monocauls is not due to bushfire or mining activities (despite the fact that they concern 55% and 43% of evaluated monocaulous species, respectively), but rather introduced herbivores. Threat from herbivores is indeed higher than expected by chance in the monocaulous flora, probably because the single meristem and few large leaves of these plants make browsing particularly damaging (see Costes et al., 2013; Charles-Dominique et al., 2017).

Another important factor influencing the risk of extinction of monocaulous species is their preference for the rainforest understory and ultramafic substrate. Habitat conservation is a fundamental element of species protection (Rohlf, 1991; Shilling, 1997) but also for maintaining genetic diversity and evolutionary process (Lawler et al., 2015). However, New Caledonian rainforests, and particularly the relictual and fragmented rainforests on ultramafic substrate, are particularly threatened (Jaffré, 2005). Mining activities on the archipelago increasingly impact the native vegetation on ultramafic substrate (Jaffré, 2005; Wulff et al., 2013; Ibanez et al., 2017a). Rainforests have been drastically reduced (Sloan et al., 2014; Birnbaum et al., 2015b) and are critically fragmented (Jaffré et al., 1998; Ibanez et al., 2017a). This habitat loss is of particular concern for rainforest species, of which monocaulous taxa are an important functional group.

Finally, the significantly higher proportion of monocaulous species assessed as data deficient (DD, 16%) illustrates the lack of knowledge of this growth habit. The rarity of monocaulous species worldwide and their peculiar morphology (large leaves, stout stems and a single growing apex) make monocauls particularly relevant for studying ecological and evolutionary processes (see Chapter 6) but constraint their representation in herbarium collections leading to taxonomic shortfalls (see Chapter 4).

5.4.6 Environmental contingency and ecological opportunities in New Caledonia

Whether a high incidence of monocauly is unique to New Caledonia is difficult to assess as comparative data are scarce. In a meta-analysis including more than 20,000 vascular plant species, Chomicki et al. (2017) found 118 origins of monocauly while we found a mean of 38 (and up to 49 for the New Caledonian flora alone (and this just using a genus-level phylogeny). Current knowledge on plant architecture would suggest that ca. 2% of species are unbranched globally (Chomicki et al., 2017), i.e. less than one third of what occurs in the New Caledonian flora. The question of the evolution of monocauly, however, remains puzzling as it depends on the definition of this habit. For instance, Chomicki et al. (2017) did not consider the Cook’s architectural model in their study but included all monocotyledonous species. While quantitative data for other floras are not available, the strong convergence toward a growth habit that is considered to be rare both globally (Hallé et al., 1978) and regionally (Schmid, 1979, 1990) suggests that monocauly is parts of the New Caledonia’s functional disharmony. Schmid (1981) even considered that the diversity and abundance of this habit are one of the most striking characteristic of New Caledonian rainforests. This is supported by the exceptional rate of endemism in the monocaulous flora (99%) which is by far higher than expected by chance. The repeated evolution of monocauly in New Caledonia among distantly related lineages suggests environmental contingencies peculiar to the archipelago.

Rainforest density – We found a significant pattern of contingent evolution between monocauly and occurrence in rainforest areas, indicating a preferential evolution of monocauly in this habitat. Sixty-five percent of monocaulous species grow exclusively in rainforest and only 11% have never been observed in this vegetation. Consequently, monocaulous species account for a substantial part of rainforest diversity (12.3% of woody species) and much more if we only consider understory species. An ecological preference for the understory of rainforests among taxa whose architecture corresponds to a monocaulous habit has yet been suggested (Corner, 1949; D'Arcy, 1973; Hallé, 1974; Hallé et al., 1978; Schmid, 1981). Monocauls support large, mostly simple leaves (Corner, 1949; Chapter 6). This could be an adaptation to low-resource environments where low-cost large leaves could be advantageous compared to more costly branches in buffered conditions (Givnish and Vermeij, 1976; Givnish, 1979). This is particularly true in dense, shady rainforest understory where lateral branches are mechanically constrained by dense neighbouring vegetation. New Caledonian rainforests appear to have higher stem densities than other Southwest Pacific rainforests (Jaffré and Veillon, 1990; Jaffré and Veillon, 1995; Ibanez et al., 2014; Ibanez et al., 2017b), probably related to the frequency and intensity of tropical cyclones (Ibanez et al., 2018a). Competition for space and light in this highly congested environment might have favoured the unidirectional space exploration and large leaves of monocaulous species. Moreover, unbranched or sparsely-branched species are less affected by debris fall or the domino effect of falling trees during cyclones. The fact that palms and tree ferns are also particularly abundant in New Caledonian rainforests (Ibanez et al., 2017b) is consistent with these hypotheses, both groups being dominated by unbranched architectures. We believe that these forest structural and dynamic features have been important driver of the convergence toward monocauly in New Caledonia.

Rainforest history – Large simple leaves, inherent to the monocaulous habit, have cheaper construction costs than twigs (see above) but are disadvantageous in arid and cold conditions due to their thicker boundary layer, which slows thermoregulation (Givnish, 1979; Wright et al., 2017). Accordingly, we found that 79% of monocaulous species occurring in dry vegetation had compound leaves or functionally similar phyllomorphic branches (not shown). Large, drought-sensitive leaves have probably constrained the distribution of monocauly to humid and shady environments, which provide buffered thermal and hydric condition (Givnish, 1979, 1987, 1988). New Caledonia has been suggested to have several rainforest refuges for some drought sensitive groups such as Palms (Pintaud et al., 2001) or basal Angiosperms (Poncet et al., 2013; Pouteau et al., 2015; Tournebize et al., 2017) during Pleistocene climatic fluctuations (Bowler et al., 1976; Hope and Pask, 1998; Stevenson and Hope, 2005). These paleoclimatic events caused important drought-related species extinctions in other Southwest Pacific rainforests, particularly in Australia (Byrne et al., 2011), which is considered as the principal source area for New Caledonian flora (Morat, 1993; Swenson et al., 2014; Thomas et al., 2014). As such, besides presenting environmental contingencies that promoted the evolution of monocauly, New Caledonian rainforest could have acted as refugia for such drought sensitive plants that disappeared from adjacent regions. After the last glacial episode, ecological opportunities provided by new vacant habitat, are likely to have promoted the diversification of some monocaulous lineages already present and triggered the evolution of monocauly in others through niche partitioning (e.g. *Atractocarpus*, Chapter 6).

Ultramafic substrates **–** Monocauly appears to have evolved preferentially on ultramafic substrate, an unsuspected result given the neglegible difference between the proportion of branched and monocaulous species occurring on this substrate (44% and 47%, respectively). These ultramafic rocks are rare globally but cover ca. one third of New Caledonia (Paris, 1981; Isnard et al., 2016) and are thought to have initially covered all of the main island (Pelletier, 2006). Soils derived from ultramafic rocks are diverse but share several characteristics, including their low nutrient content and high concentrations of potentially bioavailable toxic trace elements, implying physiological tolerance among plants that grow on them (Jaffré, 1976, 1980; Isnard et al., 2016). As such, ultramafic substrates appear to be largely responsible for the floristic disharmony between the New Caledonian archipelago and adjacent regions (Jaffré, 1993; Pillon et al., 2010; Isnard et al., 2016). Veillon (1976) suggested that these constraining edaphic conditions could be responsible for the high proportion of orthotropic, slow-growing stems with distally clustered-leaves, as showed by Virot (1956). Deploying large leaves might indeed be no more costly than producing an equivalent photosynthetic area on several twigs (Givnish, 1995; Wright et al., 2006). In this sense, monocauly might be seen as a structural reduction of a more complex branched architecture resulting from selection under constraining edaphic conditions. A phenomena referred to as “architectural pauperization” was proposed for *Cecropia obtusa*, a branched tree (generally conforming to the Rauh’s architectural model) that becomes monocaulous on bare, eroded and humus-free soils (Barthélémy, 1988). Consequently, the convergence toward monocauly observed in the New Caledonian flora could also have been triggered by preferential evolution of this habit on the locally common but globally rare ultramafic substrate. Interestingly, several clades rich in monocaulous species (e.g. Malpighiales, Apiales, Ericales, Gentianales, Sapindales) have been shown to be over-represented in New Caledonia, probably as a result of exaptation to ultramafic substrate (Pillon et al., 2010). In some of these clades (e.g. Malpighiales, Ericales, Gentianales) nickel hyper-accumulation, a specialization associated with adaptation to ultramafic substrates, is common (Pillon et al., 2010; Jaffré et al., 2013).

Lack of browsers **–** Threats associated with IUCN Red List risk of extinction status suggest that monocaulous species are more sensitive to introduced herbivores than branched taxa. Recent studies actually showed that plant architecture significantly contribute to structural defenses: the more intrinsically branched is a plant, the more effective is the protection (Costes et al., 2013; Charles-Dominique et al., 2015; Charles-Dominique et al., 2017). As such, the absence of native browsers in New Caledonian rainforests may have provided an ecological opportunity for the evolution of monocauly. This exposed growth habit could then be considered as a syndrome of insular naivety. To our knowledge, horned terrestrial turtles (Meiolaniid) are the only known native browsing vertebrate that were present in New Caledonia and survived until the Holocene (Anderson et al., 2010; White et al., 2010). As another large terrestrial vertebrate, the bird *Sylviornis neocaledonicae* (Poplin and Mourer-Chauviré, 1985), which was probably not a browser (Mourer-Chauviré and Balouet, 2005; Worthy et al., 2016), horned turtles probably lived in the coastal plain and dry forest (Anderson et al., 2010), where monocauls are infrequent. Accordingly, monocaulous species of *Cyanea* (Campanulaceae) in Hawaii where browsing birds were present, have thorn-like prickles to protect the stem (Givnish, 1994). By contrast, New Caledonian flora account for very few armed species, the vast majority of which are climbers (Bruy et al., 2018).

5.4.7 Conclusions and future directions

Monocauly in New Caledonia appears to represent a remarkable functional convergence, involving different plant architectural models. Environmental contingencies present in the archipelago (e.g. rainforest stem density, ultramafic substrate, glaciation-driven habitat vacancy) might have provide a favorable background for the evolution of monocauly, did not face strong negative selection pressures such as the presence of large browsers or pronounced seasonality. Changes in growth habit may in turn alter the selective environment of other trait attributes (cauliflory, rhythmic growth) and drive their evolution. The moderate phylogenetic clustering of monocauly indicates some potential prerequisites that have not been highlighted in the present study. An important prerequisite that remains to be tested is plant architecture because the currently available data are insufficient. The New Caledonian flora seems to include many sparsely-branched plants in addition to monocauls, and some architectural models (Corner's, Rauh's, Attims', Leuwenberg's, Chamberlain's, see Veillon, 1976) seem to be particularly well represented. The architectural background of a group could act as a key driver in the diversification of growth habit, and New Caledonia is undoubtedly an appropriate case study to investigate this.

More globally, monocaulous species appear to comprise an important functional group in rainforest understory habitats, as probably occurs in other areas such as Gabon (Hallé and Hallé, 1965) and Papua New Guinea (Hallé, 1974). However, the monocaulous habit remains largely overlooked and further comparative studies are needed to gain insight into the ecological and evolutionary history of monocaulous plants throughout the tropics.

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Chapter 6 — Evolution of plant architecture, functional diversification and divergent evolution in the genus *Atractocarpus* (Rubiaceae) for New Caledonia

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Abstract:

The diversification of ecological roles and related adaptations in closely related species within a lineage is one of the most important processes linking plant evolution and ecology. Plant architecture offers a robust framework to study these processes as it can highlight how plant structure influences plant diversification and ecological strategies. We investigated a case of gradual evolution of branching architecture in Atractocarpus spp. (Rubiaceae), forming a monophyletic group in New Caledonia that has diversified rapidly, predominantly in rainforest understory habitats. We used a transdisciplinary approach to depict architectural variations and revealed multiple evolutionary transitions from a branched (Stone's architectural model) to a monocaulous habit (Corner's architectural model), which involved the functional reduction of branches into inflorescences. We propose an integrative functional index that assesses branching incidence on functional traits influencing both assimilation and exploration functions. We showed that architectural transitions correlate with ecologically important functional traits. Variation in ecologically important traits among closely relatives, as supported by the architectural analysis, is suggestive of intense competition that favored divergence among locally coexisting species. We propose that Pleistocene climatic fluctuations causing expansion and contraction of rainforest could also have offered ecological opportunities for colonizers in addition to the process of divergent evolution.

Keywords: Branching index, Convergence, Corner's rules, Gardenieae, Island, Rainforest, Treelet, Understory

6.1 Introduction

Convergent and divergent evolution are widely recognized as important drivers of plant diversification at large scale (Givnish and Sytsma, 1997; Gianoli, 2004; Drummond et al., 2012; Couvreur et al., 2015; Givnish, 2016). Well known examples of large scale convergence in plants (i.e. the appearance of phenotypic similarities among distantly related taxa) include the evolution of a cushion growth habit in alpine environments (Boucher et al., 2012; Aubert et al., 2014; Boucher et al., 2016), rosette-shrubs in islands (Carlquist, 1974; Givnish, 2010; Lens et al., 2013), climbing mechanisms in lianas (Sousa-Baena et al., 2014; Sousa-Baena et al., 2018), and succulence in arid environments (Ogburn and Edwards, 2010; Arakaki et al., 2011). These and others examples demonstrate that similar habitats or micro-habitats can produce selective pressures that favor some morphological and physiological trait attributes. Another evolutionary process, sometimes linked with convergence, is the diversification of ecological roles among closely related species, i.e. divergent evolution, which results in the exploitation of different ecological resources (see e.g. Bramwell, 1975; Givnish et al., 2009; Givnish et al., 2014). Convergent and divergent evolution have been attributed to morpho-physiological traits, whose gradual evolution or rapid innovation can lead to adaptive radiation, sometimes involving increased diversification rates (Givnish and Sytsma, 1997; Givnish et al., 2014; Couvreur et al., 2015). A striking feature of convergent and divergent evolution is that it often involves variation in growth habit, which represents the ultimate form of a plant expressed in its physiognomy (Warming, 1909). Growth habit results from the integration of a set of traits, e.g. branching pattern and structure, body size and shape, position of inflorescences, and anatomy, among others, which have generally been studied independently (see e.g. Carlquist, 1984; Rowe and Speck, 2005; Givnish et al., 2009; Isnard et al., 2012; Wagner et al., 2014). Few work has, however, used the integrative approach provided by plant architecture to study the evolution of plant growth habit.

Plant architecture characterizes the spatial arrangement and specialization of structures (morphological origin, branching pattern, axis categorization) and their evolution during ontogeny (Hallé et al., 1978; Barthélémy and Caraglio, 2007). As such, it can highlight how plant structure impacts plant diversification and can help identify evolutionary processes underlying plant evolution (Bateman, 1994, 1999; Sussex and Kerk, 2001; Meyer-Berthaud et al., 2010). Architectural studies have shown that plants are modular organisms comprising elements that can differ in their organization and functions (Hallé et al., 1978; Barthélémy and Caraglio, 2007). For instance, in many tree and treelet species, the trunk functions primarily for exploration and to provide support, while branches are involved in assimilation and reproduction. Plant architecture thus influences spatial and temporal exploitation of resources (Smith et al., 2014). Some architectural traits have been shown to impact plant fitness, either directly (Küppers, 1989; Millet et al., 1999; Charles-Dominique et al., 2010; Charles-Dominique et al., 2012; Millan, 2016; Charles-Dominique et al., 2017) or in interaction with other functional traits (Pérez-Harguindeguy et al., 2013; Trueba et al., 2016). Among the best known examples are Corner's rules, which stipulate that "the greater the ramification, the smaller become the branches and their appendages" (leaves, flowers, and fruits, Corner, 1949). This statement points toward an effect of plant architecture on leaf size and linked architecture and plant ecological strategies (White, 1983a; Ackerly, 1996). To date, approaches linking plant architecture and function are scarce although some architectural indexes can assess interesting strategies such as defense against herbivores ("Index of caginess", Charles-Dominique et al., 2017) or leaf-to-stem relation that trigger flowering ("Index of axialisation", Lauri, 1988; Lauri and Kelner, 2001).

Despite the functional importance of plant architectural traits, little is known about their evolution (Kurmann and Hemsley, 1999; León Enriquez et al., 2008). In a recent review, Chomicki et al. (2017) investigated the evolution of plant architecture for several groups. Their results showed preferential transitions between models, suggesting pre-requisite morphological ability for the evolution of a given plant architecture. In contrast, some model transitions seem never to occur, suggesting that genetic constraints might prevent them. Chomicki et al. (2017) did not, however, investigate processes involved in plant architectural evolution. Bateman (Bateman and DiMichele, 1994; Bateman, 1999) argued that the changes involved in the transition from one architecture to another are too important and deep for such transitions to take place gradually. Rather, such evolution is suggested to occur preferentially by saltation, which involves the direct shift from one competitive architecture to another without passing through intermediate states associated with lower fitness. Other authors have proposed the notion of an "architectural continuum" (Oldeman, 1974; Barthélémy et al., 1989), suggesting a continuous transition from one model to another in some groups (Hallé et al., 1978). In the context of this diversity of possible models to explain evolution in plant architecture, detailed studies within individual clades that combine results from molecular phylogenetic work with detailed architectural analysis may be particularly informative.

Atractocarpus Schltr. & K.Krause (Gardenieae, Rubiaceae), a Pacific genus of about 40 species, of which 32 are endemics to New Caledonia (Mouly et al., *submitted*), is ideally suited to study the evolution of plant architecture and to test hypotheses regarding the role of architecture in plant ecological diversification. Especially since a recently published phylogeny based on comprehensive sampling is available for the genus (Mouly et al., *submitted*). Most members of this genus are treelets occurring in the understory of tropical and subtropical rainforests, and they exhibit substantial variation in branching pattern (Tirvengadum and Sastre, 1979; Robbrecht and Puff, 1986), ranging from monocaulous (i.e. unbranched) to well-branched species, including

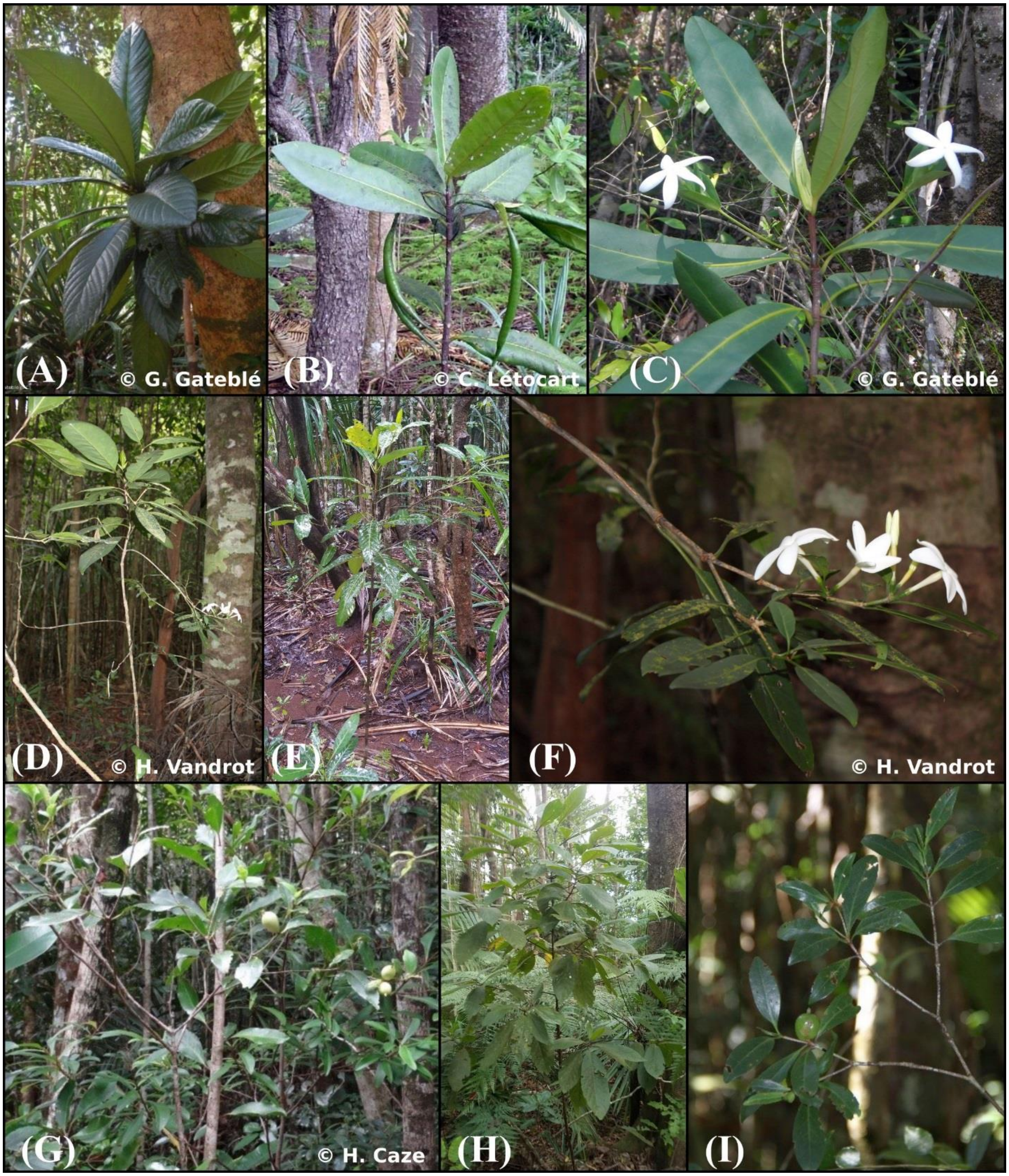

FIGURE 6.1 – Photographs of different *Atractocarpus* species in their environment showing variability in growth habit and lateral axis. Monocaulous species: **(A)** *A. confertus*, **(B)** *A. bracteatus*, **(C)** *A. bracteatus*. Intermediate species: **(D)** *A. ngoyensis*, **(E)** *A. ngoyensis*, **(F)** *A. ngoyensis*. Branched species: **(G)** *A. pseudoterminalis*, **(H)** *A*. sp. nov. 10, **(I)** *A. pseudoterminalis*.

various intermediate states (Figure 6.1). The New Caledonia members of *Atractocarpus*, which originated from a single colonization event that occurred ca. 2.4 Myr ago (Mouly et al., *submitted*), has the highest diversification rate of any genus studied to date (1.17 species species^{-1} Myr^{-1}), approaching that of the well-known Hawaiian lobelioid genus *Cyanea* on the island of Maui (Hawaiian lobelioids; 1.36 species species-1 Myr-1, Givnish et al., 2009).

The presence of a high diversification rate combined with architectural diversity is thought to provide an indication of ecological diversification, a situation that is often associated with island colonization (Silvertown, 2004; Silvertown et al., 2005). In groups adapted to growing in the forest understory, light is a variable and limiting resource, and in response, plants have deployed various growth strategies related to leaf photosynthesis and the economization of carbon. To quantify the architectural gradient from monocaulous (unbranched) to well-branched species, we developed a new “functional branching index”, which assesses branching incidence on functional traits that influence assimilation and exploration functions. Considering each understory species of *Atractocarpus* in New Caledonia, we analyzed correlations between architecture and traits associated with key ecologically significant functions (viz., photosynthesis, hydraulic, mechanics, and dispersal). We investigated the evolution of plant architecture (branched vs. unbranched) in forest understory species and its impact on the exceptional diversification rate of the genus. Finally, we explored how ecological opportunities might stimulate the diversification of architecture through spatial differentiation in resource use (niche partitioning) in closely related species following the colonization of New Caledonian rainforests.

6.2 Material and methods

6.2.1 Sampling

We sampled all the 27 known rainforest species of *Atractocarpus* occurring in New Caledonia (list of taxa in Appendix 2). For Ancestral Character Estimation (ACE), three Australian *Atractocarpus* species and one species in each of the most closely related genera for which DNA sequences were available (Mouly et al., 2014; Mouly et al., *submitted*) were included as outgroups.

Individuals were sampled in 20 rainforest sites occurring on *Grande Terre*, New Caledonia's main island (Appendix 2).

6.2.2 Branching index and plant architectural traits

Based on the observation that an observed architectural gradient might result from differential allocation in branch length and supported leaf area (Figure 6.1), we used two functional branching indexes based on the differentiation of function from branches to trunk (Corner, 1958). Given that photosynthetic function can be approximated by leaf area (Pérez-Harguindeguy et al., 2013) and exploration function by stem length (Barthélémy and Caraglio, 2007; Smith et al., 2014), branching indexes were calculated as follows:

(i) Photosynthetic branching index: $\frac{Leaf\ area\ supported\ by\ branches}{Total\ leaf\ area\ (branches+trunk)}$

(ii) Exploration branching index: $\frac{Branches\ cumulated\ length}{Total\ stem\ length\ (branches+trunk)}$

A value of zero indicates that photosynthesis and exploration are assumed only by the trunk and that branches (lateral exploration) are lacking, which corresponds to the monocaulous habit, physiognomically defined as "trees with a single trunk or visible stem of the plant" (Hallé et al., 1978). The higher the value of the index, the greater the functional role played by branches. We built a single integrative branching index that expresses the architectural gradient by combining these two variables using Principal Component Analysis (correlation between photosynthetic and exploration branching indexes: rho = 0.86) employed in the *ade4* package for R (Dray and Dufour, 2007).

Species were segregated into three architectural classes (Monocaulous, Intermediate, and Branched) using Wilcoxon signed-rank tests that enable detection of breaks in the distribution of the integrative branching index.

Using morphological criteria reviewed by Barthélémy and Caraglio (2007), we then described main traits commonly used in architectural analyses (growth process, branching pattern, position of reproductive structures, etc.) for the 27 New Caledonian species of *Atractocarpus*. The number of individuals studied varied from more than a hundred in some species (e.g. *A. pseudoterminalis*, *A. ngoyensis* and *A. bracteatus*) to twelve in *A. sezitat*, a rare species whose habitat is highly disturbed by introduced herbivores. All species were studied at different ontogenetic stages (from very young plants to senescent adults) except *A. sezitat* and *A.* sp. nov. 12, for which no young plants could be found.

6.2.3 Plant functional traits

We tested the correlation of 14 traits with branching index. The traits were selected to reflect important features of plant ecological strategies (Table 6.1). They were measured on five individuals per species and, when possible (e.g. for leaf and internode traits), five times per individual. The selection of individuals was standardized for environment (rainforest understory) and for ontogeny following three criteria: (i) recently mature individuals, (ii) non reiterated individuals (see Oldeman, 1974; Barthélémy and Caraglio, 2007), and (iii) non-traumatized trunks. It was not possible to locate individuals meeting all three conditions for *A. sezitat* and *A.* sp. nov.

TABLE 6.1 – Functional traits measured for 25 *Atractocarpus* species. References are given to justify the interest of each trait for corresponding functions.

Trait	Abbreviation	Unit	Formula	Related function	References
Trunk traits					
Slenderness ratio	sr	Ø	$\frac{Plant\ height}{Plant\ basal\ diameter}$	Geometric feature of buckling resistance	Alméras et al. (2004); Niklas et al. (2006); Homeier et al. (2010)
Specific wood density	swd	$g.cm^{-3}$	$\frac{Wood\ dry\ mass}{Wood\ fresh\ volume}$	Growth rate, drought resistance and mechanical reinforcement	Pérez-Harguindeguy et al. (2013); Wright et al. (2007); Olson et al. (2009)
Specific stem density	ssd	$g.cm^{-3}$	$\frac{Stem\ dry\ mass}{Stem\ fresh\ volume}$	Growth rate, capacitance, mechanical reinforcement	Pérez-Harguindeguy et al. (2013); Díaz et al. (2016)
Internode diameter	internode_d	cm	$\sqrt{Min\ IN\ diameter \times Max\ IN\ diameter}$	Growth rate, mechanical reinforcement	Vertessy et al. (1995); Schuerger et al. (1997); Olson et al. (2009)
Internode length	internode_l	cm	Ø	Growth rate, leaf spacing	Weijschedé et al. (2007); Dong et al. (2010)

Proportion of pith	%_pith	Ø	$\frac{Area\ of\ pith}{whole\ section\ area}$	Primary growth, stem biomechanics	Carlquist (1974); Niklas (1992); Levionnois et al. (2018)
Proportion of wood	%_wood	Ø	$\frac{Area\ of\ wood}{whole\ section\ area}$	Secondary growth, stem biomechanics	Penfound (1931); Schuerger et al. (1997); Hummel et al. (2007)
Proportion of cortex	%_cortex	Ø	$\frac{Area\ of\ cortex}{whole\ section\ area}$	Storage	Pérez-Harguindeguy et al. (2013)
Huber value	hv	Ø	$\frac{Wood\ area\ at\ POM}{LF\ area\ above\ the\ POM}$	Allocation of wood to leaf area deployed	Penfound (1931); Gleason et al. (2012); Pérez-Harguindeguy et al. (2013)
Mean leaf area	mean_la	cm^2	Ø	Energy balance, hydraulic demand	Poorter et al. (2009); Pérez-Harguindeguy et al. (2013); Ackerly (2004)
Specific Leaf Area	sla	cm.g^{-1}	$\frac{Leaf\ fresh\ area}{Leaf\ dry\ mass}$	Allocation of biomass to light harvesting	Pérez-Harguindeguy et al. (2013); (Westoby et al., 2002)

Whole plant trait					
Total leaf area	total_la	cm^2	$(BR\ mean\ LF\ area \times Number\ of\ BR) + (Mean\ area\ of\ TR\ LF \times Number\ of\ TR\ LF)$	Energy balance, hydraulic demand	Pérez-Harguindeguy et al. (2013); Díaz et al. (2016)
Leaf number	nb_leaf		$Number\ of\ TR\ LF + (BR\ mean\ number\ of\ LF \times Number\ of\ BR)$	Light harvesting	Duncan and Hesketh (1968); White (1983a)
Fruit trait (herbarium measure)					
Fruit volume	fruit_vol	cm^3	$Core\ fruit\ length \times (Core\ fruit\ width)^2$	Dispersal, reproductive allocation	Cornelissen (1999); Cornelissen et al. (2003)

IN: internode, POM: point of measurement, LF: leaf, BR: branch, TR: trunk

12 due to small population sizes and habitat degradation, so these taxa were removed from this analysis. We concentrated our sampling in the apical part of the trunk because (i) this enabled standardization of physiological age and (ii) unbranched and branched species can be compared only on the basis of the main stem. Moreover, variation in resource allocation and anatomy between unbranched and branched species might be more prevalent toward the apex, where large leaves are deployed (Carlquist, 1974). Stem and leaf measurements were standardized as follows. Leaf traits (SLA, leaf area) were measured on the five youngest, fully expended leaves of the main axe (trunk). Wood was collected below the terminal leaf tuft for the measurement of anatomical traits (proportion of tissues, specific wood density, and specific stem density). Internode length and diameter were measured on the five youngest, well-developed trunk-internodes (before secondary growth). Branch traits (cumulated length, leaf number, leaf area) were measured on two representative branches per individual and the total number of branches was counted.

Most of the individuals studied in the field were infertile, so fruit traits were measured on herbarium specimens (NOU and P, Herbarium acronyms follow Thiers, *continuously updated*). We selected undamaged and unflattened fruits from which length and diameter were measured. As *Atractocarpus* fruits are often ellipsoid to tubular (Puttock, 1999), these two dimensions are used to approximate fruit volume (Table 6.1). A total of 592 fruits were measured, and only the five largest fruits per taxon (four for *A. confertus* and *A. sessilifolius*) were used to ensure that values from only mature fruits were included in our analyses. One of the species, *A.* sp. nov. 6, is a very rare species whose fruits have never been observed; it was consequently excluded from the fruit volume dataset.

6.2.4 Data analysis

Phylogenetic tree – The molecular phylogeny of Mouly et al. (*submitted*) was used for analysis. This ultrametric phylogenetic tree was constructed under Bayesian Inference using one nuclear (*ITS*) and two chloroplastic (*trnTL*, *rpl32*) loci. Since the current study focused on rainforest species, we pruned the five dry forest and maquis species using the R software (Ver. 3.4.3).

Phylogenetic signal – We assessed phylogenetic independence of measured traits (Felsenstein, 1985) using two complementary statistics calculated under a Brownian Motion (BM) model of evolution. Pagel's Lambda (Pagel, 1999; Freckleton et al., 2002) is widely used for low rates of type I error and robustness, even for poorly or moderately informative phylogenies (Freckleton et al., 2002; Münkemüller et al., 2012). Because this statistic loses statistical power when used on small phylogenies (< 30 tips, Freckleton et al., 2002), we also used Blomberg's Kappa (Blomberg et al., 2003; Kembel, 2009) that is less robust but more appropriate for small taxonomic sampling (until 20 taxa, Kamilar and Cooper, 2013). Both statistics were calculated considering intraspecific variation using the *phytools* package for R (Revell, 2012).

Trait correlations and functional characterization – We used phylogenetic regression based on the method proposed by Ives et al. (2007) and implemented in the *phytools* package for R (Revell, 2012) to test whether architectural variation was correlated with functional specialization. Using maximum likelihood, this method fits bivariate models taking into account both phylogenetic framework and intraspecific variation. The response variable was the integrative branching index, and the explanatory variables were all other functional traits (Table 6.1). Significance of relations was tested using a likelihood ratio test between the model and a model constrained with a slope of zero.

To characterize the functional space of each architectural classes, we performed a Principal Component Analysis. We used the species arithmetical mean of each functional traits (branching

TABLE 6.2 – Models fitted for trait based diversification analysis. Bold lines represent models with lowest AICc.

Model	Speciation rates	Extinction rates	Transition rates	AICc
1	≠	≠	≠	-46.72
2	**=**	**=**	**=**	**-50.59**
3	≠	=	=	-49.59
4	≠	≠	=	-49.56
5	≠	=	≠	-46.72
6	=	=	≠	-46.16
7	=	≠	≠	-46.16
8a	M = I ; B ≠	=	=	-50.58
8b	I = B ; M ≠	=	=	-50.50
8c	M = B ; I ≠	=	=	-49.59
9a	M = I ; B ≠	0	=	-50.58
9b	I = B ; M ≠	0	=	-50.50
9c	M = B ; I ≠	0	=	-49.59
10	**=**	**0**	**=**	**-50.59**
11	≠	0	=	-49.59

M: Monocaulous, I: Intermediate, B: branched index excluded), and functional differences between architectural classes (Monocaulous, Intermediate, Branched) were tested with a permanova (*Vegan* package for R, Oksanen et al., 2018).

Ancestral Character Estimation **–** To determine the putative ancestral architectural class of *Atractocarpus* and infer the evolution of architecture in the genus, Ancestral Character Estimation (ACE) was performed. We assigned an architectural class to each of the 11 outgroup species based on published descriptions (Fosberg, 1987; Smith and Darwin, 1988; Fosberg et al., 1993; Puttock, 1999; Wong, 2004; Zahid and Wong, 2004, 2010; Tong et al., 2013), herbaria specimens (P, K, BM, E) and available photos. The ACE were performed using a maximum likelihood method under the *ape* package for R (Paradis et al., 2004). Three possible models of evolution fitted the data characteristics: (i) equal transition rates between classes (ER), (ii) different transition rates between classes but with equal rates for reversions (SYM), and (iii) different rates for every transition (ARD). The best model was selected using the corrected Akaike Information Criterion (AICc).

Trait Based Diversification **–** To test whether one of the architectural classes has contributed more than the others to the diversification of New Caledonian *Atractocarpus* (by increasing speciation rates and/or decreasing extinction rates), we used the Multiple State Speciation Extinction (MuSSE) framework (Fitzjohn et al., 2009) as implemented in the *diversitree* package for R (Fitzjohn, 2012). For this analysis, outgroups were dropped from the phylogeny to consider only the 27 rainforest *Atractocarpus* species. Fifteen models of diversification were used, each differing in whether or not of speciation, extinction and transition rates were equal between classes (Table 6.2). Model selection was done according to AICc.

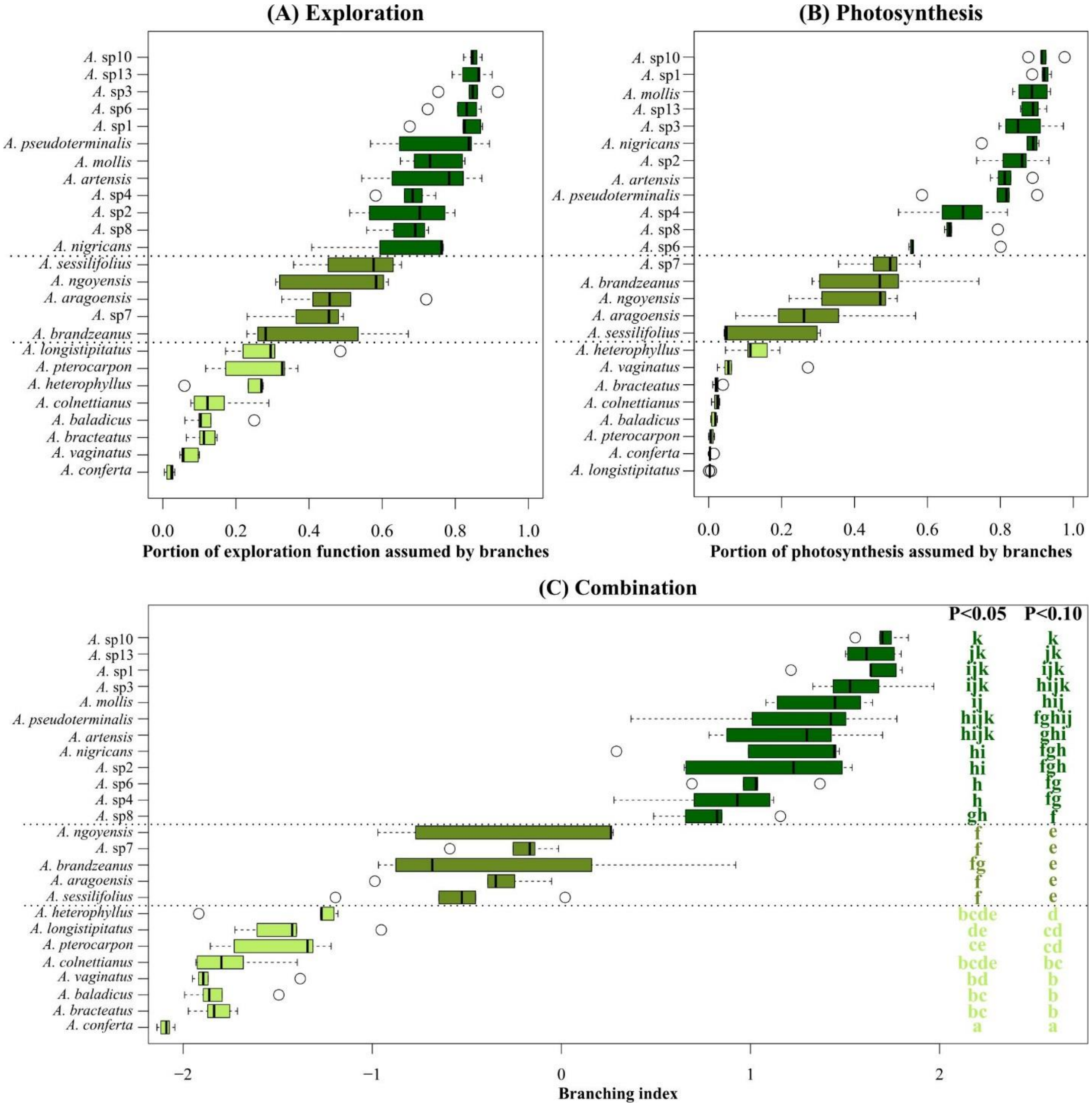

FIGURE 6.2 – Branching indexes calculated on the base of **(A)** exploration function, **(B)** photosynthetic function and **(C)** the combination of both, for 25 *Atractocarpus* species. Letters in **(C)** correspond to the result of the Wilcoxon test; species with shared letters are not significantly different for a given risk of error.

6.3 Results

6.3.1 Branching index

Branching indexes confirmed the existence of a morpho-functional gradient from branched to monocaulous species of *Atractocarpus*, for both exploration and photosynthetic functions (Figure 6.2-A, B). For both indexes, interspecific variation was too gradual to allow the partitioning in distinct classes, but when combined (i.e. using the branching index), three distinct architectural groups could be differentiated (Wilcoxon tests: $P < 0.1$, Figure 6.2-C), viz. the branched, intermediate and monocaulous architectural classes. On average, branched species had 82% of photosynthesis and 76% of exploration provided by branches, versus 36% and 45%, respectively, for intermediate species, and 3% and 16% for monocaulous species.

6.3.2 Architectural characterization

The architecture of New Caledonian *Atractocarpus* species involves two axis categories: (i) a trunk (C1), i.e., an orthotropic monopodium with continuous indeterminate growth, and (ii) "branches" (C2), i.e., orthotropic sympodia with terminal sexuality conferring rhythmic growth (Table 6.3, Figure 6.3). The sympodial branching of C2 always originates in a hypotonic (i.e. on the lower surface) or amphitonic position, resulting in upward flower exposure (Figure 6.1). The only qualitative architectural variation observed between species concerned the branching position of C1, which was continuous for some monocaulous species while diffuse for others. Two main quantitative architectural traits varied greatly among species, the number of modules per branch and the length of modules, which decreased in monocaulous species (Table 6.3, Figures 6.3, 6.4). For example, *A. longistipitatus* is a monocaulous species whose C2 comprise many very short modules (apart from the first one). By contrast, *A. bracteatus* is also monocaulous but its C2

TABLE 6.3 – Architectural traits of 27 *Atractocarpus* species.

	Taxon	*A. mollis*	*A.* sp10	*A.* sp8	*A.* sp1	*A.* sp6	*A.* sp13	*A.* sp3	*A. nigricans*	*A. pseudoterminalis*	*A. sezitat*	*A.* sp4	*A.* sp12	*A. artensis*	*A.* sp2	*A. aragoensis*	*A. ngoyensis*	*A. brandzeanus*	*A.* sp7	*A. sessilifolius*	*A. longistipitatus*	*A. baladicus*	*A. bracteatus*	*A. pterocarpon*	*A. heterophyllus*	*A. colnettianus*	*A. vaginatus*	*A. conferta*
	Architectural class	**Branched**														**Intermediate**					**Monocaulous**							
	Number of AC	2														2					2							
C1	Growth pattern	Indeterminate														Indeterminate					Indeterminate							
	Growth periodicity	Continuous														Continuous					Continuous							
	Branching pattern	Monopodial														Monopodial					Monopodial							
	Growth direction	Orthotropic														Orthotropic					Orthotropic							
	Reproduction	Absent														Absent					Absent							
	Branching position	Diffuse														Diffuse					Diffuse			Continuous				
C2	Growth pattern	Determinate														Determinate					Determinate							
	Growth periodicity	Rhythmic														Rhythmic					Rhythmic							
	Growth direction	Orthotropic														Orthotropic					Orthotropic							
	Reproduction	Terminal														Terminal					Terminal							
	Branching position	Rhythmic acrotone														Rhythmic acrotone					Rhythmic acrotone				na			
	Branching pattern	Sympodial														Sympodial					Sympodial				na			
	Number of relay	1-2														1-2					1-2				na			
	Number of internode / module	2 (-3)								2-3						2-3			2 (-3)	2	2				2			1
	Max. number of module / branch	56	48	46	42	41	38	38	31	71	48	30	29	28	25	25	19	12	16	46	26	5	5	9	5	1	1	1
	Mean length of module (cm)	5.5	4.8	6.5	8.9	9.2	7.8	7.6	7	5.9	6.9	6.5	7.7	14.8	11.5	6.3	12.9	15	7.1	2.4	1.5	12.1	8.1	4.5	8.5	5.9	5.1	1.7

AC: Axis category, C1: First axis category (trunk), C2: Second axis category ("branches")

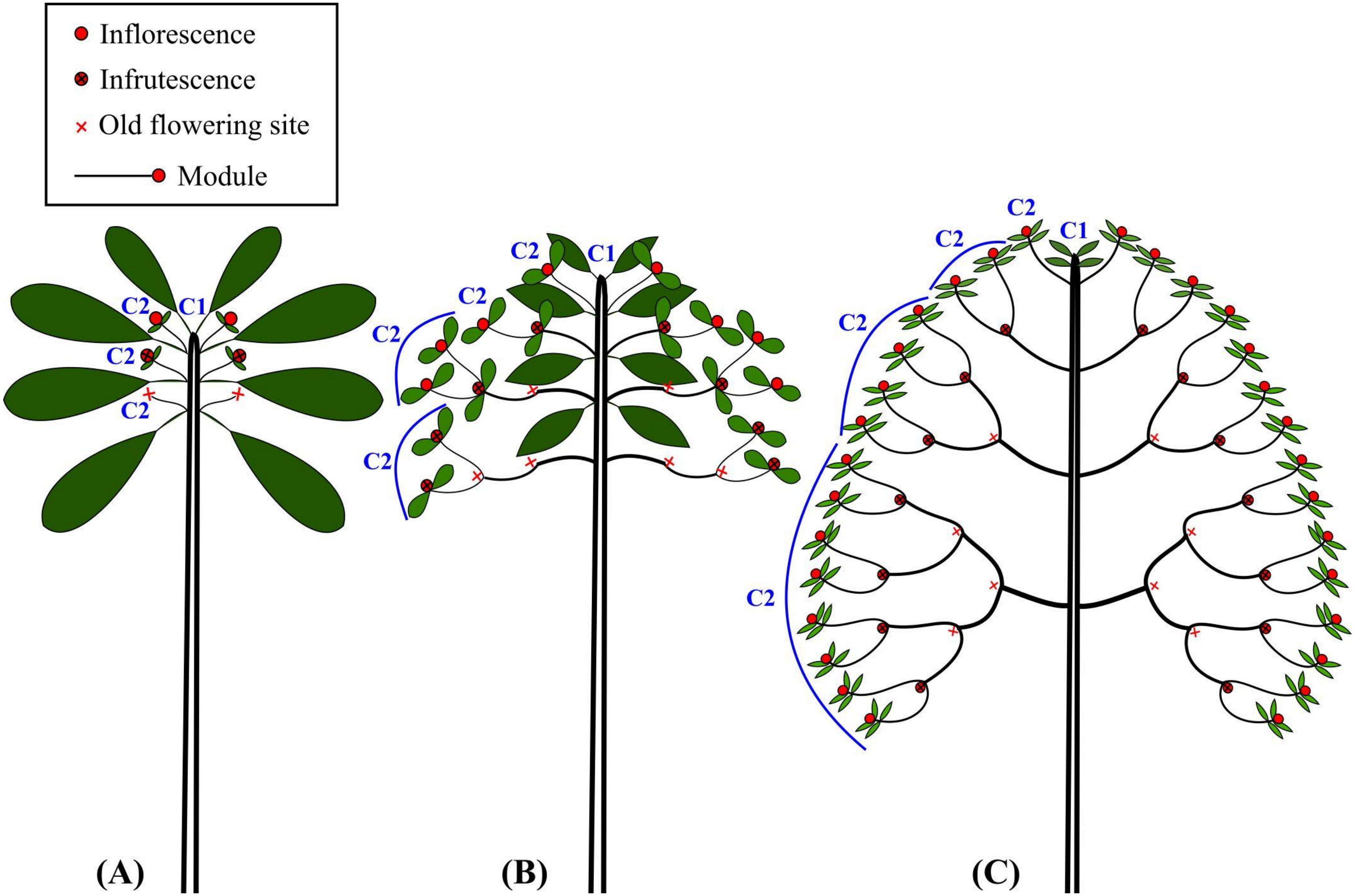

FIGURE 6.3 – Schematic representation of the three main architectural classes found in the rainforest understory species of *Atractocarpus*: **(A)** Monocaulous, **(B)** Intermediate **(C)** Branched.

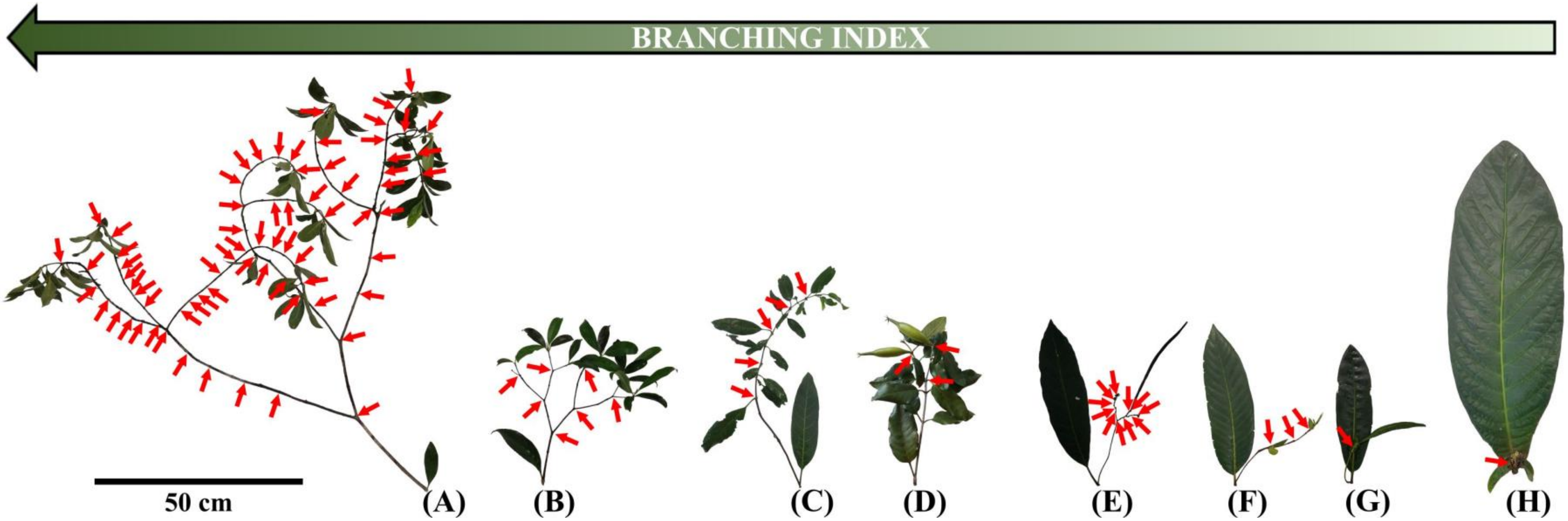

FIGURE 6.4 – Photographs of branches with their axillary leaves (i.e. from trunk) for height *Atractocarpus* species with different branching degrees. Arrows indicate apical death, i.e. flowering sites (for *A. longistipitatus* **(E)**, only half of apical death has been represented). Branched species: **(A)** *A. pseudoterminalis*, **(B)** *A.* sp. nov. 4. Intermediate species: **(C)** *A. ngoyensis*, **(D)** *A. brandzeanus*. Monocaulous species: **(E)** *A. longistipitatus*, **(F)** *A. pterocarpon*, **(G)** *A. bracteatus*, **(H)** *A. confertus*.

comprise a single long module (Figure 6.4). The number of internodes per module vary little in the genus but tend to be reduced in monocaulous species, with an extreme case of one node per module in *A. confertus* (Table 6.3). All species showed the ability to develop delayed reiterate on damaged or aged individuals.

6.3.3 Functional characterization

Phylogenetic signal varied substantially depending on which statistic was used (Lambda or Kappa, Table 6.4). This was probably due to the small size of our phylogeny (25 terminals), since the statistics differ in sensitivity to the number of terminals (Freckleton et al., 2002; Kamilar and Cooper, 2013). Blomberg's Kappa captures significant phylogenetic signal for stem specific density, proportion of pith, Huber value, and mean leaf area, whereas Pagel's Lambda captures significant signal for internode diameter (Table 6.4). Among all measured functional traits, only the branching index had a highly significant phylogenetic signal calculated with both Pagel's Lambda and Blomberg's Kappa.

Several functional traits were significantly related to the branching index (Table 6.5), including biomechanics (e.g., slenderness ratio, internode diameter) as well as photosynthesis (e.g. leaf area, SLA), hydraulics (e.g. Huber value), and even dispersal (fruit volume). These correlations between architecture and functions were confirmed by PCA and Permanova ($P = 0.016$), which showed significant differences between the functional space occupied by the three architectural classes (Figure 6.5). Intermediate species were confounded between the two other architectural classes, but monocaulous and branched species appeared to be functionally very different. In comparison to monocaulous species, branched taxa tend to have numerous small leaves, higher SLA, smaller fruits and, smaller internode diameters with a lower proportion of wood, but a higher wood area-leaf area ratio (Huber value). The monocaulous *A. confertus* (the lowest point on Figure

TABLE 6.4 – Phylogenetic signals of measured traits across the phylogeny of 25 *Atractocarpus* species (24 for fruit volume). Signal were tested with Pagel's Lambda (left) and Blomberg's Kappa (right). Bold lines represent significant phylogenetic signal following a 0.05 risk of error.

Trait	Lambda	p-value	Kappa	p-value
Branching index	**1.013**	**< 0.001**	**1.132**	**0.002**
Slenderness ratio	0.748	1	0.251	0.539
Specific wood density	0.447	1	0.429	0.242
Specific stem density	0.813	0.265	**0.607**	**0.029**
Internode diameter	**0.442**	**0.047**	0.533	0.076
Internode length	0	1	0.127	0.946
Proportion of pith	0.277	0.427	**0.603**	**0.021**
Proportion of wood	0.595	1	0.399	0.39
Proportion of cortex	0.488	1	0.418	0.27
Huber Value	0.589	0.998	**< 0.001**	**0.035**
Total leaf area	0.765	1	0.006	0.165
Leaf number	1.105	1	0.001	0.157
Mean leaf area	1.105	0.064	**0.031**	**0.003**
Specific Leaf Area	0	1	0.042	0.405
Fruit volume	0	1	0.002	0.356

TABLE 6.5 – Results of phylogenetical generalised least square. Bold lines represent significant relation between corresponding trait and branching index following a 0.05 risk of error.

Trait	log(L)	beta	p.value
Slenderness ratio	**-150.3**	**-3.1**	**0.004**
Specific wood density	-0.635	-0.003	0.157
Specific stem density	4.982	-0.0002	0.290
Internode diameter	**-35.90**	**-0.09**	**0.018**
Internode length	-85.30	0.3	0.169
Proportion of pith	0.397	0.03	0.112
Proportion of wood	**1.477**	**-0.0009**	**0.002**
Proportion of cortex	-2.600	-0.01	0.094
Huber value	**-295.9**	**3587**	**< 0.001**
Total leaf area	-282.5	288.8	0.351
Leaf number	**-165.2**	**37.2**	**< 0.001**
Mean leaf area	**-203.3**	**-85.6**	**0.008**
Specific Leaf Area	**-162.9**	**15.9**	**< 0.001**
Fruit volume	**-180.5**	**-3.8**	**0.021**

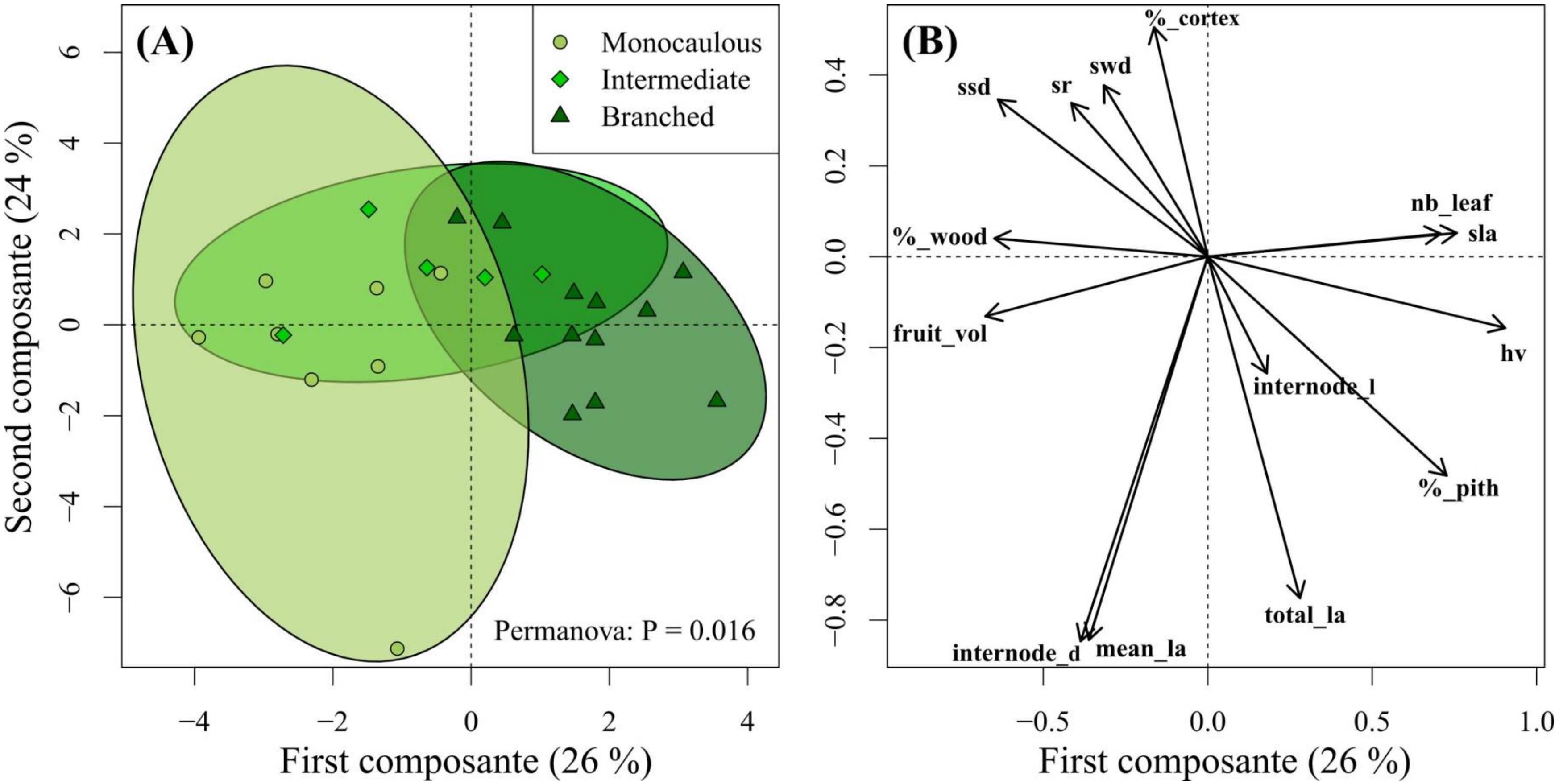

FIGURE 6.5 – Projection of **(A)** species and **(B)** traits on the two first axis of Principal Component Analysis (see Table 6.1 for trait abbreviations). Ellipses represent the 95% confidence interval for each architectural classes. Functional differences between architectural classes were tested with Permanova.

6.5) was distinct from the other *Atractocarpus* species examined in having numerous very large leaves, leading to a disproportionately higher total leaf area (up to 2.4 m^2 *versus* a mean of 0.5 m^2 for the other species).

6.3.4 Ancestral Character Estimation

All considered outgroup species belonged to the branched architectural class, except for the Fijian *Sukunia pentagonoides* (Seem.) A.C.Sm, which is monocaulous. Among the three possible models of evolution that fitted the data, the best supported one was that of equal transition rates between classes (ER), with an AICc of 84.4 versus 96.1 and 104.2 for SYM and ARD, respectively. According to this model, the ancestral architecture of *Atractocarpus* was most likely branched (probability = 0.98, Figure 6.6), and the monocaulous habit evolved two or three times in the two main New Caledonian clades (referred to as “monocaulous clade A” and “monocaulous clade B” in Figure 6.6), ca. 1.4 and 0.9-0.6 Myr ago respectively. In each clade, species with an intermediate architecture are closely related to monocaulous species, the only exception being *A. brandzeanus*, whose closest relatives are branched. Conversely, pairs of sister or closely related species never showed branched and monocaulous habit.

6.3.5 Trait based diversification

Following the IACc, models 2 and 10 are the best fitted, in which speciation and transition rates are equal for each state and extinction rates are equal or null (Table 6.2). This means that diversification was not greater among the members of any of the architectural classes during the evolution of *Atractocarpus* in New Caledonia.

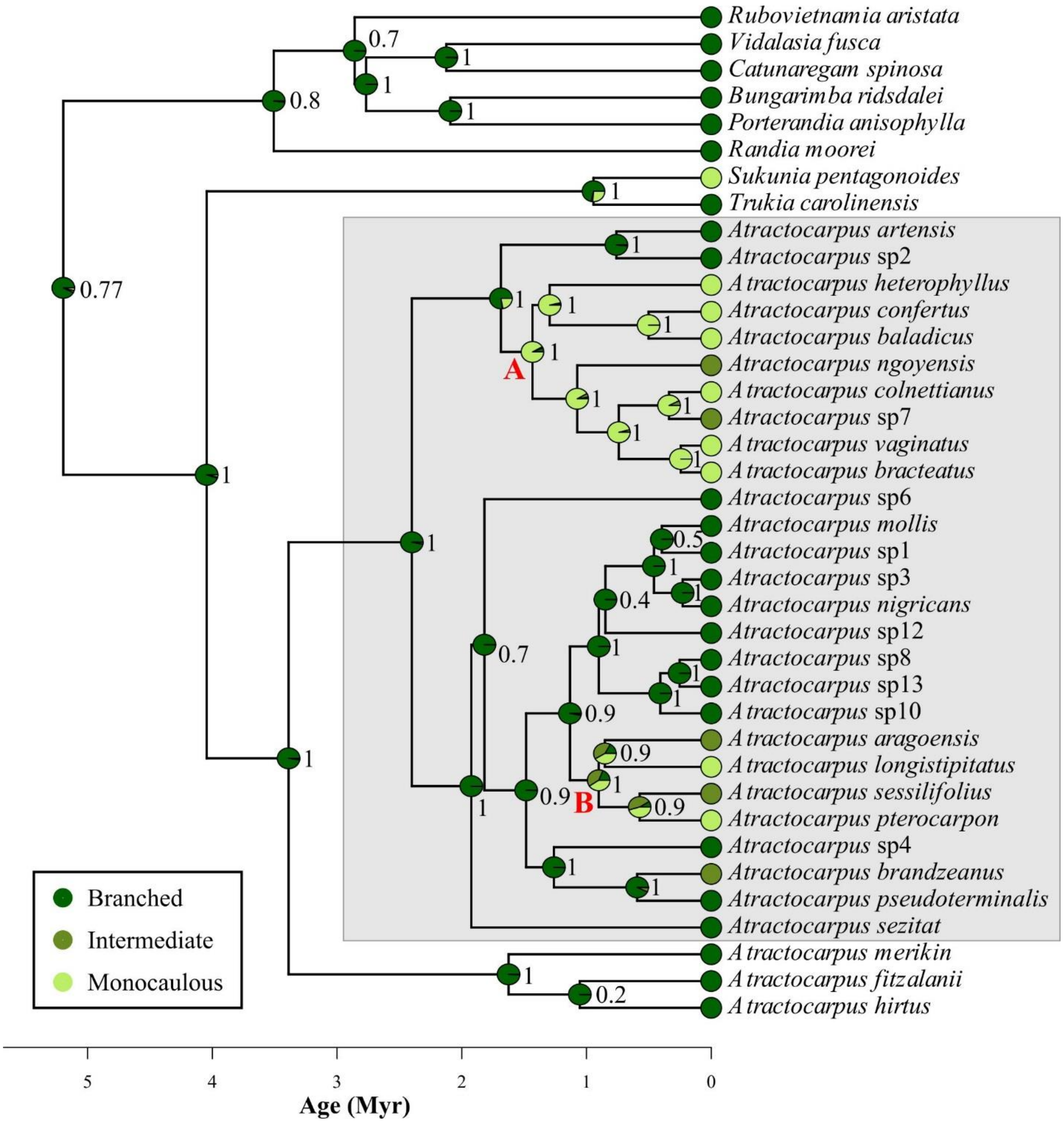

FIGURE 6.6 – Estimation of ancestral architectural class in the genus *Atractocarpus*. Numbers correspond to the Bayesian probability for each reconstituted node. Grey box highlights New Caledonian clade. Letters (A, B) highlight major clades were shifts from branched to monocaulous or intermediate architecture operate.

6.4 Discussion

6.4.1 Evolution of plant architecture

Despite the diversity of growth habits in the genus *Atractocarpus*, ranging from well branched to monocaulous species, the architectural construction of members of the group is fairly homogenous. Differences between species mainly result from quantitative variations in which the number of modules per branches and module length tend to increase with increasing branching index.

The measurement of functionally explicit variables (branch length and leaf area) that link plant architecture and function (Lauri, 1988; Lauri and Kelner, 2001; Charles-Dominique et al., 2017) showed that variation of growth habit in *Atractocarpus* is correlated with a gradual variation from branched species, for which photosynthesis and exploration are largely assumed by branches, toward monocaulous species, for which these functions are assumed by the trunk. The reduced C2 in monocaulous species supports a limited number of small leaves (on average 4 leaves of 9 cm^2) and are dedicated almost exclusively to reproduction. These “axes” are functionally closer to inflorescences than branches (Van Steenis, 1963) and are often considered as such by taxonomists (e.g. Fosberg et al., 1993; Puttock, 1999).

The branched architectural class appears to be ancestral in *Atractocarpus* and our results indicated at least two independent origins of monocauly in New Caledonia. Other examples of derived monocauly have recently been revealed in flowering plants (Chomicki et al., 2017; Barrabé et al., 2018). The intermediate architectural class is evolutionary closer to the monocaulous habit since intermediate and monocaulous species are always sister taxa or very close relatives. There is a high probability that the putative ancestor of “monocaulous clade B”, had an intermediate architecture. This insight, as well as the architectural gradient observed among extant species, suggests a gradual evolutionary transition from the branched architecture toward monocauly through an intermediate architectural class. Reversion from a monocaulous architecture toward an intermediate one appears to have been possible (e.g. *Atractocarpus* sp. nov. 7) but full reversion to a branched architecture was not observed.

The similarity of developmental origin and the gradual quantitative architectural variation of lateral axes (C2) across closely related taxa suggest a homologous origin of these axes in the *Atractocarpus* species studied here (see Nozeran, 1955; Rossignol and Rossignol, 1985; Haicour et al., 1989). A homologous origin between vegetative and inflorescence axes has been suspected in several groups such as Ranunculaceae and Papaveraceae (Stebbins, 1973), as well as several families of Alismatales (Posluszny and Charlton, 1993, 1999) and Pandanales (Rudall and Bateman, 2006), though none of these studies combined architectural analysis with molecular phylogenetic results.

Only a few studies to date have explored evolutionary links between architectural models (see Chomicki et al., 2017). In New Caledonia *Atractocarpus*, we found recurrent transitions from Stone's model for branched species (with C2 functioning as branches) to Corner's model for monocaulous species (with C2 functioning as inflorescences), although the limit between them remains fuzzy, as illustrated by species whose architecture is intermediate. The variation observed in branching index across species illustrates an 'architectural continuum' (Oldeman, 1974; Barthélémy et al., 1989) rather than saltational evolution involving rapid and profound change in architecture (Bateman and DiMichele, 1994; Bateman, 1999). Nothing suggests that the intermediate architectural class confers lower fitness (i.e., represents a fitness valley) compared to monocaulous or branched architecture, particularly in situations where the environment (rainforest understory) varies gradually. Saltation from one model to another might take place when gradual changes are impossible, for example in the colonization of contrasted habitats (Bateman and DiMichele, 1994). Gradual variation between and within models has already been noted (Hallé et al., 1978), suggesting that preferential transition between models might occur.

The two independent origins of monocauly inferred in *Atractocarpus* illustrate two different evolutionary pathways involved in the transition from branches into inflorescences. In “monocaulous clade A”, reduction in the branching index occurred through a reduction in the number of modules, while in “monocaulous clade B”, module length is involved. Architectural analysis actually showed that the two species with intermediate architecture and the two monocaulous species belonging to the clade B are those with the higher number of modules (up to 46 for the intermediate *A. sessilifolius* and 26 the for monocaulous *A. longistipitatus,* i.e. as much as certain branched species) and with shorter module length (excluding the monocaulous *A. confertus*). This type of morphological reduction observed at the module level in *Atractocarpus* could affect any elementary level of organization in other plant groups (e.g. annual shoots, growth units, metamers, etc.).

The iterative gradual transition of axillary structure (C2) from branches to inflorescences occurs as a functional reduction of vegetative growth and a change in the timing of flowering. Such evolutionary changes, often result from growth heterochrony (Smith, 2001). In the case of New Caledonian *Atractocarpus*, the axillary structure (C2) of descendants is either a truncated part (in “monocaulous clade A”) or a miniaturized copy (in “monocaulous clade B”) of that of their ancestors. This suggests heterochronic evolution through “neoteny” in the first case and through “proportional dwarfism” in the second (Gould, 1977; Alberch et al., 1979; Smith, 2001), but more details of the ontogenetic sequences are required to test these hypotheses in *Atractocarpus*.

In this context, our original approach showed that a careful study of low organization levels is needed to depict the evolution of plant architecture. This involves a deep characterization of architectural units (Edelin, 1977, 1984), combining qualitative and quantitative traits.

6.4.2 Branching index, Corner's rules, and ecological strategies

In the original *Durian theory*, Corner (1949, 1953-1954) proposed two fundamental rules governing plant morphology: (i) *Axial conformity*, stipulating that "the stouter, or more massive, the axis in a given species, the larger and more complicated its appendages"; and (ii) *Diminution on ramification*, stipulating that "the greater the ramification, the smaller become the branches and their appendages". *Axial conformity* is by far the most studied since the leaf size - twig size and fruit size - leaf size spectra are among the best-documented (White, 1983b; Bond and Midgley, 1988; Brouat et al., 1998; Cornelissen, 1999; Brouat and McKey, 2001; Westoby et al., 2002; Preston and Ackerly, 2003; Westoby and Wright, 2003; Pickup et al., 2005; Sun et al., 2006; Normand et al., 2008). Large leaves and fruit carried by a large single stem, as seen in monocaulous species, illustrate one extremity of this spectrum.. The second rule (*diminution of ramification*), has received much less consideration (but see White, 1983a; Ackerly and Donoghue, 1998). Our results agree with this statement, as we have shown that internode diameter, as well as fruit and leaf size, are negatively correlated with branching index, even with phylogenetic corrections. Beyond Corner's rules, we found a strong correlation between branching index and several functional traits related to various ecological strategies in areas with a similar habitat (i.e. rainforest).

We found that branching index tends to be correlated with ecologically important dimensions (Mooney, 1972; Grime, 1974; Grime et al., 1988; Westoby et al., 2002). The large leaves of monocaulous species increase light interception in shady understory (Poorter, 1999; Rozendaal et al., 2006), their low SLA and Huber value are likely associated with low photosynthetic capacity (Field and Mooney, 1986; Shipley et al., 2005; Poorter and Bongers, 2006; Rozendaal et al., 2006; Pérez-Harguindeguy et al., 2013) and their small internode length can result from a slow growth rate (Mooney, 1972; Chuah, 1977; Grime et al., 1988; Westoby et al., 2002). Monocaulous species are likely skewed toward a high resource conservation strategy (Grime et al., 1997; Díaz et al., 2004; Díaz et al., 2016) suited to the shady understory of rainforest.

In sparsely branched to unbranched species, a distal part of the stem with thicker diameter and higher wood proportion was found to be suited to supporting large and numerous energetically costly leaves (higher leaf area and SLA). However, higher wood area does not fully compensate for high total leaf area of the main stem since the Huber value (the ratio of wood area to leaf area) was positively correlated with branching index. Detailed anatomical studies, particularly on vessel size and density, are needed to understand the hydraulic and mechanical trade-off involved in the pervasive link between leaf area, stem thickness and branching intensity (Lehnebach et al., 2018).

6.4.3 Divergence and ecological opportunities in New Caledonian rainforests

New Caledonian *Atractocarpus* appear to be the result of a single colonization event (Mouly et al., *submitted*) and the archipelago is the center of diversity for the genus. Island colonization is a two steps process involving dispersal and successful establishment (Silvertown, 2004). The large, fleshy fruits of *Atractocarpus* suggest a rather limited ability for long-distance dispersal. Such niche preemption, claimed to act as a major driver of monophyly and diversification in island floras (Silvertown, 2004), could have prevailed in the diversification of the New Caledonian clade of *Atractocarpus*. Its young age (estimated at 2.4 My) coincides with colonization during late Pleistocene, a period of intense climatic Fluctuation (Bowler et al., 1976; Hope and Pask, 1998; Stevenson and Hope, 2005). Increasing evidence supports the persistence of taxa in rainforest refugia during the Pleistocene in New Caledonia (Pintaud et al., 2001; Pillon, 2012;

Nattier et al., 2013; Poncet et al., 2013; Pouteau et al., 2015; Tournebize et al., 2017). Climatic fluctuations causing expansion and contraction of rainforests could also have offered ecological opportunities for new colonizers. Other diversified rainforest clades in New Caledonia have been shown to result from recent colonization (e.g. palms, Pintaud et al., 2001; Pillon, 2012). Similarities in form and physiology among close relatives, as suggested by our character state reconstruction and architectural analysis, are suggested to involve intense competition that favors divergence among locally coexisting species (Givnish, 2016). In support of this, we found notable variation in module length and number between sisters species, even when they belong to the same architectural class. In *Atractocarpus,* variation in growth habit is correlated with a gradual switch in assimilation function from branches to trunk, and is associated with a vertical differentiation of major functions. Leaf arrangement in monocaulous species results in important overlap that impacts photosynthesis, while stem slenderness suggests a rather small structural investment in vertical support. Branched species tend to increase light harvesting and reduce leaf overlap (via increase branch length), a strategy that require more investment in stem tissue (Givnish, 1995), as allocation to non-leaf structures might increase with ramification. *Atractocarpus* species thus exhibit a gradient of foraging for light in which leaf size and disposition vary with branching index.

New Caledonian rainforests are characterized by a low canopy (ca. 20 m) and trees with small crowns (Blanchard et al., 2016), two structural features that increase the number and intensity of sunflecks (Chazdon and Pearcy, 1991). A low canopy and its corollary, reduced forest stratification, could result in stronger competition within a given stratum. These forest features (high sunfleck variability, reduced stratification) favor niche partitioning through a gradient in architecture and related functional traits. Moreover, limited dispersal of the large fruits of *Atractocarpus* might interact with niche partitioning to promote divergent evolution. Finally, divergent selection may be especially favored in permissive environments where competition prevails over the external environment or in the colonization of islands where resources are underutilized (Givnish, 2016). New Caledonia exhibits both components of divergent selection: (i) climatically permissive rainforests and (ii) ecological opportunities offered by recent climatic fluctuations. Divergent selection, caused by competition among closely related taxa, leads to adaptive radiation, i.e. the rise of a diversity of ecological roles and related adaptations in different species among a lineage (Givnish, 2016). The theory of niche pre-emption holds that adaptive radiation creates a barrier that inhibits the establishment of closely related taxa, thus reducing the likelihood of repeated colonization.

6.4.4 Conclusions

Despite the fundamental importance of plant architecture, little work has been done to integrate this aspect into key domains of plant science such as evolution and functional ecology. However, increasing availability of information on ecologically important traits and molecular phylogenies provides a basis for testing and developing new concepts. Our study clearly highlights evolutionary processes behind architectural transitions and their link to plant ecological strategy and perhaps also to diversification. We have shown that gradual transition from one architecture to a very different one is possible through morpho-functional reduction of morphological units. Quantifying plant architecture through functional indexes appears to offer a promising avenue toward further understand the implications of architectural variation on plant fitness under different environmental conditions. Based on such an index, our study provides a functional definition of monocauly that is ecologically and evolutionary more explicit than one based solely on physiognomy (cf. Hallé et al., 1978; Chomicki et al., 2017): we define monocaulous species as self-supporting woody plants whose cardinal functions (e.g., assimilation and exploration) rely on a single apparent stem.

Although our work focused on a small clade, it opens new perspectives and proposes a general framework for further understanding evolution of plant architecture and its functional implications in other plant groups and other geographical areas, and at larger scales. We believe that Pleistocene climatic fluctuations have played a major role in the evolution of monocauly and more widely in shaping the current diversity of the New Caledonian flora. This hypothesis now needs to be tested at a larger phylogenetic scale in New Caledonia, as the monocaulous habit, which occurs repetitively in many different groups (Veillon, 1976; Schmid, 1979, 1990), has much to offer to understand the evolution, biogeography and ecology of this “very old Darwinian island” (Grandcolas et al., 2008).

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Chapter 7 — Back to Corner: functional characterization and leaf – stem scaling in monocaulous plants

In preparation article

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7.1 Introduction

Monocauly (i.e. unbranched habit) in woody plants is a globally rare phenomenon but represents a case of evolutionary convergence (Chapter 5) that has much to offer to our understanding of metabolic implications and selective advantage of large leaves and limited branching patterns (Chapter 6). Monocaulous plants have a single apparent woody stem with large leaves concentrated toward the apex (Corner, 1949; Hallé et al., 1978). They conform to four architectural models (Corner's, Holttum's, Chamberlain's and Cook's) (Chapter 5). Thus, while the vast majority of woody growth habits (e.g. tree, treelets, lianas) present several more or less specialized axis (axis categories, see Barthélémy and Caraglio, 2007), the cardinal functions (photosynthesis, water transport, mechanics, storage) are carried by a single stem in monocaulous plants (Chapter 6). This particular architectural design might entail a stronger interdependence of traits and contrasting functional behavior of stems and leaves compared to branched species. Though, morpho-anatomical traits of woody monocaulous plants have virtually not been investigated (but see Chapter 6) and their functional characteristics remain unclear.

Strategic dimensions given by correlation of two or more ecologically important traits (Westoby et al., 2002; Westoby and Wright, 2003; Wright et al., 2004; Wright et al., 2007; Osnas et al., 2013; Olson et al., 2018) are considered as main drivers of plant evolution and functional diversity worldwide (Díaz et al., 2004; Poorter and Bongers, 2006; Díaz et al., 2016). As such, identifying extreme points in these multivariate correlations of functional traits should bring strong insights into the selective advantage of increasing some leading dimension. As an ultimate state of branch reduction, the monocaulous habits stand out at the extremity of the branching order – leaves size spectrum known as an element of Corner's rules (Corner, 1949, 1953-1954). The second statement of Corner's rules, "diminution on ramification", indeed proposed that "the greater the ramification, the smaller become the branches and their appendages" (Corner, 1949). This statement has however been poorly investigated (but see White, 1983a; Ackerly and Donoghue, 1998; Westoby and Wright, 2003, Chapter 6).

A more widely studied spectrum is the leaf size – twig size spectrum (Westoby and Wright, 2003), also known as leaf – stem scaling (e.g. Yang et al., 2009). It corresponds to the first statement of Corner's rules, i.e "axial conformity", proposing that "the stouter, or more massive, the axis in a given species, the larger and more complicated its appendages" (Corner, 1949). It arises from the observation of Sinnott (1921) and Corner (1949) on the general correlation between individual leaf size and pith (i.e. primary meristem size) or stem diameter respectively. This relationship, confirmed by numerous studies (White, 1983b, a; Bond and Midgley, 1988; Brouat et al., 1998; Cornelissen, 1999; Brouat and McKey, 2001; Preston and Ackerly, 2003; Westoby and Wright, 2003; Sun et al., 2006; Normand et al., 2008, Chapter 6), has been extended to twig or plant levels as the foliage – stem scaling (e.g. Brouat et al., 1998; Sun et al., 2006; Olson et al., 2009; Smith et al., 2017; see Lehnebach et al., 2018). If the universality of these relationships is obvious, the functional relations linking foliage area and stem area, and individual leaf area and stem area, remain poorly debated. Leaf area and stem diameter are alternatively linked by hydraulic (Chuah, 1977; White, 1983a; Preston and Ackerly, 2003; Sun et al., 2006; Normand et al., 2008), mechanic (White, 1983a; Niklas, 1992; Normand et al., 2008; Olson et al., 2009; Levionnois et al., 2018a) and photosynthesis (Primack, 1987; Cornelissen, 1999) functions. Attempts to identify the relative importance of each function remain scarce (Normand et al., 2008; Levionnois et al., 2018a). This debate needs further anatomical studies to quantify the structure-function relationships responsible for foliage – stem scaling (Lehnebach et al., 2018, Chapter 6).

The selective advantage of monocauly in rainforest has been questioned by several authors (e.g. Richards, 1966; D'Arcy, 1973). Some insights suggest that sparsely-branched trees with large leaves are fast-growing and preferentially growth in first stage of forest succession (White, 1983a; Ackerly, 1996). By contrast, in forest understory, monocaulous species might not benefit from growth advantage but would rather exhibit a conservation resource strategy compared to their branched relatives (Chapter 6). Anatomical properties of monocauls has mainly been investigated in rosette-tree and rosette-shrub species through the phenomenon of secondary woodiness. These plants appeared to have large pith and cortex (Carlquist, 1974; Mabberley, 1974a; Hallé et al., 1978; Meinzer and Goldstein, 1986; Mosbrugger, 1990) and thin wood characterized by an important proportion of parenchyma (Carlquist, 1962; Mabberley, 1974a; Aldridge, 1978; Mosbrugger, 1990). But these anatomical features seem different from some rainforest monocaulous species, which showed a thick cylinder of dense wood and have not evolved from herbaceous ancestors (Chapter 6).

In this study, we compared functional traits, from micro-anatomical to whole plant scale, of monocaulous species and their branched relatives growing in the understory of New Caledonian rainforest. This site was selected because of the exceptional diversity in monocaulous plants providing a wide phylogenetic spectrum for the selection of species (Chapter 5). Our aim was to compare the functional strategy of monocaulous plants with closely related species using several dimensional traits associated with mechanical, hydraulic and physiological functions. Monocaulous species were also compared to the TRY Plant trait Database (Kattge et al., 2011) for important trait coordination. Through multi-level anatomical investigation (from cell to tissue) we also investigated the functional explanation of the universal leaf – stem and foliage – stem scaling.

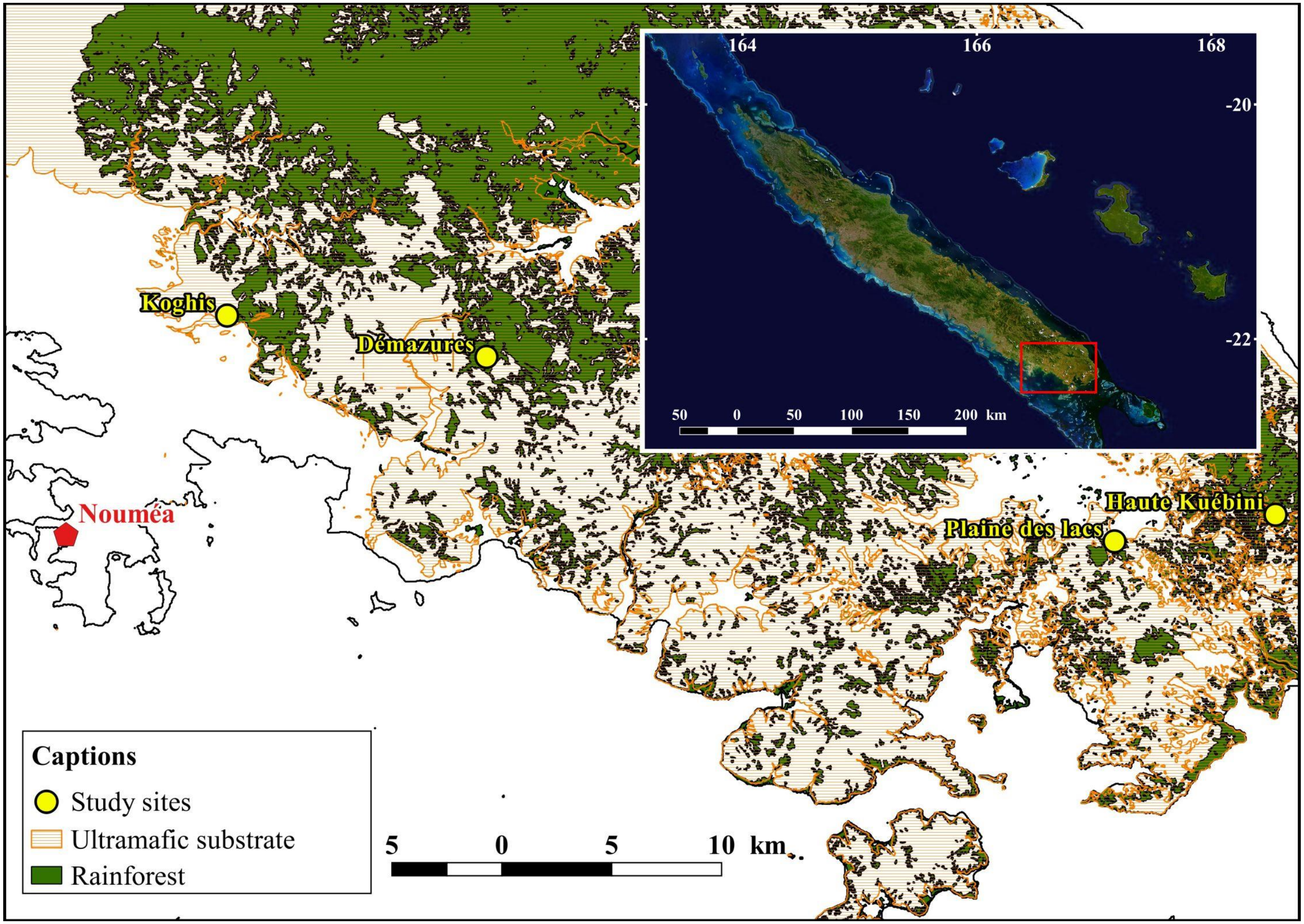


FIGURE 7.1 – Map of New Caledonia and location of study sites in the South of main island. Layer of Ultramafic substrate from DIMENC/SGNC-BRGM (2010). Layer of rainforest from Birnbaum et al. (unpublished data).

TABLE 7.1 – List of sampled taxa, study sites and architectural models. Asterisks indicate monocaulous architectural models.

Taxon	Family	Voucher	Study site	Architectural model
Atractocarpus bracteatus Schltr. & K.Krause	Rubiaceae	Bruy 133	Plaine des lacs	Corner*
Atractocarpus ngoyensis (Schltr.) Mouly		Bruy 139	Plaine des lacs	Stone
Melicope lasioneura (Baill.) Baill. ex Guillaumin	Rutaceae	Bruy 137	Plaine des lacs	Corner*
Melicope glaberrima Guillaumin		Bruy 597	Koghis	Rauh
Litsea ripidion Guillaumin	Lauraceae	Bruy 610	Haute Kuébini	Corner*
Litsea triflora Guillaumin		McPherson 4599	Haute Kuébini	Rauh
Bocquillonia spicata Baill.	Euphorbiaceae	Bruy 131	Plaine des lacs	Corner*
Bocquillonia rhomboidea (Schltr.) Airy Shaw		Bruy 229	Plaine des lacs	Aff. Koriba
Cleidion lasiophyllum Pax & K.Hoffm.	Euphorbiaceae	Bruy 169	Démazures	Corner*
Cleidion vieillardii var. *vieillardii* Baill.		Bruy 140	Plaine des lacs	Rauh
Phelline comosa Labill.	Phellinaceae	Bruy 604	Plaine des lacs	Corner*
Phelline lucida Vieill. ex Baill.		Bruy 414	Koghis	Rauh
Tapeinosperma gracile Mez	Primulaceae	Bruy 172	Démazures	Corner*
Tapeinosperma robustum Mez		Bruy 122	Koghis	Rauh
Balanops pancheri Baill.	Balanopaceae	Bruy 132	Plaine des lacs	Chamberlain*
Balanops vieillardii Baill.		Pillon 610	Koghis	Aff. Koriba
Pittosporum pronyense Guillaumin	Pittosporaceae	Bruy 164	Plaine des lacs	Chamberlain*
Pittosporum deplanchei Brongn.& Gris		Bruy 607	Haute Kuébini	Leeuwenberg
Phyllanthus francii Guillaumin	Phyllanthaceae	Bruy 128	Plaine des lacs	Cook*
Phyllanthus koghiense Guillaumin		Bruy 603	Koghis	Roux

7.2 Material & methods

7.2.1 Study site and sampling

Located in the Southwest Pacific Ocean (20-23 °S, 164-167 °E, Figure 7.1), New Caledonia benefits from a subtropical climate (Maitrepierre, 2012). The study was undertaken in four locations in the southern part of the main island (*Grande Terre*, Figure 7.1) in understory of evergreen rainforest of low and mid-elevation on ultramafic substrate (Jaffré et al., 2012). All sites were on ferralitic soils (i.e. Ferralsols) overlying peridotite. These soils are characterized by low concentration of P, K, and Ca, imbalanced Mg/Ca ratio, high concentration of potentially bioavailable toxic trace elements (Ni, Mn, and low ion exchange capacity; Jaffré, 1993; L'Huillier and Edighoffer, 1996; Isnard et al., 2016). These locations were chosen because all taxa are abundant, allowing more reliable comparisons. Elevation ranged from 200 m (*Haute Kuébini*) to 550 m (*Koghis*) and mean annual pluviometry from 2200 mm.yr^{-1} (*Koghis*) to 3000 mm.yr^{-1} (*Plaine des Lacs*) (Météo-France, 2007).

Twenty species in 10 different genera were sampled (one monocaulous and one branched species in each genus). To ensure phylogenetical independence of results, each genus was selected from different families covering seven orders (Table 7.1). Only genera *Bocquillonia* and *Cleidion* belong to the same family (Euphorbiaceae) but belong to different tribes (Wurdack et al., 2005).

Five individuals per species were sampled between September 2016 and Mars 2017. In order to limit ontogenetic effect and allow for reliable comparison, selection of individuals was standardized as follows: (i) recently mature individuals were selected based on the observation of inflorescences/fruits or scars, (ii) only non-reiterated individuals (see Oldeman, 1974; Barthélémy and Caraglio, 2007) and (iii) non-traumatized trunks were selected. Fully expanded leaves were sampled in distal parts of the plants (Figure 7.2). All samples (Figure 7.2) were placed in hermetic

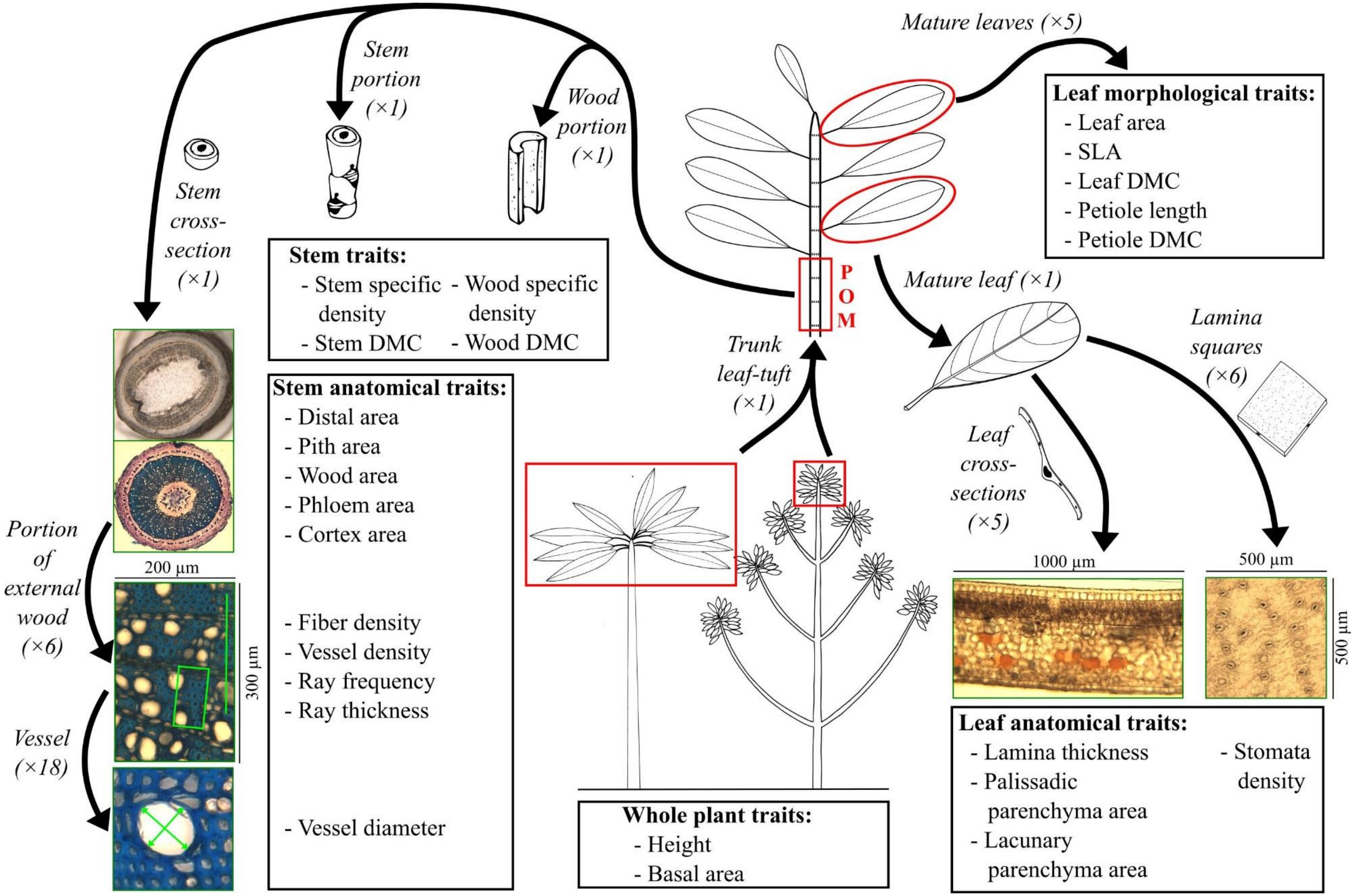


FIGURE 7.2 – Summary of sampling procedure and trait measurement protocol. DMC: Dry Matter Content, POM: Point of Measurement, SLA: Specific Leaf Area.

bags, and stored in a cool and wet environment during transportation to the lab. Measurements were carried within max. 24 hours after sampling. Leaves were not separated from stem until measurement.

7.2.2 Traits analyzed

All traits (Table 7.2) were measured from five individual per species (Figure 7.2). Whole plant stem traits (plant height and basal area) were measured *in situ* with a measuring tape, a caliper and eventually a TRUPULSE 360R Telemeter for taller plants.

For the measurement of leaf traits, fresh mass of lamina were measured with a precision balance. Length of petioles (PL) was measured with a measuring tape. Leaf laminas (petiole removed) were scanned at 300 pp and leaf area (LA) was calculated with the *imageJ* software through the *LeafArea* package for R (Masatoshi, 2017). Laminas were dried at 50 °C for 72 hours and their dry masses were measured to calculate specific leaf area (SLA) and leaf dry matter content (LDMC).

For the measurements of stem traits, sampling was done at Point Of Measurement (POM) which is located directly under the trunk leaf-tuft (Figure 7.2). This POM was selected because (i) branched and monocaulous species could only be compared for trunks, (ii) it makes a direct link between stem anatomy and distal leaf traits (e.g. Huber Value) and (iii) distal parts of the plant are supposed to be approximately of same age. The portion of stem situated at POM (5-6 cm long) was sampled and separated in (i) one 2-3 cm long portion of stem, (ii) one 2-3 cm long portion of wood (pith and cortex pulled-out), (iii) one cross-section of stem used for anatomical measures (see below) (Figure 7.2). The fresh and dried (at 50°C for 72h) mass, and fresh volume (using the water displacement method) of stem and wood portion were measured to calculate Stem Specific Density (SSD), Stem Dry Matter Content (SDMC) and Wood Specific Density (WSD) (see Table 7.2 for trait values calculations). For leaf anatomical measurements, one leaf per individual was measured (Figure 7.2). Procedure followed the IAWA requirements as close as possible (Wheeler et al., 1989; Baas et al., 2004). Anatomical characters were investigated through freehand cross-sections on material fixed in 70 % ethanol. To examine photosynthetic and non-photosynthetic tissues of the limb, unstained transversal cross-sections (Figure 7.2) were mounted in water. Leaf thickness (LT) and area of palisade and spongy mesophyll were measured on five 1000-µm-wide fields of view. Stomata density (SD) was measured from leaf impression (nail polish) of a lamina, avoiding veins, on six fields of view of 250000 µm². For all observations we used a Leica DM5000B binocular microscope or Leica M165C stereo microscope depending on anatomical elements. Both were mounted with a Leica EC3 camera for photography. Traits were measured from photographs with the *imageJ* software (Schneider et al., 2012). The two species of *Bocquillonia* presented too much ornamented leaf abaxial epiderm to enable leaf impression; in this case, stomata density was measured on photographs performed with scanning electron microscope (FEI Quanta 200 FEG).

Leaf anatomical traits (Figure 7.2, Table 7.2) have not been measured yet on all sampled species. LT, ratio of palisade mesophyll area to spongy mesophyll area (PSR) and SD was only measured on genera *Atractocarpus* (Rubiaceae), *Bocquillonia* (Euphorbiaceae), *Litsea* (Lauraceae), *Phelline* (Phellinaceae) and *Tapeinosperma* (Primulaceae). The five other genera will be measured subsequently to complete the dataset.

For stem anatomical traits (Figure 7.2, Table 7.2), different scales were used. Macro-anatomy (cross-sectional area, area of pith, wood, phloem and cortex) was measured regarding the total cross-section either with stereo microscope (in this case, section was finely sanded) or binocular microscope depending on stem size. For micro-anatomy, approximately 30-µm-thick transverse sections were made with a vibratome (Microm HM650V) and were prepared according

TABLE 7.2 – List of measured traits. References are given to justify the interest of each trait for corresponding functions. n=replicate(s) per individuals

Trait	Abbreviation	n	Units	Formula	Related function	References
Whole plant traits						
Slenderness ratio	SR	1	Ø	$\frac{Plant\ height}{Plant\ basal\ diameter}$	Geometric feature of buckling resistance	Alméras et al. (2004); Niklas et al. (2006); Homeier et al. (2010)
Tapering	T	1	$cm.m^{-1}$	$\frac{Basal\ diameter - Distal\ diameter}{Plant\ height}$	Geometric feature of buckling resistance	Poorter and Werger (1999); Niklas (2000)
Huber value	HV	1	Ø	$\frac{Wood\ area\ at\ POM}{Mean\ leaf\ area\ \times Nb\ of\ leaf\ above\ POM}$	Allocation of wood to leaf area deployed	Penfound (1931); Gleason et al. (2012); Pérez-Harguindeguy et al. (2013)
Apical (POM) stem traits						
Distal stem area	S_{area}	1	µm²	Ø	Mechanical reinforcement (geometrical)	Vertessy et al. (1995); Westoby and Wright (2003); Olson et al. (2009)
Pith area	P_{area}	1	µm²	Ø	Primary stem diameter	Sinnott (1921); Eggert (1961); Chapter 6
Stem dry matter content	SDMC	1	Ø	$\frac{Stem\ dry\ mass\ at\ POM}{Stem\ fresh\ mass\ at\ POM}$	Growth rate, mechanical reinforcement	Shipley and Vu (2002); Pérez-Harguindeguy et al. (2013)
Specific stem density	SSD	1	$g.cm^{-3}$	$\frac{Stem\ dry\ mass\ at\ POM}{Stem\ fresh\ volume\ at\ POM}$	Growth rate, capacitance, mechanical reinforcement	Pérez-Harguindeguy et al. (2013);

						Díaz et al. (2016)
Proportion of pith	$Pith_p$	1	Ø	$\frac{Area\ of\ pith}{Whole\ section\ area}$	Primary growth, stem biomechanics	Carlquist (1974); Niklas (1992); Levionnois et al. (2018)
Proportion of wood	$Wood_p$	1	Ø	$\frac{Area\ of\ wood}{Whole\ section\ area}$	Secondary growth, stem biomechanics	Penfound (1931); Schuerger et al. (1997); Hummel et al. (2007)
Proportion of phloem	$Phloem_p$	1	Ø	$\frac{Area\ of\ phloem}{Whole\ section\ area}$	Photosynthate exchange	Ewers and Fisher (1991); Hölttä et al. (2009); Santini et al. (2012)
Proportion of cortex	$Cortex_p$	1	Ø	$\frac{Area\ of\ cortex}{Whole\ section\ area}$	Storage	Pérez-Harguindeguy et al. (2013)
Apical (POM) wood traits						
Specific wood density	WSD	1	$g.cm^{-3}$	$\frac{Wood\ dry\ mass\ at\ POM}{Wood\ fresh\ volume\ at\ POM}$	Growth rate, drought resistance and mechanical reinforcement	Pérez-Harguindeguy et al. (2013); Wright et al. (2007); Olson et al. (2009)
Fiber density	FD	6	μm^{-2}	Ø	Wood mechanical resistance	Baas et al. (2004); Beeckman (2016)
Vessel diameter	V_d	18	μm	$\sqrt{(major\ vessel\ diameter} \times minor\ vessel\ diameter)$	Hydraulic efficiency / cavitation risk	Sperry et al. (2007); Beeckman (2016); Hacke et al. (2017)
Vessel density	VD	6	μm^{-2}	Ø	Hydraulic efficiency / cavitation risk	Zanne et al. (2010); Hacke et al. (2017);

						Levionnois et al. (2018)
Hydraulically weighted mean vessel diameter	Dm	1	μm^2	$\frac{\sum_{Vessel=1}^{18} Vd^5}{\sum_{Vessel=1}^{18} Vd^4}$	Hydraulic efficiency	Tyree et al. (1994); Kolb and Sperry (1999); Ewers et al. (2000))
Theoretical conductivity	K_{th}	1	$kg.m^{-1}.s^{-1}.MPa^{-1}$	$\pi \times \sum_{Vessel=1}^{18} \frac{Vd^4}{128 \times \eta}$	Hydraulic efficiency	Tyree and Zimmermann (2002); Martinez-Cabrera et al. (2011)
Theoretical specific conductivity	K_{s-th}	1	$m^4.MPa^{-1}.s^{-1}$	$Kth \times VD \times Wood\ area$	Hydraulic efficiency	Pfautsch et al. (2018)
Ray frequency	RF	6	μm^{-1}	Ø	Exchanges, Carbon storage	Morris et al. (2016); Plavcová et al. (2016); Carlquist (2018)
Ray thickness	RT	1	Nb of cells	Ø	Exchanges, Carbon storage	Morris et al. (2016); Plavcová et al. (2016); Carlquist (2018)
Leaf traits						
Mean Leaf area	LA	5	m^2	Ø	Energy balance, hydraulic demand, mechanical constriants	Poorter et al. (2009); Pérez-Harguindeguy et al. (2013); Ackerly (2004)
Specific Leaf Area	SLA	5	$m^2.g^{-1}$	$\frac{Fresh\ lamina\ area}{Leaf\ dry\ mass}$	Allocation of biomass to light harvesting; growth rate	Pérez-Harguindeguy et al. (2013); Westoby et al. (2002)

Leaf dry matter content	LDMC	5	Ø	$\frac{Leaf\ dry\ mass}{Leaf\ fresh\ mass}$	Structural allocation; growth rate	Hodgson et al. (2011); Pérez-Harguindeguy et al. (2013)
Petiole length	PL	5	cm	Ø	Reducing autoshading; leaf mechanic	Takenaka (1994); Weijschedé et al. (2007)
Lamina thickness	LT	5	µm	Ø	Photosynthetic rate; leaf mechanic	Díaz et al. (2004); Pérez-Harguindeguy et al. (2013)
Ratio of leaf parenchyma	PSR	5	Ø	$\frac{Palisade\ mesophyll\ area}{Spongy\ mesophyll\ area}$	Hydraulic capacity; Gaz exchange	Grubb et al. (1975); Sack and Frole (2006); Terashima et al. (2011)
Stomata density	SD	6	µm^{-2}	Ø	Gaz exchange	Grubb et al. (1975); Farquhar and Sharkey (1982); Xu and Zhou (2008)

to the following protocol: (i) 10-20 minutes in 20% bleach to decolorize tissues, (ii) 5 minutes in water to remove bleach, (iii) 2 minutes in acetic acid to facilitate colorant fixation, (iv) 5-10 seconds in Toluidine blue to colorize different tissues and (v) fast rinsing with water. The external portion of wood were photographed to measure wood anatomical traits. Vessel density (VD) was measured in six 60000 µm² fields of view. Fiber density (FD) was measured in six 5000 µm² fields of view. Ray frequency (RF) was measured as the number of rays crossing six 200-µm-long tangential segments. Ray thickness (RT) is the maximal thickness of ray for one individual in number of cells as recommended by IAWA (Wheeler et al., 1989; Baas et al., 2004). Vessel diameter (V_d) was measured as the geometrical mean of the minimum and maximum vessel diameter (Figure 7.2) for 18 vessels randomly selected in external wood.

We further calculated hydraulically weighted mean vessel diameter (Dm), theoretical conductivity (K_{th}) and theoretical specific conductivity ($K_{s\text{-}th}$) (see Table 7.2 for formulas and references) based on micro-anatomical traits.

7.2.3 Data analysis

Comparison between monocaulous and branched species – The effect of monocaulous architectural models (Corner’s: 7 species, Chamberlain’s: 2 species, Cook’s: 1 species) and leaf composition (simple: 8 species, compound: 1 species, phyllomorphic branch: 1 species) on functional traits were tested beforehand through permanova (*Vegan* package for R, Oksanen et al., 2018). The effect of both factors was non-significant ($P > 0.063$). Although this absence of difference could be due to the unbalanced representation of architectural models and leaf types, these factors were not statistically controlled in subsequent analyses.

Trait differences between monocaulous and branched species were tested through mixed effects anovas performed with the *nlme* package for R (Pinheiro et al., 2017). Fixed explanatory variable was the growth habit (monocaulous or branched) and response variables were all other functional traits (Table 7.2), and were logarithmically transformed when necessary. Random variables were genera and individual (nested in genera) for traits with several replicates per individual.

Stem size – leaf size allometries were investigated through linear regression at three different levels; (i) at the level of phytomer by considering distal pith area (primary meristem diameter) – mean leaf area relationships (Sinnott, 1921), (ii) at individual-leaf level by considering distal stem area (including secondary growth) – mean leaf area relationships (leaf – stem scaling, e.g. Westoby and Wright, 2003; Sun et al., 2006) and (iii) at leaf-tuft level by considering distal stem area – total leaf area relationships (foliage – stem scaling, e.g. Brouat et al., 1998; Olson et al., 2009). For each regression, data was log-transformed and differences in slopes and intercepts between monocaulous and branched species were tested by adding growth habit and their interactions in linear models (Ancovas).

Comparison with the TRY Database – To test if functional differences observed between New Caledonian monocaulous and branched species were consistent when compared to other species in other geographical areas, functional trait values were extracted from the TRY Plant trait Database (Kattge et al., 2011). We focused on two standardized and widely measured plant traits to approximate: (i) resource acquisition strategy in relation to leaf size (SLA – LA relationship), both traits are at the center of the worldwide leaf economic spectrum (Wright et al., 2004; Osnas et al., 2013; Edwards et al., 2014), and (ii) hydraulic investment in relation to deployed leaf area (Huber value – V_d relationship). For each functional dimension, linear regressions were performed with 95% prediction intervals and the functional space occupied by monocaulous plants and their 95% prediction ellipse were added on the global spectrum.

Huber value (HV) represents sapwood area to leaf area ratio and is widely used to investigate hydraulic constraints on wood anatomy (Pickup et al., 2005; Wright et al., 2006; Pérez-Harguindeguy et al., 2013). V_d is widely used to approximate hydraulic efficiency in plants (Zanne et al., 2010; Beeckman, 2016), as hydraulic conductivity is a fourth-power function of the vessel diameter (Hagen-Poiseuille law, Tyree and Zimmermann, 2002). All freely available data from the TRY database where both traits were measured came from the compilation of Choat et al. (2012) and involve tree or shrub species. After removing some bottle tree species such as *Brachychiton australis*, for which anatomy is too much atypical, the used dataset included 163 pairs of measures.

Data where LA and SLA were measured such as previously described came from 10 published studies (Shipley, 1995; Pyankov et al., 1999; Shipley and Vu, 2002; Cavender-Bares et al., 2006; Swaine, 2007; Baraloto et al., 2010; Laughlin et al., 2010; Milla and Reich, 2011; Frenette-Dussault et al., 2012; Auger and Shipley, 2013). Given that relationships between leaf traits varied little with growth habit (Wright et al., 2004; Milla and Reich, 2007), herbs and lianas were considered as well as woody autoportant species in analysis. Only arborescent monocotyledons (e.g. palmae), of which a majority is unbranched, were removed from the dataset leading to a total of 18863 observations.

Anatomical implication of foliage – stem scaling – To disentangle functional implication of the foliage area – stem size relationships and particularly relative importance of hydraulic, mechanic and storage constraints, anatomical structures were partitioned following their functions and their relationship with foliage size was independently assessed at different levels.

At the stem level, whether variation in S_{area} was more related to total leaf area or to total leaf fresh mass was tested. Univariate and multivariate linear regressions were performed with foliage area and/or foliage mass as explanatory variables and S_{area} as the response variable.

Differences in the slope between the two regressions were tested with Pillai's trace test (Pillai, 1955) as implemented in the *car* package for R (Fox and Weisberg, 2011). Higher effect of foliage area, with a surrogate of evapotranspiration rate and photosynthetic resource capture, would suggest higher constraints in water conduction and/or metabolic rates on the variation of stem size. Higher effect of foliage mass would suggest stronger mechanical constraints on the stem, implying resistance adjustment through stem size.

At the tissue level, the relative contribution of the major stem tissues to the increase in foliage area with stem size was analyzed. Pith area, xylem area, phloem area and cortex area were each regressed against total leaf area and slope differences were tested through Pillai's trace tests. A higher contribution of pith would suggest stronger mechanical constraints (through second moment of inertia, Niklas, 1992) in the foliage – stem relationship; a higher contribution of phloem or cortex would suggest a strongest role of photosynthate transport and storage (Kozlowski, 1992). Wood is a highly multifunctional tissue (Evert, 2006; Beeckman, 2016) and its higher contribution to the foliage – stem relationships has to be further explored through cell-types contribution (vessel, fiber and parenchyma).

Therefore, at the wood level the relative contribution of the major cell types to the variation in foliage area was tested. Number of vessels (hydraulic function), fibers (mechanical function) and rays (storage function) in the total wood cross-section were respectively regressed against total leaf area. Slope differences between these three regressions were tested through Pillai's trace tests.

7.3 Results

7.3.1 Functional differences between monocaulous and branched species

Several morpho-anatomical traits are significantly different between monocaulous and

TABLE 7.3 – Results of mixed effect anovas. A positive value in "Value monocaulous" indicates higher traits value for monocaulous than for branched species. Bold lines represent significant relations between growth habit and the corresponding trait following a 0.05 risk of error.

	Trait	n	Log likelihood	Value monocaulous	P.value
Stem traits	**S_{area}**	**100**	**-113.4**	**1.0893**	**< 0.001**
	P_{area}	**100**	**-153.1**	**0.9816**	**< 0.001**
	SR	**100**	**-80.2**	**0.243**	**0.011**
	T	**100**	**-88.2**	**-0.384**	**< 0.001**
	SDMC	100	115.7	-0.0136	0.300
	SSD	100	98.3	-0.014	0.370
Macro-anatomy	$Pith_p$	100	-78.1	-0.1078	0.262
	$Xylem_p$	**100**	**80.2**	**0.0869**	**< 0.001**
	$Phloem_p$	100	207.9	-0.0055	0.268
	$Cortex_p$	**100**	**96.8**	**-0.0483**	**0.003**
Wood traits	WSD	100	76	-0.034	0.088
	FD	**600**	**-272.9**	**-0.2887**	**< 0.001**
	RF	**600**	**1430.3**	**-0.0082**	**0.002**
	RT	100	-124.3	0.18	0.224
	V_d	**1800**	**245.8**	**0.2061**	**< 0.001**
	VD	**600**	**-495.3**	**-0.3977**	**< 0.001**
Hydraulic traits	**HV**	**100**	**-69.8**	**-0.2625**	**0.004**
	Dm	**100**	**-5.9**	**0.2257**	**< 0.001**
	K_{th}	**100**	**-134.7**	**0.9457**	**< 0.001**
	$K_{s\text{-}th}$	**100**	**-164.3**	**1.9414**	**< 0.001**
Leaf traits	**LA**	**500**	**-200.6**	**1.1603**	**< 0.001**
	PL	500	-165.1	0.1856	0.291
	LDMC	**500**	**785.4**	**-0.0568**	**< 0.001**
	SLA	500	170.4	-0.0708	0.183
	LT	**251**	**222.6**	**0.2175**	**< 0.001**
	PSR	251	-8.3	0.12	0.198
	SD	**301**	**1654.2**	**-0.0017**	**0.026**

DMC: dry matter content, SD: specific density, SLA: specific leaf area

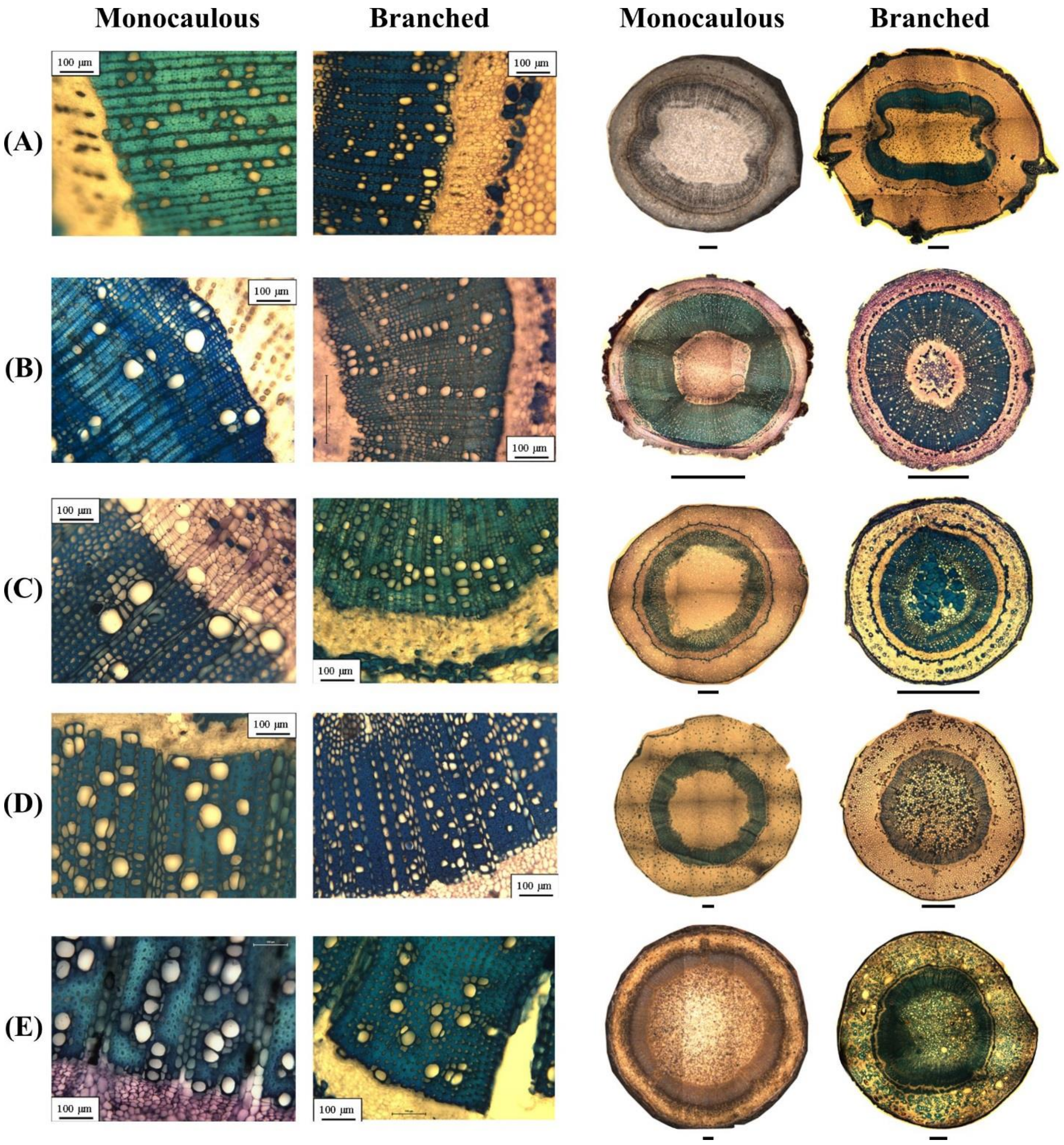


FIGURE 7.3 – Comparison of micro-anatomy (left) and macro-anatomy (right) between monocaulous and branched species in five of the ten studied genera. **(A)** *Atractocarpus*, **(B)** *Bocquillonia*, **(C)** *Litsea*, **(D)** *Phelline*, **(E)** *Tapeinosperma*. For macro-anatomical photographs, each bar is 1 mm long.

branched plants (Table 7.3). Monocaulous plants exhibited slender and less tapered stem, suggesting less mechanical reinforcement. They tended to have thicker apical cross-sections, both at primary growth (P_{area}) and after the onset of secondary growth (S_{area}) (Figure 7.3). This larger S_{area} was associated with a higher proportion of xylem, and not pith, while branched species allocated relatively more in cortex tissue. WSD, SSD and SDMC were not significantly different between monocaulous and branched species. Wood of monocaulous species was characterised by larger vessels and a lower FD, VD and RF in comparison to branched species (Figure 7.3). HV was lower in monocaulous plants, implying lower wood area dedicated to the supply of the distal leaf area with water and minerals. This was, at least partially, compensated by higher values of traits related to hydraulic capacity (V_d, Dm, K_{th}, $K_{s\text{-}th}$). Leaves were by far larger for monocaulous plants but no significant difference in SLA was found. This could result from higher LT but lower LDMC in monocaulous plants as SLA is an inverse function of LDMC and LT (Hodgson et al., 2011). Allocation in the palisade and spongy mesophylls did not differ between growth habits, but monocauls tended to have lower SD. These results need to be confirmed by a complete sampling (currently only half of the species has been measured for these traits).

Leaf area and stem area scaled positively for monocaulous and branched species at phytomer level (Figure 7.4-A), at individual-leaf level (Figure 7.4-B) and at leaf-tuft level (Figure 7.4-C). This observed scaling was not significantly different between growth habit at phytomer (Figure 7.4-A) and leaf-tuft levels (Figure 7.4-C), whether considering slopes (Ancova, $P = 0.24$ and $P = 0.74$ respectively) or y-intercepts (Ancova, $P = 0.099$ and $P = 0.94$). The scaling was different between growth habit at individual leaf level (Figure 7.4-B), LA increased more rapidly with S_{area} for branched species (Ancova, $P = 0.01$) that have significantly smaller leaves for a given stem size (lower y-intercept, Ancova, $P = 0.007$). Total leaf area explained a greater variability of

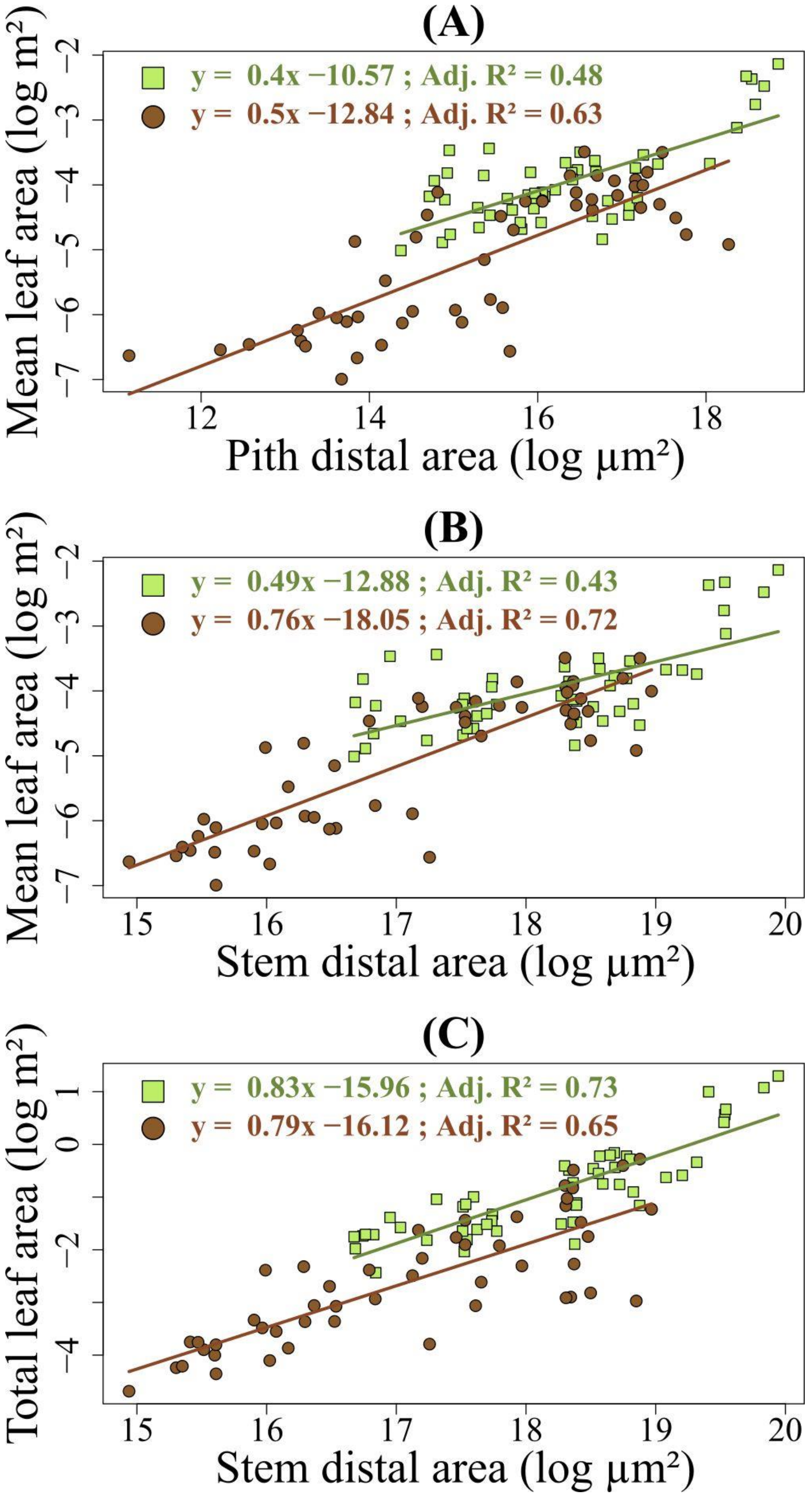


FIGURE 7.4 – Leaf – stem relationship for monocaulous and branched species considering **(A)** individual leaf and pith area, **(B)** individual leaf area and stem area at point of measurement and **(C)** whole leaf-tuft area and stem area at point of measurement. Green squares correspond to monocaulous species and brown circles to branched species.

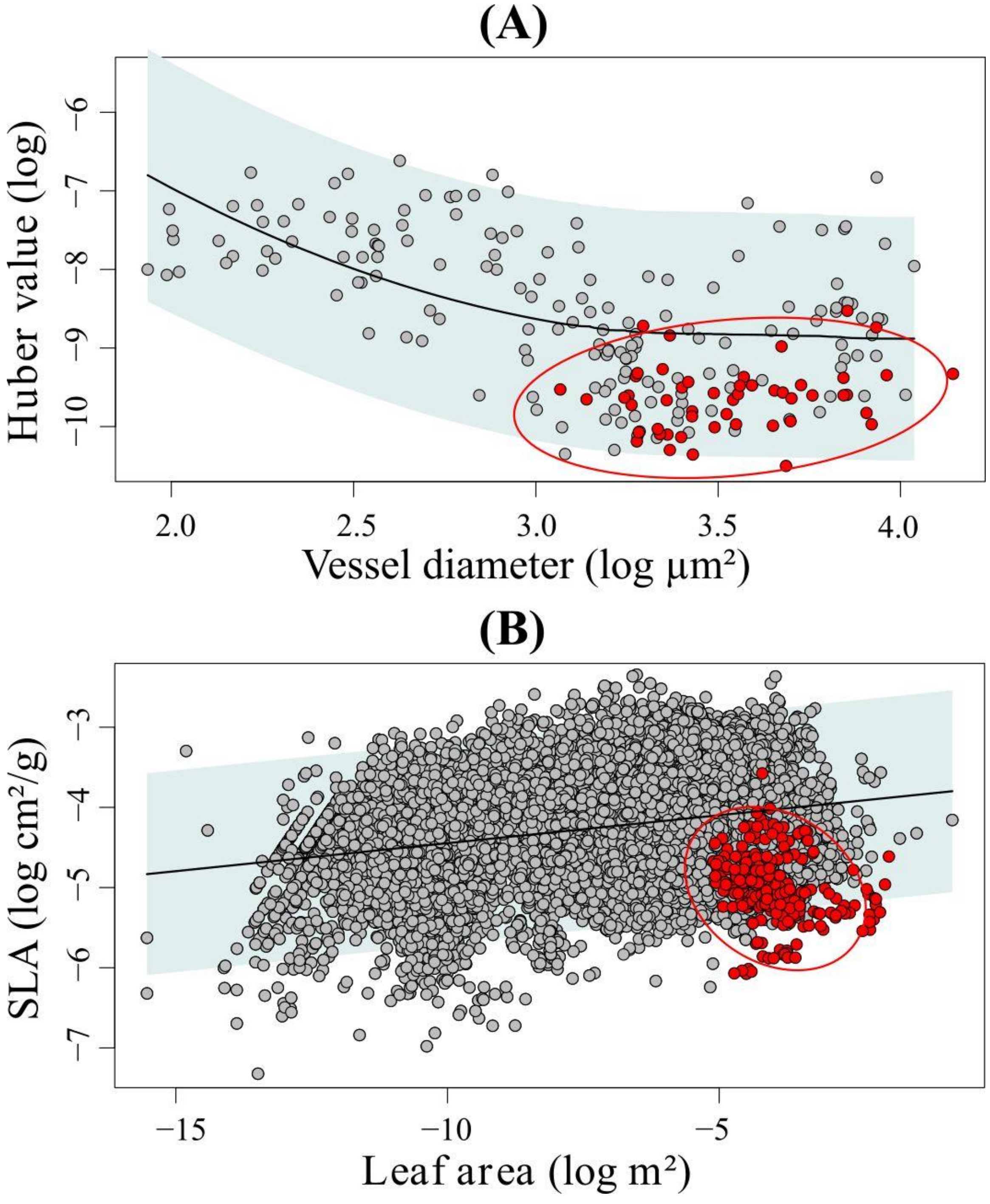


FIGURE 7.5 – Comparison between monocaulous plants and worldwide plants (TRY database) for **(A)** hydraulic comportment and **(B)** photosynthetic comportment. Black lines represent linear regression of branched species with 95% prediction interval in blue. Red points and ellipses represent monocaulous individuals and their 95% prediction ellipses.

stem distal area than mean leaf area.

When data for monocaulous plants was compared to a larger diversity of species, growth habits and environmental conditions from the TRY database, the New Caledonian monocaulous occupied a corner position on the trait coordination spectrum. Globally, HV decreased logarithmically with increasing V_d (logged data, Figure 7.5-A). This trend was mainly due to an increasing variation in HV when V_d increased: since large vessels facilitate hydraulic capacity, they are suited for both high and low ratio of xylem to distal leave area while small vessel elements are more strongly associated with high ratio of wood to distal leaves. Within this global scaling, monocaulous appeared to be extremes in having both relatively large vessels and low leaf area to wood area ratio. LA and SLA scaled positively in a linear way (logged data, Figure 7.5-B): at large scale, the larger the leaf, the lower the structural investment. In this context, New Caledonian monocaulous appeared peculiar in having extreme leaf size but low SLA as shown by ellipse largely exceeding the global 95% prediction interval.

7.3.2 Anatomical implication of foliage – stem scaling

S_{area} scaled positively with both total leaf area and total leaf mass (Figure 7.6). Both traits were strongly correlated and association with stem size was high in both cases (slopes > 0.97, adjusted $R^2 > 0.74$), but slope was significantly higher for foliage mass than for foliage area (Pillai's trace test, $P < 0.001$) suggesting greater importance of mechanical constraints on the foliage – stem size relationship.

The area of each stem macro-anatomical tissues (pith, xylem, phloem and cortex) scaled positively with total leaf area (Figure 7.7). Slopes of regressions were significantly higher for pith and xylem areas than for cortex and phloem areas, even if the adjusted R^2 of the pith area – foliage area relationship was quite low (adjusted $R^2 = 0.57$).

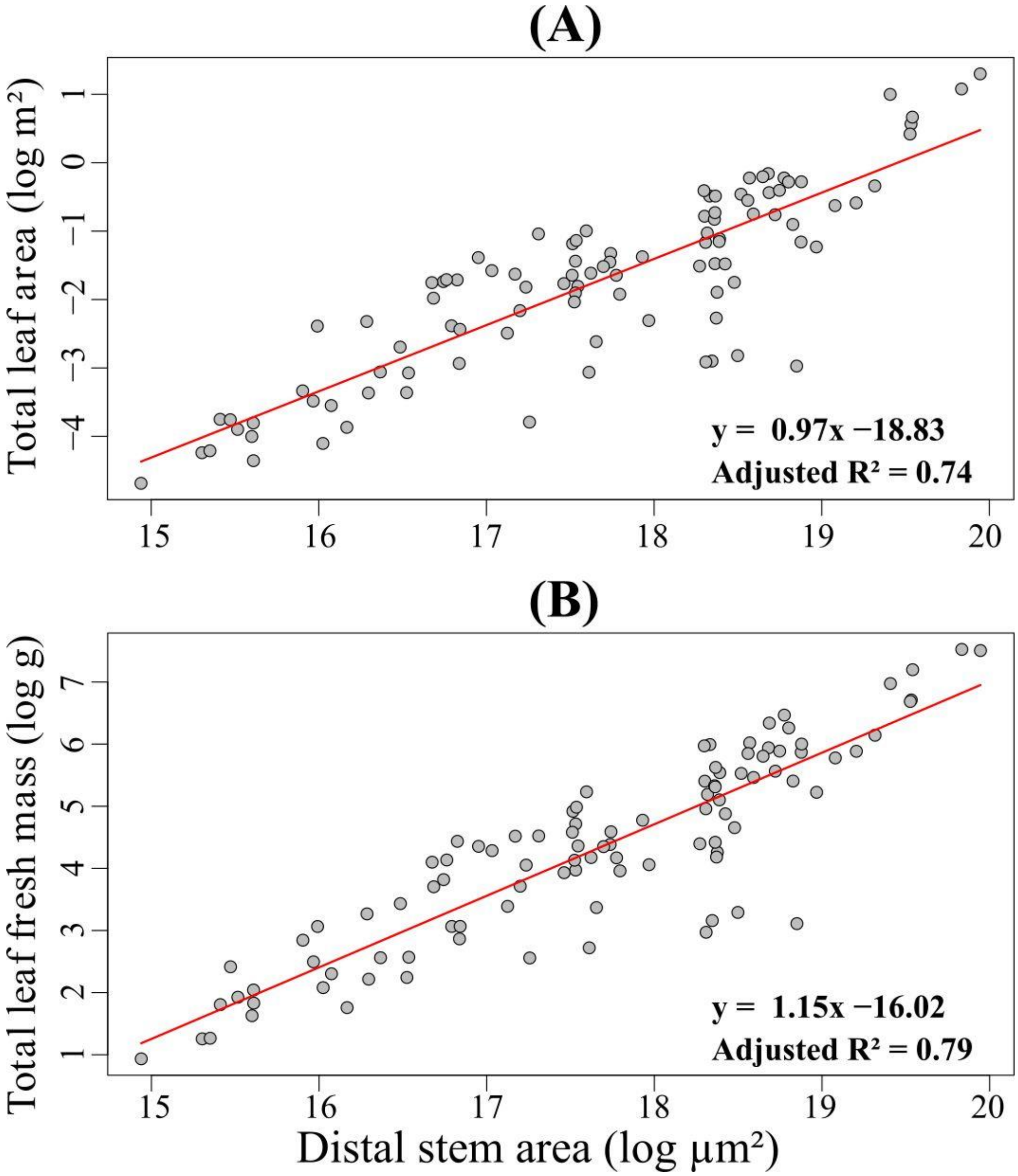


FIGURE 7.6 – Relationship between stem area and **(A)** total leaf area or **(B)** total leaf mass.

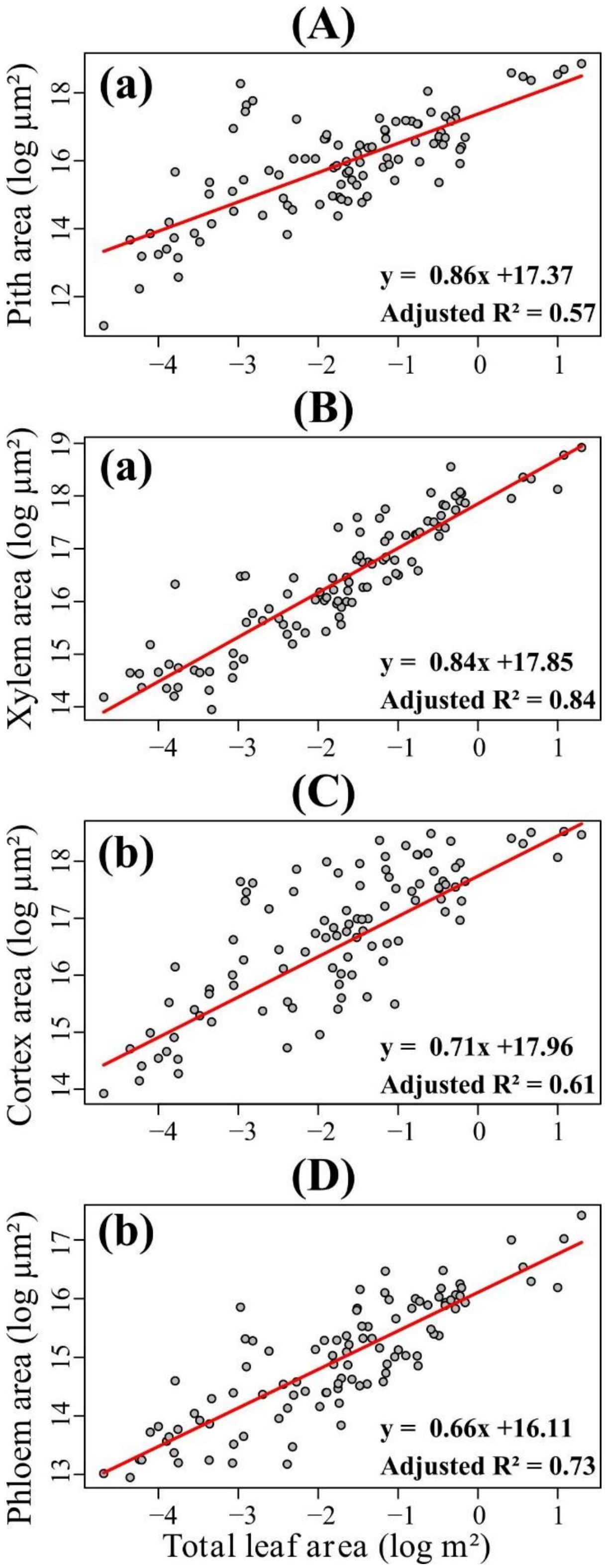


FIGURE 7.7 – Relationship between total leaf area and **(A)** pith area, **(B)** xylem area, **(C)** cortex area or **(D)** phloem area. Lowercase letters on graphs indicate the results of Pillai's trace test: regressions with shared letters do not have different slopes following a 0.05 risk of error.

Vessel and fiber number showed a significant positive relationship, with similar slope, with total leaf area (logged data, Figure 7.8). The relationship was also significantly positive but much less pronounced for the number of rays.

7.4 Discussion

7.4.1 Toward a functional characterization of rainforest monocaulous habit

Whereas major functions of most trees and treelets are partitioned between axis categories (trunks, branches, twigs, see Barthélémy and Caraglio, 2007), monocauls are characterized by a single trunk assuming all essential functions (Chapter 6). This particular architectural design involved functional constraints leading to contrasting functional behavior of stems and leaves between growth habits (branched versus monocaulous).

Biomechanics **–** Carlquist (1974) suggested that distal parts of monocaulous stems might possess a wood cylinder configuration that would maximize strength because of the large and numerous leaves. We found a strong difference in both LA and S_{area} between monocaulous and branched species, as well as a significant relation between S_{area} and total leaf mass that confirms the mechanical reinforcement of upper stem in response to apical mass for both growth habit. Thicker apical diameter in monocaulous species however results from higher wood fraction and not pith fraction as previously suggested for other monocaulous models (Carlquist, 1974; Mabberley, 1974a; Hallé et al., 1978; Meinzer and Goldstein, 1986; Mosbrugger, 1990). As shown by the position of monocaulous plants along a two-dimensional spectrum related to hydraulic strategies, they tend to have low wood to distal leaf area ratio (HV). Increasing wood area fraction, compared to their branched counterparts, is probably to be related to the hydraulic and mechanical demand of large and numerous leaves (see below). When considering only monocaulous species,

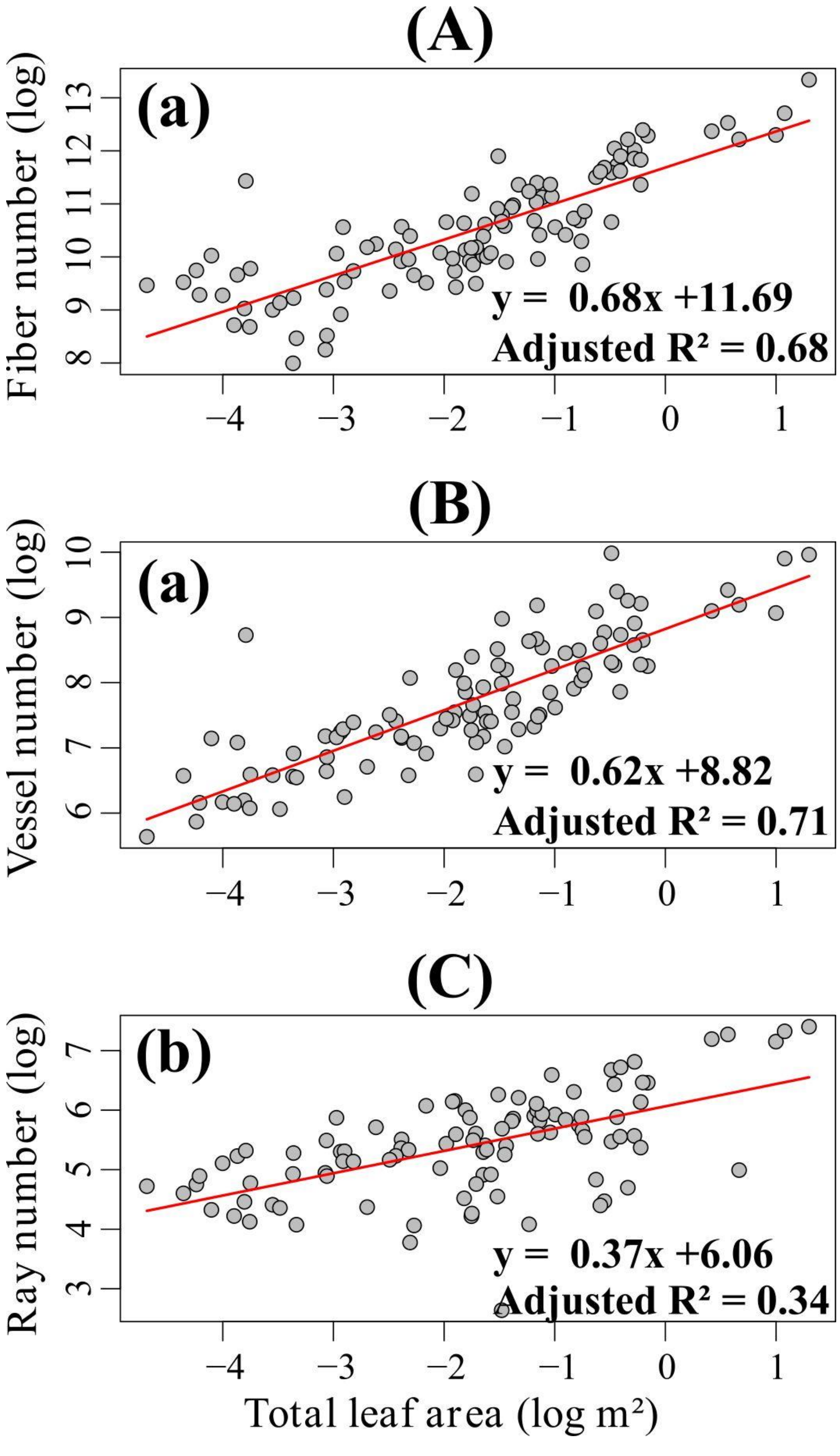


FIGURE 7.8 – Relationship between total leaf area and **(A)** fiber number, **(B)** vessel number or **(C)** ray number in wood cross section. Lowercase letters on graphs indicate the results of Pillai's trace test: regressions with shared letters do not have different slopes following a 0.05 risk of error.

we found only weak correlation between WSD and total leaf area (Spearman correlation test: rho = -0.12, P = 0.41) or wood traits such as FD (rho = 0.10, P = 0.48), V_d (rho = -0.26, P = 0.07) or VD (rho = 0.24, P = 0.09) while these correlations are significant for closely related branched species (not shown) and often supported in literature (e.g. Mencuccini, 2003; Ackerly, 2004; Cavender-Bares et al., 2004; Santiago et al., 2004; Pickup et al., 2005; Wright et al., 2007; Zanne et al., 2010). These results support the view that geometric adjustment of the stem, rather than micro-anatomical variation, is involved in the response to the biomechanical and hydraulic demand of the monocaulous habit.

At the whole plant level, monocaulous species tended to deploy higher slenderness ratio (SR), whose mechanical stability depends on mechanical reinforcement (E, bending modulus) and static-load (P) (Niklas, 1992; Niklas et al., 2006). As for the mechanical stability of a column, SR is proportional to $(E/P)^{1/2}$ (Niklas et al., 2006), and reducing P through lack of branching could be sufficient to ensure mechanical stability of slender stems. Higher SR in monocaulous species indeed means that they would be more vulnerable to global elastic buckling induced by self-loading, i.e. if E is low or P is high. But lower tapering of monocaulous stem, resulting for thicker apical portion, suggests lower critical buckling lengths for a given bending modulus (Niklas et al., 2006). Preliminary results seem to indicate that there is no relationship between slenderness ratio/tapering and bending modulus at the base of monocaulous stems, i.e. no mechanical reinforcement (unpublished data). Monocaulous species are however variables in their biomechanical behaviors, with for instance maximal values of bending modulus ranging from 4000 to 10000 MPa, and different E to diameter relationships (unpublished data). Further biomechanical investigations should bring more information on the diversity of mechanical strategies related to anatomical construction.

***Hydraulics* –** We found that monocauls deployed less xylem per distal leaf area and wider vessels than their branched congeners and species from the TRY database. This condition could involve plant hydraulics, in regard to the deployment of a large distal leaf area, as wider vessels could compensate hydraulically for a proportionally narrower xylem area (Ewers and Fisher, 1991; Pickup et al., 2005; Wright et al., 2006). This is because K_{th} scales with the fourth power of V_d (Hagen-Poiseuille law), thus a slight increase in V_d causes a disproportional increase in conductivity and modifies the wood area needed to conduct water at a given rate (Tyree and Zimmermann, 2002). By contrast, VD is not linked with HV (rho = -0.09). The counterpart of this increased hydraulic efficiency through vessel size rather than density is the potential increase in cavitation risk, as embolism can be (indirectly) related to vessel diameter (Tyree and Sperry, 1989; Hacke et al., 2000; Poorter et al., 2010). This phenomena is however supposed to be rare in the buffered rainforest understory (see Wright et al., 2006) where most monocaulous species are found (Chapter 5).

***Leaves economics* –** As empirically suggested by Corner (1949), monocaulous plants have larger leaves than branched relatives. In a more global spectrum, monocaulous plants from our dataset ($6\times10^3 – 1.5\times10^5$ mm²) have among the largest leaves recorded worldwide (TRY Database, Figure 7.5). The global data indicate that SLA increases with LA, while the trend is reversed for monocaulous plants (Spearman correlation test: rho = -0.2, $P < 0.001$, Appendix 3). Several authors found similar relationship when comparing species from similar sites (Westoby and Wright, 2003). In monocaulous plant, this could be attributed to the greater construction cost of large leaves or long leaf lifespan, both being often interrelated (Wright et al., 2004; Sack et al., 2012). SLA of monocaulous species did however not significantly differ from congeneric branched species, but was nevertheless in the lower range of the worldwide spectrum for similar leaf size, suggesting low acquisition of nutrient and conservation of resource (Wright et al., 2004). As such, SLA does not bring much information on the ecological strategy that differentiates monocaulous and branched habit in similar environment. The components of leaf dry mass – thickness and density (LDMC as surrogate) – adjust more independently from the environment and might provide better insights into the components of functional strategies (Niinemets, 1999). We indeed found that leaves of monocaulous species tend to be thicker with a lower LDMC. Low LDMC could mean that the fraction of the leaf volume occupied by mesophyll – where CO_2 fixation takes place – is higher, though photosynthetic activity is more tightly correlated with SLA (Nadal et al., 2018). But monocaulous species tend to have a lower SD, rather suggesting less efficiency in CO_2 capture. Further works on the economy of light harvesting and biomass partitioning should bring more light on the economy of leaves in monocaulous plants (support investments, leaf chemical and structural characteristics, Niinemets, 1999; Niinemets et al., 2007).

For leaves, in a given microclimate and soil watering, stomatal and boundary layer conductance determine the transpiration rate (Sack et al., 2003). Large leaves, with thicker boundary layers, must face slower thermal regulation as – all else being equal – they have larger leaf-to-air temperature difference (Wright et al., 2017). This condition is mostly critical in hot, drier and sunny environment, where large leaves would fail to regulate transpiration rate (Givnish, 1987). In rainforest understory, the physiological constraints of large leaves are largely buffered (perhaps virtually lacking), favoring the deployment of large photosynthetic area, and its corollary reduced branching pattern, to increase light capture at cheaper cost. Using models and different scenarios, Smith et al. (2017) predicted that partitioning a given total leaf area in few large leaves is economically more interesting than in several small leaves (maximization of return on twig-leaf investment). Another selective advantage of the large-leaved monocaulous habit could then be related to growth advantage associated with lower structural cost at plant level (no branching, lower wood fraction and slightly lower stem area per total foliage, though not significant). Such growth advantage is susceptible to be particularly pronounced on the nutrient poor ultramafic substrate (Jaffré, 1993; L'Huillier and Edighoffer, 1996; Isnard et al., 2016) where monocauly preferentially evolved (Chapter 5).

***Carbohydrate storage* –** Carbohydrates are stored in all parts of plants, but the more largely used tissue in ligneous non-liana Angiosperms is ray parenchyma (Loescher et al., 1990; Kozlowski, 1992; Morris et al., 2016; Carlquist, 2018). Monocauls presented a lower ray density and ray thickness was not significantly different following growth habit. The relative allocation in ray parenchyma is consequently higher in branched species but monocauls have a higher proportion of wood, leading to a higher absolute number of rays (on average 395 against only 243 for branched species, not shown). Proportion of cortex is higher in branched species possibly involving further implication of this stem tissue in carbohydrate storage. Despite these slight differences in storage traits, storage function remain very difficult to approximate with soft traits (Hodgson et al., 1999; Weiher et al., 1999) and because storage location varies according to species. Actually, carbohydrate storage implies a wide variety of tissues including pith parenchyma, wood ray parenchyma, wood axial parenchyma, cortex parenchyma and bark. And the relative contribution of each tissue is likely to vary following plant systematic position (Kozlowski, 1992; Carlquist, 2018). Contrary to hydraulics and biomechanics, storage function could be allocated in other organs or axis categories than the trunk (e.g. roots) and if it is the case for some of the studied species, differences of storage allocation between growth habits could be hidden.

7.4.2 Toward a functional explanation of the foliage – stem scaling

We found a strong relation between stem (shoot) area and leaf area (individual and total) confirming the universal leaf – stem and foliage – stem scaling. Beyond confirming the consistence of the pattern across organization levels (phytomer level, individual leaf level, twig level), we further showed that the relationship stays mainly unchanged across growth habits (monocauls vs. branched) in similar environments, for a wide range of leaf areas (from 6×10^2 to 1.5×10^5 mm^2). Only the stem area – individual leaf area showed differences in slopes and intercepts between monocaulous and branched species: monocauls had higher individual leaf area for a given stem area but leaf area increased more rapidly with increasing stem area in branched species. The linear log-log relation between stem area and leaf area (at all levels) means that leaf area increases disproportionately with stem area (Niklas, 1994), as showed in other studies (Bond and Midgley, 1988; Brouat and McKey, 2001; Westoby and Wright, 2003; Normand et al., 2008, but see Brouat et al. 1998). The relationship was stronger at foliage level than at individual-leaf level, confirming that stem-leaves relationship is more strongly governed by total leaf area than individual leaf area (Brouat et al., 1998; Westoby et al., 2002).

The foliage – stem scaling has been hypothesized to result from a leaf to stem metabolic dependency alternatively involving hydraulics (Chuah, 1977; White, 1983a; Preston and Ackerly, 2003; Sun et al., 2006; Normand et al., 2008), mechanics (White, 1983a; Niklas, 1992; Normand et al., 2008; Olson et al., 2009; Levionnois et al., 2018a) and photosynthesis (Primack, 1987; Cornelissen, 1999). In our study, the metabolic constraint seems to operate mechanically, as we found a stronger response of apical stem area to increasing foliage mass, representing mechanical constraints, than to increasing foliage area, representing hydraulic and photosynthetic constraints. The strong correlation of foliage area with pith area also supports the mechanical hypothesis. Actually, the increased contribution of pith put mechanically important tissues (wood, cortical fibers) at the periphery of the stem, where they have a disproportionate mechanical contribution to whole stem stiffness at lower carbon cost (Niklas, 1992). This geometrical strategy was yet suggested as important in the relation between foliage area and stem size (White, 1983a). Wood area is also strongly correlated with the variation in foliage area (more than phloem or cortex). The increase of wood area appears to be an important mechanism for the adjustment of stem size over foliage size because it allows the concomitant increase of several essential functions (hydraulic, mechanic and storage). In our case, this adjustment of wood seems more linked with an increase in the number of vessels and fibers rather than in the number of rays. More generally, the lower relationship between total leaf area and photosynthate-storage related tissues (wood rays, phloem, and cortex) showed that this function only little contributes to the foliage – stem scaling.

The stronger importance of the mechanical function in the adjustment of stem size to leaf area is consistent with other studies (Normand et al., 2008; Levionnois et al., 2018a) but must depends on the environment. In our study sites, mean annual precipitations were higher than 2200 mm.yr^{-1} (Météo-France, 2007). Even if a long dry annual period occurs in New Caledonia (Maitrepierre, 2012), this is not critical for rainforest understory where individuals were sampled. These moist and shaded conditions make hydraulic and photosynthetic constraints on stem size marginal which probably result in prevailing mechanical over hydraulic constraints.

To summarize, our results suggest that the universal foliage – stem scaling (in rainforest) is mainly due to an increase in pith and wood fraction in response to mechanical static load imposed by numerous large leaves. But this does not explain why there is a modal correlation between stem area and individual leaf area (Westoby et al., 2002). The possible reason is that total leaf area (and mass) is more correlated with individual leaf area than with leaf number (Falster and Westoby, 2003; Westoby and Wright, 2003; Smith et al., 2017), as shown by our dataset (linear regressions with total leaf area: Adjusted $R^2 = 0.87$ for individual leaf area against 0.28 for leaf number).

Moreover, even if total leaf area is equal, biomechanical constraints are not necessarily similar when leaf area is made up of few large leaves or many small leaves. Whereas mass imposed by small leaves are distributed closely to the supporting axis, mass of large leaves are distributed further away from the axis leading to higher biomechanical constraints on stem (longer level arm). Such higher biomechanical constraints of leaves appear as a major drivers of foliage – stem scaling), and could also explain the universal leaf size – stem size spectrum in rainforest understory.

Another well-developed theory came from the redundant observation of a negative correlation between leaf area and wood density (e.g. Cavender-Bares et al., 2004; Santiago et al., 2004; Pickup et al., 2005; Wright et al., 2007) or young modulus (Olson et al., 2009; Trueba et al., 2016). Olson et al. (2009) argue that for a constant total leaf area (and therefore a hypothetical similar amount of photosynthates), large-leaved plants have lower stem density because they have longer internodes (i.e. "leaf spacing"), thus needing thicker stems for biomechanical adjustment. The proposed biomechanical adjustment through stem diameter is coherent with our above hypothesis and our results support the negative relation between leaf size and wood density (Spearman correlation test: rho = -0.31, P = 0.002, Appendix 3). But we do not think that this correlation is due to longer internode in large-leaved species. Virtually all studies that investigated both leaf size and internode length did not find a positive correlation between the two traits (Chuah, 1977; Ashton, 1978; Barcellos de Souza et al., 1986; Lauri, 1988; Poorter and Rozendaal, 2008, Chapter 6). This hypothesis is also in contradiction with Corner's rules (Corner, 1949) predicting that small-leaved trees ("leptocaulous") have longer internodes than large-leaved ("pachycaulous") trees. A similar total leaf area does not necessarily imply similar carbon production and carbon allocation strategies could be different between large-leaved and small-leaved species. For example, a significant part of photosynthates is allocated to fruit production (Niklas and Enquist,

2003) which seems higher in large-leaved species (Primack, 1987; Cornelissen, 1999, Chapter 6).

7.4.3 New Caledonian monocauls, a special case of monocauly?

Despite being achieved through various structural ways (Corner's, Holttum's, Chamberlain's and Cook's architectural models) (Hallé et al., 1978, Chapter 5), the monocaulous habit remains consistent in both physiognomical and functional aspects. We considered a reasonable phylogenetical diversity but only a single habitat (rainforest), where most of the New Caledonian monocaulous taxa occur (89%, Chapter 5). In that sense our work depicts monocauly associated with tropical rain forest understory fairly well. The few species occurring in open habitat (maquis) are likely to provide more insight into adaptation to the monocaulous habit, i.e. do they exhibit lower leaf area? Lower SLA value? Does transpiration rate influence wood anatomy and do we observe different strategies of apical mechanical reinforcement?

The few published data about monocauls comes from studies about rosette-trees, of which the majority is monocaulous. However, beyond their large leaves and thick stems, their stem anatomy seems very different from our monocaulous species. Rosette-trees present a disproportionate proportion of pith (Cotton, 1944; Carlquist, 1974; Mabberley, 1974a; Hallé et al., 1978; Meinzer and Goldstein, 1986; Mosbrugger, 1990), a thin and highly parenchymatous wood (Cotton, 1944; Mabberley, 1974a; Aldridge, 1978) and a large cortex (Cotton, 1944; Mabberley, 1974a; Hallé et al., 1978; Mosbrugger, 1990). These contrasting strategies obviously result from different evolutionary backgrounds and environmental factors. Most previously studied monocaulous species evolve from herbaceous ancestors (e.g. *Espeletia* for Meinzer & Goldstein, *Cyanea* for Carlquist, *Dendrosenecio* for Cotton, *Echium* for Aldridge) and are adapted to dry (Böhle et al., 1996; Lens et al., 2013) or frosty (Hedberg and Hedberg, 1979; Meinzer and Goldstein, 1986; Givnish, 2016) conditions. At the opposite monocaulous species in New

Caledonia most likely evolved from woody ancestors (Barrabé et al., 2018; Chapters 5,6) and are suited to moist and shady understory. As such, our study illustrated a virtually unknown ecology of monocaulous plants, occurring in several tropical regions throughout the world (e.g. Gabon, Hallé and Hallé, 1965; Panama, D'Arcy, 1973; or New guinea, Hallé, 1974), where they could represent an important fraction of the understory diversity (Hallé and Hallé, 1965).

Chapter 8 — General Discussion and Conclusions

8.1 Monocauly in New Caledonia: evolutionary convergence and an element of the archipelago's functional disharmony?

New Caledonia is well known for the outstanding distinctiveness of its flora, characterized by a marked taxonomic and functional disharmony compared to adjacent regions (Morat et al., 1994; Jaffré, 1995; Carpenter et al., 2003; Pillon et al., 2010; van der Ent et al., 2015; Trueba, 2016). In this study, we found that 182 species are monocaulous, belonging to 41 genera, 30 families and 15 orders. As such, 5.5% of the flora and 9% of the woody flora are monocaulous (Chapter 5). Whether this high diversity of monocaulous species and lineages is part of New Caledonia's functional disharmony is difficult to assess given the lack of data for other floras. We established a reliable list of monocaulous species, but some taxa (about twenty) still have to be thoroughly checked. A similar intensive work (based on a similar definition of monocauly) is needed for other regions such as Australia and New Guinea, recognized as the main sources for New Caledonian flora (Morat, 1993; Swenson et al., 2014). This could be especially interesting for New Guinea, which was also previously suggested as being particularly rich in monocaulous plants (Hallé, 1974).

The occurrence of monocauly in 9% of the woody flora is by far lower than suggested by Veillon (1976), who found 112 of the 575 species he considered (19.5%) to conform to monocaulous architectural models (Corner's, Holttum's, Chamberlain's and Cook's). This discrepancy might principally result from the inclusion of monocotyledons and ferns in the work of Veillon (1976). In addition, his work was based on an opportunistic sub-sampling of the flora, which induced a bias in favor of monocaulous species for which architecture is comparatively easy and quick to describe. However, 5.5% of the entire flora (and 9% of the woody flora) nevertheless represents a significant portion for a growth habit recognized as rare both regionally (Schmid, 1979) and globally (Hallé et al., 1978; Chomicki et al., 2017). The contribution of monocauly is even more remarkable when considering only rainforest vegetation, in which it represents respectively 10.7% and 12.4% of rainforest-facultative and rainforest-restricted woody non-monocot species. For comparison, the monocaulous flora (including monocots and ferns) was suggested to account for only 2% of the world's flora as a whole (Chomicki et al., 2017) and the divaricated flora of New Zealand, recognized as the most outstanding syndrome for this island, accounts for 10% of the woody flora (Greenwood and Atkinson, 1977).

Whether this outstanding diversity of monocaulous species in New Caledonia translates into a high abundance and density of species with this habit in ecosystems is difficult to assess. Despite intensive forest inventories carried over the last few years in New Caledonia (Ibanez et al., 2014; Birnbaum et al., 2015a; Birnbaum et al., 2015b; Ibanez et al., 2017b; Ibanez et al., 2017a; Blanchard et al., *submitted*), abundance and distributional data for monocaulous species are lacking because most ecological censuses considered trees with a DBH > 5 cm or DBH > 10 cm. We investigated the representativeness of monocaulous species in the New Caledonian Plant Inventory and Permanent Plot Network (NC-PIPPN, Ibanez et al., 2014). The results indicated that only 24% of New Caledonian monocaulous species were represented in the database, against 46% for branched tree species (Ibanez et al., 2014). Most monocaulous species (41%) were represented by less than 3 individuals in the database and 80% of them never exceeded 10 cm in diameter. While this apparent rarity may also be due to restricted distribution and small plot sizes, small DBH

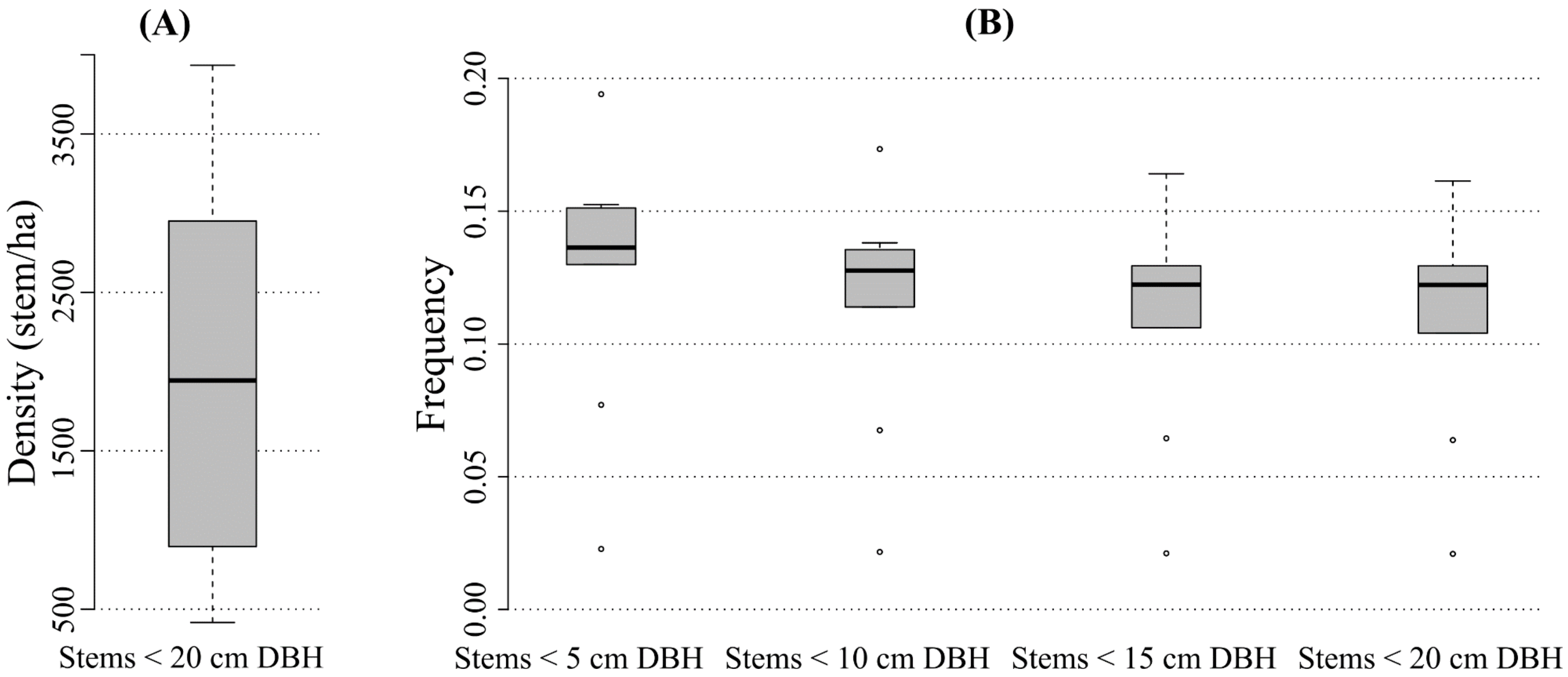


FIGURE 8.1 – Data of density (A) and frequency (B) for monocaulous plants in nine rainforest plots of 0.048 to 0.124 ha (total size = 0.576 ha). Plots are located in the south-east of the main island on ultramafic substrate from 240 m to 940 m elevation (see Read et al. 2000 for the detailed method).

indicates that monocaulous plants are mainly represented by old individuals. This confirms that monocaulous species have in general a DBH lower than 5 cm and that standardized forest inventories are not adapted for the study of this growth habit and more generally for the study of understory species. Despite this, monocaulous species were present in 45% of the plots and could represent up to 100% of the understory species in some cases. A less extensive study analyzed structure, diversity and composition of different rainforests measuring all stems > 1.3 m high in nine plots (Read et al., 2000). Plots were located in the south-east of the main island, on ultramafic substrate, from 240 m to 940 m elevation, and ranged from 0.048 to 0.124 ha (total size = 0.576 ha). Extraction of monocaulous species from this dataset confirm that 95.2% of stems are thinner than 5 cm DBH and 99.1% thinner than 10 cm DBH. The stem density of monocaulous plants is highly variable (ranging from 417 to 3934 stems per ha) with a mean of 2135 stems per ha (Figure 8.1-A). Monocaulous plants account on average for 12.1% (and up to 16.1%) of all stems < 20 cm DBH. The smaller the DBH threshold, the higher the frequency of monocaulous plants with an average of 13.7% (and up to 19.6%) of all stems < 5 cm DBH (Figure 8.1-B). Despite the low representability of monocaulous species in the NC-PIPPN database, and the small area sampled by Read et al. (2000) these results suggest that monocaulous plants are an abundant component of rainforest understories.

The high incidence of monocaulous species in New Caledonia could be explained by three non-exclusive mechanisms: (i) colonization of many monocaulous taxa, (ii) repeated *in situ* evolution and (iii) *in situ* diversification of monocaulous lineages (see Chapter 1 and Figure 1.1 for details).

(i) The establishment of monocaulous species from other regions would imply that the monocaulous habit is an ancestral train in New Caledonian clades. A phylogenetic reconstruction of *Atractocarpus* did not validate this hypothesis (Chapter 6), nor did the phylogeny of several other lineages such as *Oxera* (Barrabé et al., 2018), *Pycnandra* (Swenson et al., 2014; Swenson et al., 2015), *Beauprea* (He et al., 2016), *Pittosporum* (Gemmill, unpublished data), and *Tapeinosperma* (Gemmill, unpublished data). A careful review of architecture expressed in the presumed sister group of New Caledonian monocaulous genera suggests that among the 41 genera, only *Phyllanthus*, *Casearia*, *Dysoxylum*, *Plerandra* and *Meryta* might have been established in New Caledonia via a monocaulous ancestor. Current evidence consequently suggests that this mechanism (primary establishment) did not contributed significantly to extant monocaulous diversity in New Caledonia. This remain to be tested, however, and some monocaulous sister groups could have become extinct.

(ii) *In situ* repeated evolution of monocauly in different lineages seems responsible for a large part of the New Caledonian diversity in monocauls, as the habit appears rarely to have been ancestral (see above), and we identified more than 31 independent origins. However, convergent evolution must not be the only mechanism, otherwise there would be as many independent evolutions as monocaulous species.

(iii) The majority of monocaulous genera (64%) contain more than one monocaulous species (Chapter 5) and, while multiple shifts to monocauly are frequent within genera, most monocaulous clades seem to have diversified at least a little. However, there are only a few genera with several monocaulous species and no truly large monocaulous radiation has been identified yet, the largest being seven species derived from a single monocaulous ancestor in *Oxera* (Lamiaceae, Barrabé et al., 2018). In *Atractocarpus*, a single monocaulous ancestor diversified into six monocaulous species and two architecturally intermediate species (Chapter 6), and monocauly did not significantly enhance diversification rate in the clade. As such, while *in situ* diversification has contributed to the current diversity of monocaulous taxa, current evidence although suggests a low rate of species diversification among groups expressing the habit, although this question needs further investigation.

As such, convergent evolution of monocauly in New Caledonia is probably the principal mechanism leading to the remarkable diversity of monocaulous species in the archipelago (i.e. functional disharmony). Our study revealed that this new case of convergence is particularly exceptional and illustrates this type of phenomenon for the first time in New Caledonia (Chapter 5). At a larger phylogenetic and geographic scale, the monocaulous architecture (*sensu* Hallé et al., 1978, see Chapter 3) has been shown to evolve repeatedly, with 118 independent origins, across more than 20,000 vascular species (Chomicki et al., 2017). Here, we found between 31 and 49 independent origins across the woody non-monocot flora of New Caledonia (2114 species, Chapter 5), using a genus-level phylogeny. This result is no doubt highly conservative since monocauly has often evolved repeatedly within genera (Rauscher, 2002; Mort et al., 2007; Chomicki et al., 2017; Barrabé et al., 2018, Chapter 6). As a comparison, secondary woodiness in the Canary Islands – known as one of the most striking cases of convergent evolution in islands – evolved 38 times independently (based on species-level phylogenies, Lens et al., 2013).

This remarkable convergence toward monocauly in New Caledonia suggests that strong environmental contingencies have favored the evolution of this functionally and physiognomically atypical growth habit in the archipelago. To accurately address the question of which environmental factors could have facilitated the evolution of monocauly, i.e. which traits were selected, we first needed to clarify the functional implications of monocauly.

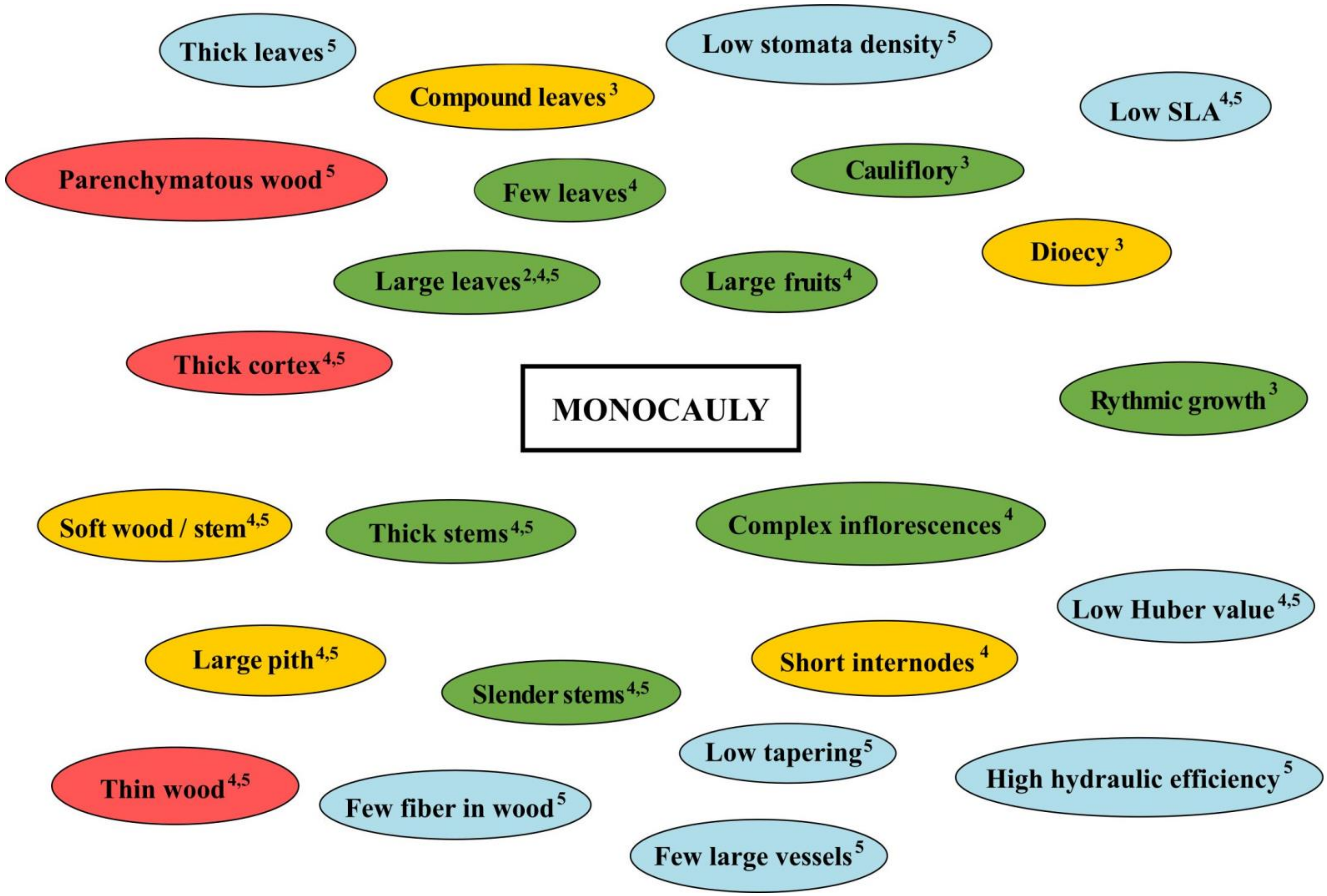


FIGURE 8.2 – Illustration of life-history traits supposed and/or showed to be associated with monocauly. Green ellipses show previously suggested traits for which we confirmed the relationship. Yellow ellipses show previously suggested traits for which we found no relationship. Red ellipses show previously suggested traits for which we found inverse relationship. Blue ellipses show not previously suggested traits for which we found a significant relationship. Letters represent chapters in which the relationship was investigated.

8.2 Ecological and evolutionary implications of monocauly

8.2.1 A well-defined functional strategy

Observations of numerous authors suggested an association between the monocaulous habit and several life history traits. Trait attributes that were empirically or indirectly linked to the monocaulous habit include large leaves, thick stem, large fruits, complex inflorescences, compound leaves, cauliflory, dioecy, few leaves, rhythmic growth, short internodes, slender stem, thin wood, thick pith, thick cortex, parenchymatous wood and soft stem tissues (see Figure 3.2). We tested all of these associations either through taxonomical work in a genera (Chapter 4), correlated evolution in the New Caledonian woody flora (Chapter 5), phylogenetic generalized least square in a genera (Chapter 6) or mixed effect anovas between pairs of co-generic species (Chapter 7). Among the 16 trait characters potentially linked to monocauly, we confirmed association for 8 of them, found no significant relationship for 5 of them and inverse relationship for 3 of them (Figure 8.2). We additionally found eight other features that appeared significantly linked to monocauly while not previously mentioned to our knowledge (Figure 8.2). The suite of trait attributes associated with monocauly appeared to be coordinated by different, sometimes conflicting, functions (Figure 8.3).

Corner's rules – The assertions of Corner (1949, 1953-1954) on the negative relation between branching intensity and (i) leaf size, (ii) stem thickness, (iii) fruit size and (iv) inflorescence complexity were confirmed by our study. (i) The relationship between branching intensity and leaf size involves a coordination between individual leaf area and leaf number since the total leaf area stays constant (Chapter 6); monocauls, being single-stemmed, have less spatial opportunity to insert leaves (less phytomers) than branched plants of the same height and, consequently, deploy larger leaves. (ii) We further showed that leaf size – stem size relationship is

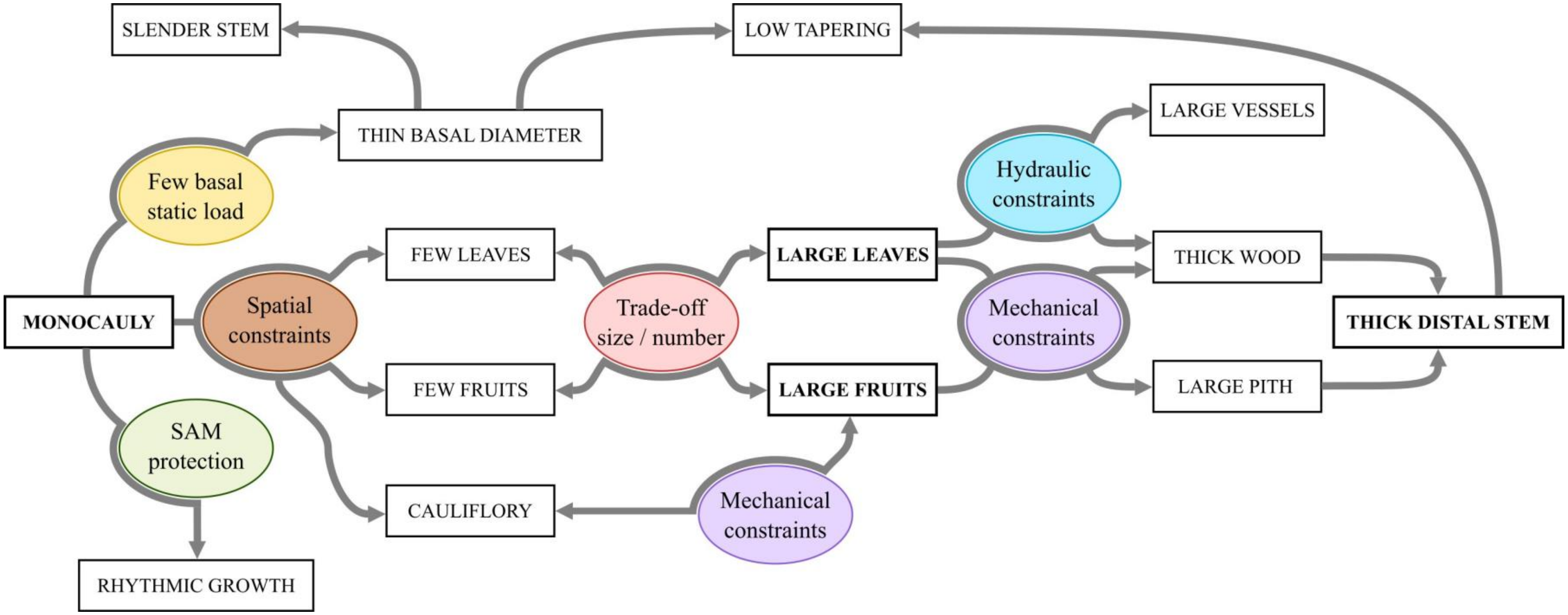
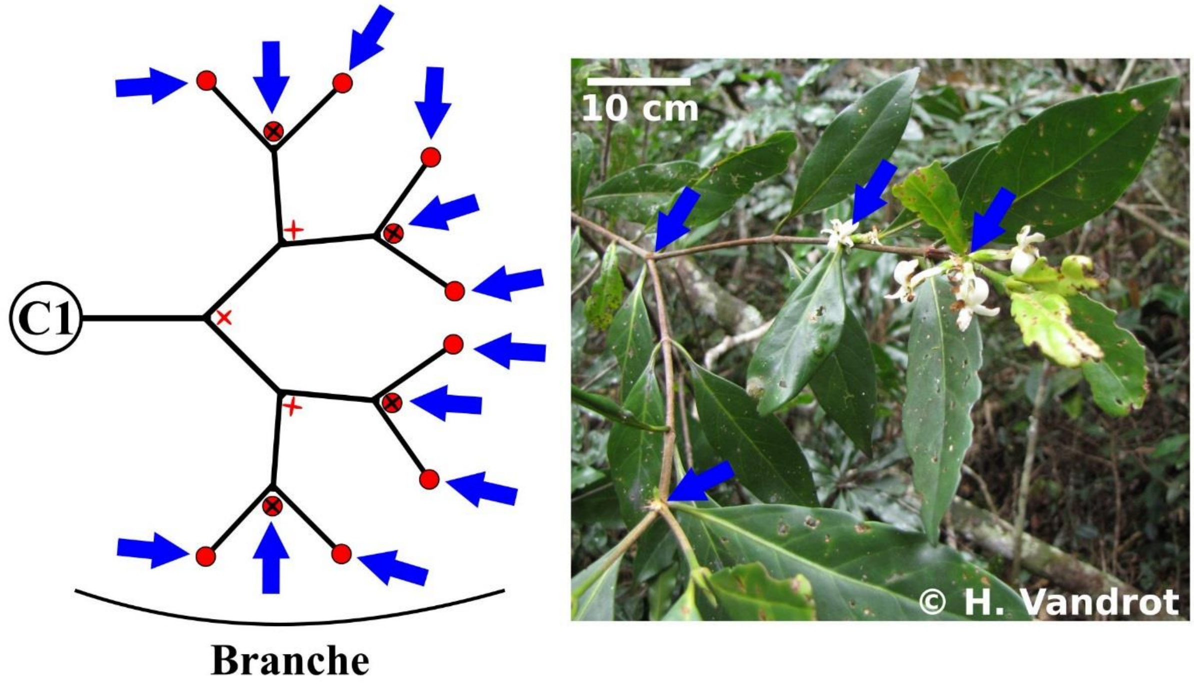


FIGURE 8.3 – Functional relationships between trait attributes associated with the monocaulous habit (compared to a branched species of the same size). Bold squares represent fundamental components of Corner's rules. SAM: Shoot Apical Meristem.

mainly driven by mechanical constraints and, to a lesser extent, hydraulic constraints (Chapter 7) as suggested by previous studies (White, 1983a; Niklas, 1992; Normand et al., 2008; Olson et al., 2009; Levionnois et al., 2018a). Increasing stem size (and wood fraction) is a response to the static load imposed by numerous apical large leaves, as the mechanical resistance of a structure is proportional to the fourth-power of its radius (Chapter 7). But the higher wood area fraction might not fully compensate hydraulically for the total leaf area of monocauls, as observed by their lower Huber value (sapwood area to leaf area ratio). The increase in wood proportion is consequently accompanied by increase in vessel diameter, leading to higher hydraulic conductivity as hydraulic conductivity is a fourth-power function of the vessel diameter (Chapter 7). (iii) The relation between the above traits (monocauly, leaf size, stem thickness) and fruit size does not appear to be due to a higher production of photosynthates by large leaves contrary to previous suggestions (Primack, 1987; Cornelissen, 1999). The equal or lower proportions of transport and storage tissues (phloem, wood parenchyma) in monocauls than in branched species suggest similar carbon exchange capacity between leaves and lower organs (Chapter 7). We further think that, as for the observed leaf size – leaf number trade-off, spatial constraints of monocaulous stem limit the number of fruits, requiring larger fruits to maintain a constant seed number (Chapter 6). Such large fruits further increase the load already imposed by large leaves and probably further influence stem thickening in monocauls (Niklas, 1993) and the higher occurrence of cauliflory (Chapter 5). (iv) By focusing on vegetative functions rather than reproductive ones, we poorly investigated the relation between monocauly and inflorescence complexity. The homology between branches of branched species and inflorescences of monocaulous species in *Atractocarpus* involves a change of scale in what is considered the inflorescence. While the simple inflorescence of branched species (a compact dichasium) is terminal on each module, the "inflorescence" of monocaulous species is rather composed of two nested dichasium (the modular axillary complex and the primary

(A) Branched species: C2 = branche



(B) Monocaulous species: C2 = inflorescence

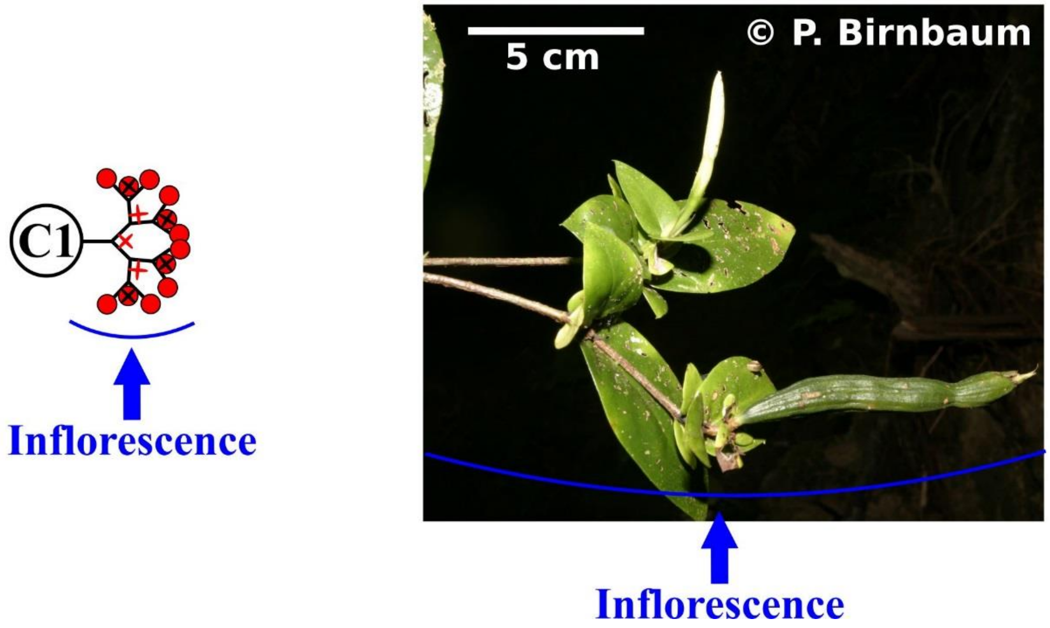


FIGURE 8.4 – Illustration of change in scale in what is considered the inflorescence for *Atractocarpus*. **(A)** In branched species, inflorescences are terminals on each module of the branche. **(B)** In monocaulous species, inflorescences are axillary on the trunk.

dichasium) (Figure 8.4). In this regard, inflorescences of monocauls could be considered as longer and more complex than those of branched species. But this case study appeared as a special case and we did not look further enough into this question to draw general conclusions.

Stem shape and mechanics – Monocauls are often noticed for their slender and little tapered stems (D'Arcy, 1973; Carlquist, 1974; Lauri, 2019). Describing a Hawaiian monocaulous species (*Cyanea leptostegia*), Carlquist (1974) noted that the stem diameter is almost equal between the basis and the apex of the plant. Distal parts were composed by a large pith and a thin cylinder of wood and basal parts by a small pith and a large cylinder of wood (Carlquist, 1974). This acropetal increase of pith in unbranched plants is also suggested in other studies (Eggert, 1961; Lauri, 1988) and confirmed by unpublished results of this thesis (Figure 8.5). As a result, we found larger pith in distal stems of monocaulous species (absolute value) compared to branched species but this increase was associated with larger wood cylinder, both tissues leading to thicker distal stems in monocauls compared to branched species (see above). But stem slenderness and tapering are also determined by plant basal diameter, which appears to be smaller for a given height in monocauls than in branched species (Figure 8.6). The higher proportion of wood in distal parts with a smaller basal diameter of monocaulous species probably involves a differential cambial activity along the stem. We suppose that this pattern results from the lack of branching which involves a lower static load along the stem of monocauls and slower basipetal diameter increment (cambial activity), leading to higher slenderness and – because of thick distal stem – lower tapering (Chapter 7, Figure 8.3). From mechanical perspectives, slenderness and low tapering can probably occur because of the lower static load inherent to the absence of branches. If true, the geometry of the stem would not require mechanical reinforcement along the stem. Unpublished results of this thesis indicated that young modulus (i.e. bending resistance) measured for basal parts of

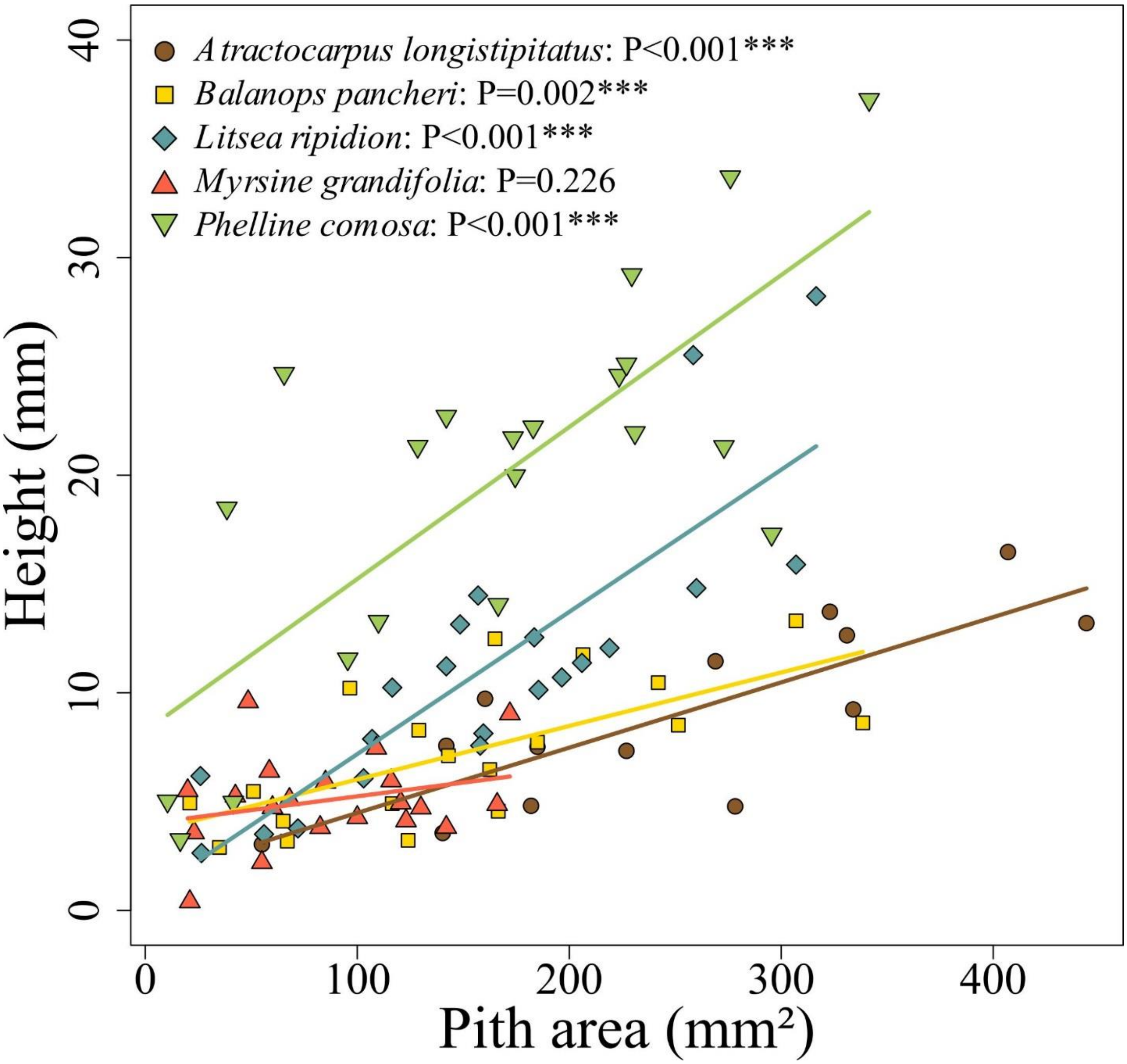


FIGURE 8.5 – Relationship between pith area and distance to the basis for five monocaulous species (five individual per species). P represent the p.values for the significance of regressions (*** $P < 0.001$, ** $P < 0.01$). Only *Myrsine grandifolia* (Primulaceae) showed non-significant increase of pith area with distance to the base but height data have a more restricted range for this species.

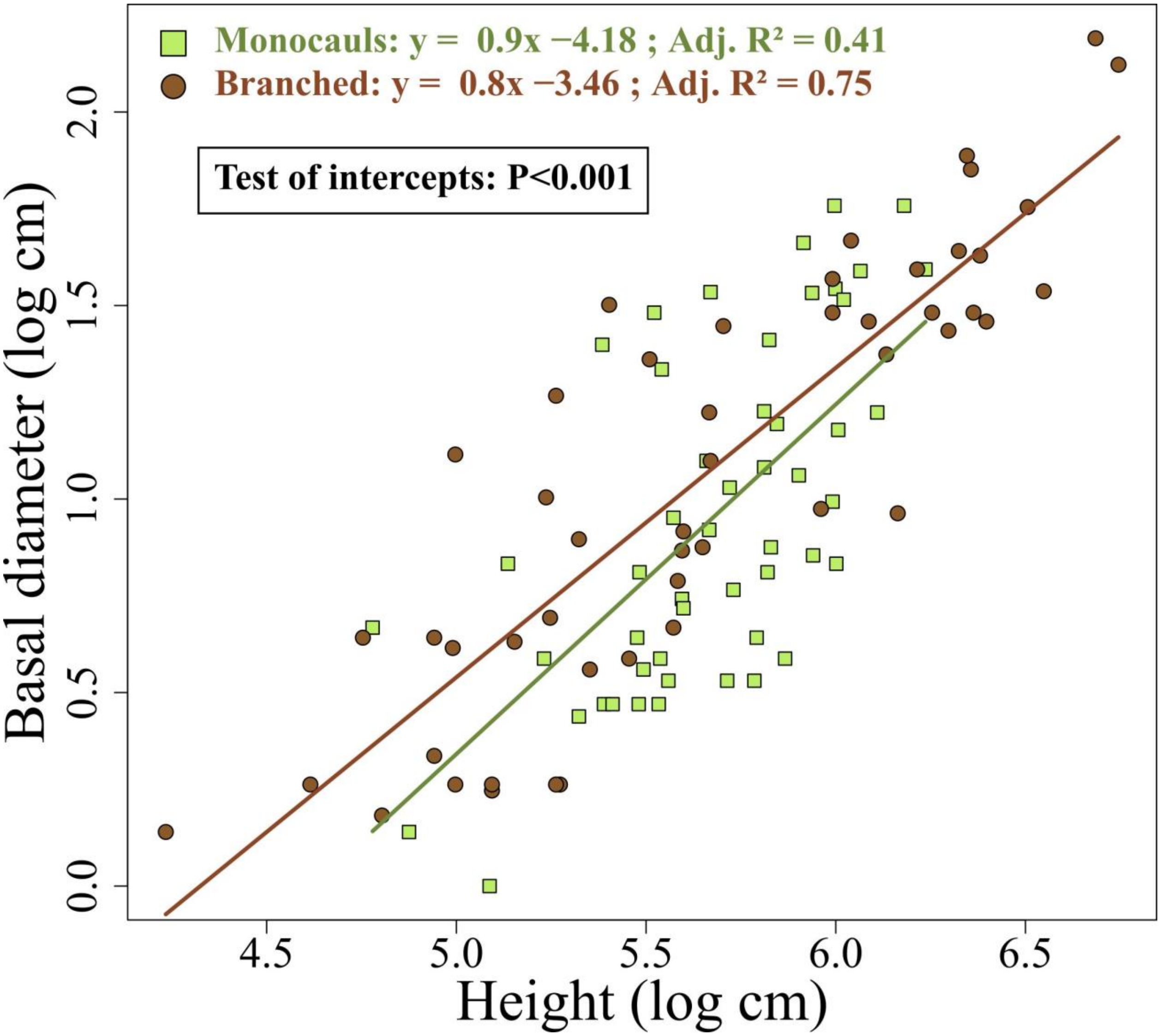


FIGURE 8.6 – Relationship between height and basal diameter for monocaulous and branched species (data from chapter 7). Monocaulous species have a significantly lower basal diameter for a given height, leading in higher stem slenderness.

monocaulous plants (between 4000 and 10000 MPa, Figure 8.7) were in the range of values measured for branches of other trees (between 5000 and 14000 MPa, Niklas, 1992). Further investigations should integrate variation in bending modulus along the stem, and height to stem allometries (Niklas and Speck, 2001; Niklas et al., 2006). In this respect, a diversity of mechanical behaviors seem to emerge in monocaulous species (Figure 8.7), whose geometrical and anatomical drivers will be investigated in a future publication.

***Photosynthesis and growth rates* –** Beyond their larger area, investigated leaf traits failed to clearly identify photosynthetic strategy of monocaulous plants (Chapter 7). Monocaulous leaves tend to exhibit lower SLA (Chapter 6), particularly for such large leaves (Chapter 7), higher leaf thickness and lower stomata density (Chapter 7). This combination of trait values suggest lower photosynthetic capacities for monocauls in comparison to their branched relatives, but this has to be confirmed by further measurements. Another publication, focusing on leaf traits diversity in one of the richest monocaulous families (the Araliaceae), is under progress and shows a relation between leaf traits and branching intensity, but divergent allocating patterns according to leaf type (simple, palmate or pinnate) (Gril, Bruy, Heinz & Isnard, *in prep.*, Appendix 4). Monocauls also tend to have shorter internodes (but only marginally significant in Chapter 6) that, together with higher secondary growth in distal stems, suggests lower primary growth rates. Several monocaulous species of different ages and growing in rainforest understory on ultramafic substrate were marked at the beginning of this thesis. The growth was too slow for the results to be interpreted in the course of the thesis. In 607 days (from 25/07/2016 to 24/03/2018), *Pittosporum pronyense* individuals produced between 0 and 1 growth unit, *Tapeinosperma gracile* between 0 and 2 growth units, *Atractocarpus bracteatus* between one and two phytomers (continuous growth, see Chapter 6) and none of the individuals of *Balanops pancheri* produced any phytomers. Growth

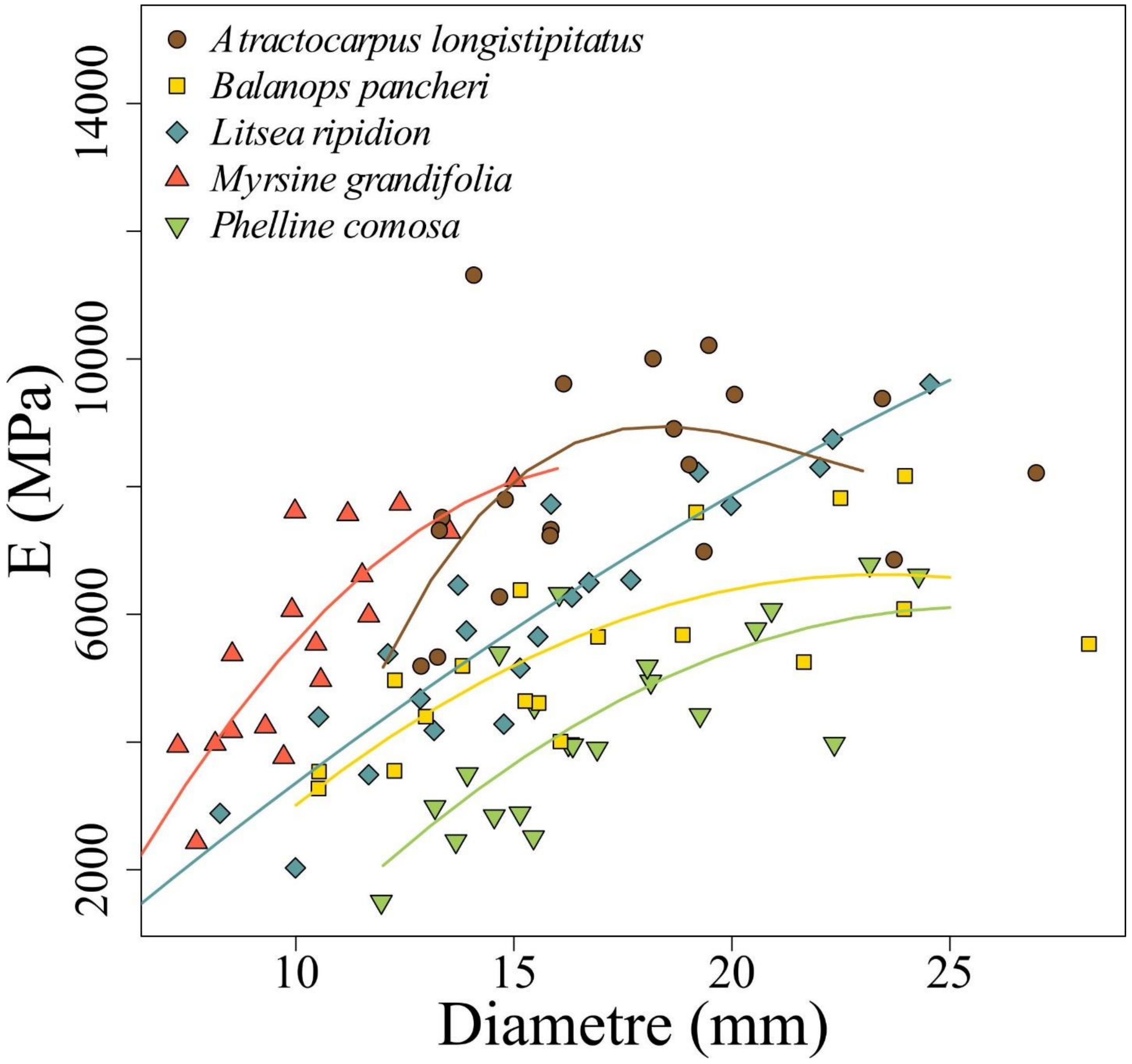


FIGURE 8.7 – Relationship between Young modulus and stem diameter for five monocaulous species.

rates seem higher for young plants than for older ones (which is, however, not yet testable). These preliminary results, which need to be further explored (effect of substrate, comparison with co-occurring branched species), together with the putative low photosynthetic capacities, suggest a marked conservative resource strategy for monocaulous species, at least higher than for branched relatives. The comparison of our SLA values with those of the TRY Database (Kattge et al., 2011) suggests that this strategy is among the most conservative in a global spectrum including other growth habits and regions of occurrence (Chapter 7).

In conclusion, as for other growth habits, monocauly is not only characterized by the lack of lateral branches but by a complex combination of inter-related traits. Spatial constraint on a single stem appeared to be the main origin of all suites of trait attributes, for which Corner's rules are one of the central themes, illustrating functional constraints of plant form evolution (Figure 8.3). Consequently, selection for a given trait attribute in a given environmental is likely to drive the variation of whole plant form and functions.

8.2.2 Environmental constraints on monocauly

Along with unbranched stems, the most remarkable functional characteristics of monocaulous plants are their large, mostly simple leaves (Chapter 5), which are among the largest worldwide (Chapter 7). Large simple leaves are disadvantaged in arid and cold conditions due to their thicker boundary layer that slows thermoregulation (Vogel, 2009; Wright et al., 2017). This physiological risk constrains the distribution of large simple leaves to humid and shady environments, providing buffered thermal and hydric conditions (Givnish, 1979, 1987, 1988). These physiological vulnerability of large leaves probably explains why monocaulous species are mainly found in rainforest (89%, Chapter 5). Possibly, the ecological limitation of monocaulous plants is reinforced by their larger vessel diameter that could be related to a greater sensitivity to drought-induced embolism. The distribution of vessel size has been shown to be strongly limited by both temperature and precipitation (Zanne et al., 2013; Pfautsch et al., 2016; Hacke et al., 2017; Olson et al., 2018). Though, drought-induced embolism is also governed by conduit structures (e.g. pit membrane density and area, Tyree and Sperry, 1989; Hacke et al., 2000; Poorter et al., 2010) which were not measured here.

Chapter 5 indicates that the branched habit occurs in all types of environments and does not seem to show preference for rainforest contrary to monocaulous species. In *Atractocarpus* for instance, only branched species "escaped" from rainforest as shown by a study including some results of this thesis (Mouly, Barrabé & Bruy, *submitted*). Nevertheless, several monocaulous species occur out of rainforest as 35% of them (63 species) have been observed at least once in other vegetation and 11% (21 species) are restricted to maquis or dry forests. The sub-sampling used in Chapter 6 and 7 focused exclusively on rainforest understory as we aimed to detect traits involved in architectural transition in similar habitat. But monocaulous species from dry environments would present interesting case studies to understand the functional limit and trait variations within the monocaulous habit. For instance, we found that 79 % of monocaulous species occurring in dry vegetation had compound leaves or functionally similar phyllomorphic branches (Figure 8.8). Dissected lamina structures are a way to reduce vulnerability inherent to large leaves in open environment by reducing both the boundary layer (accelerating thermoregulation) and drag (limiting wind damages) (Givnish, 1978; Vogel, 2009; Wright et al., 2017). Regarding species with simple leaves (21% of dry vegetation monocauls), an often unconsidered aspect of Corner's rules is that relation between branching intensity and leaf size is effective when comparing similarly sized plants. Consequently, a way to reduce leaf area while remaining unbranched is to reduce whole plant size (Figure 8.8). For example, *Argophyllum acinetochromum* (Argophyllaceae) and

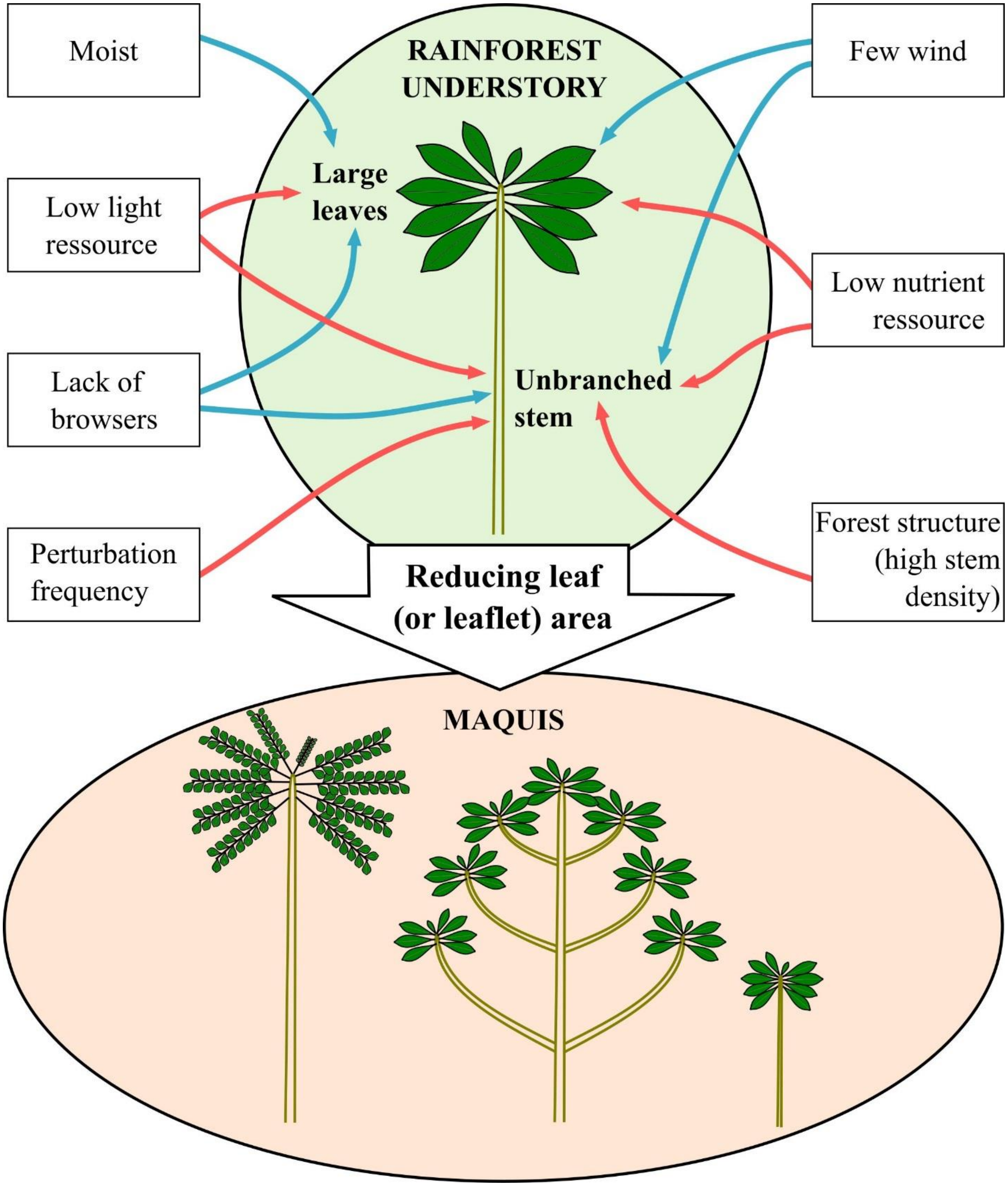


FIGURE 8.8 – Illustration of environmental conditions constraining (red arrows) or allowing (blue arrows) the occurrence of large leaves and unbranched stem in rainforest understory and illustration of three evolutionary ways for monocaulous species to colonize open and dry vegetation.

Scaevola beckii (Goodeniaceae), that are among the only monocaulous species with simple leaves from maquis are also among the smallest monocauls of the archipelago (< 1 m high), and their leaves are no larger than leaflets of co-occuring monocaulous species. Beyond reducing leaf size, plant height is also the main driver of vessel diameter worldwide (Olson et al., 2018) and small monocaulous plants are then likely to be less sensitive to drought embolism than their taller counterparts.

Modelling studies shown that, for a twig with a given total leaf area, few large leaves are economically more interesting than several small leaves (maximization of return on twig-leaf investment) (Smith et al., 2017). As a result, the monocaulous strategy, being at the extreme end of the leaf size – leaf number trade off, would be advantaged in resource poor environments (e.g. shady or with low soil fertility). Other environmental factors known to constrain leaf size are wind and browsing of which tearing probability increases with leaf size (Moles and Westoby, 2000; Vogel, 2009; Charles-Dominique et al., 2015).

8.2.3 Environmental correlates of monocauly in New Caledonia

If the evolution of monocauly is probably limited by a set of environmental conditions (Figure 8.8), several hypotheses can be proposed in regard to environmental factors that could have facilitated the evolution of monocauly in New Caledonia (Figure 8.9).

Tropical cyclones **–** New Caledonian rainforests are characterized by an outstanding high density of stems (Jaffré and Veillon, 1990; Jaffré and Veillon, 1995; Ibanez et al., 2014; Ibanez et al., 2017b), argued as the main structural characteristic that distinguish New Caledonia from other Southwest Pacific rainforests (Ibanez et al., 2017b). Recent insights suggest that this particularity is due to the high frequency and intensity of tropical cyclones in the region (Ibanez et al., 2018a). We think that such dense neighboring operate as a space constraint, somehow similar to “crown

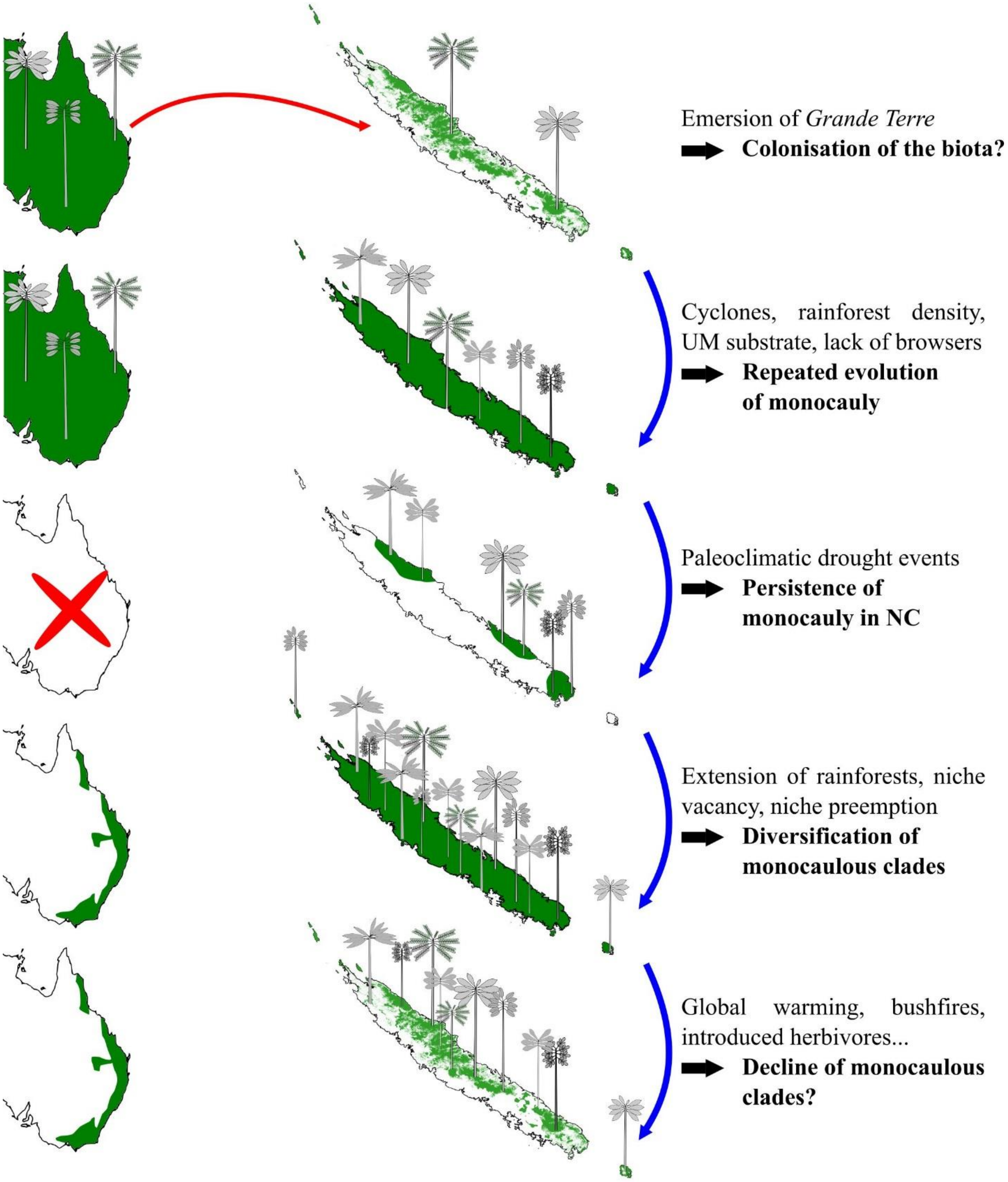


FIGURE 8.9 – Schematic illustration of main hypotheses explaining the outstanding prevalence of monocauly in New Caledonia.

shyness" (Putz et al., 1984), in which not abrasion but thigmomorphic response, favor selection toward reducing branching. In these conditions, unidirectional exploration strategy might be advantaged. Moreover, high cyclone frequency involves debris falls and damages through the domino effect, to which monocauls, lacking lateral branches, might be less sensitive (Figure 8.10). Supporting these hypotheses, palms and tree ferns are also particularly abundant in New Caledonian rainforests (Ibanez et al., 2017b), both groups being dominated by monocaulous architectures. We believe that the structural and dynamic features of these forests are important environmental contingencies of the convergence toward monocauly in New Caledonia (Chapter 5).

It is the first time that density of New Caledonian rainforest is suggested as a driver of the New Caledonian disharmony. This particularity is actually more likely to affect growth habit distribution which is known to be highly dependent on forest structure (e.g. Schnitzer, 2018). This potential effect on functional disharmony is likely to indirectly affect taxonomical disharmony through the over-representation of typically single-stemmed groups (e.g. Palms: 40 species, Tree ferns: 16 species).

Rainforest history **–** The long-time persistence of rainforest on the archipelago while they declined from adjacent regions (see Chapter 2) is supposed to be responsible for the high incidence of several drought-sensitive groups such as Palms (Pintaud et al., 2001) or basal Angiosperms (Poncet et al., 2013; Pouteau et al., 2015; Trueba, 2016; Tournebize et al., 2017). This mechanism is also likely to drive the current high representation of monocaulous lineages, through different possible scenarios. (i) Monocaulous would have survived in rainforest refugia while their regional relatives disappeared, (ii) the post-Pleistocene expansion of rainforests produced vacant niches for rainforest groups, and favored niche pre-emption in the understory, as suggested for *Atractocarpus* (Chapter 6).

FIGURE 8.10 – Illustration of the possible advantage of monocaulous species under forest perturbation. In this high elevation rainforest (Dent de Saint Vincent), only two monocaulous plant and tree ferns escaped the fall of a large tree.

Apart from the genus *Atractocarpus*, such ecological opportunities are likely to have driven the diversification of several rainforest lineages timely present in New Caledonian rainforest. Accordingly, three palms clades, strongly associated with rainforest and dominated by unbranched architecture, showed stem ages and crown ages similar to that of *Atractocarpus* (Pillon, 2012), and their current distribution was suggested to be related with Pleistocene refugia (Pintaud et al., 2001). As such, alternation in expansion and contraction of rain forests in response to climatic fluctuation during Pleistocene is likely to be an important driver of current New Caledonian biodiversity (Jaffré and Veillon, 1995; Poncet et al., 2013; Pouteau et al., 2015). More globally, late quaternary climatic change have been suggested to impact current pattern of biodiversity in islands, notably due to variations in islands area (Weigelt et al., 2016).

Edaphic constraints – The presence on one third of the territory of the worldwide rare ultramafic substrate is largely recognized as one of the main drivers of taxonomic disharmony in the New Caledonian flora (Jaffré et al., 1987; Pillon et al., 2010; Isnard et al., 2016). The constraining conditions for plant growth challenge the establishment of most species – there are for instance very few invasive species on this substrate (Jaffré, 1980; Meyer et al., 2006) – while favoring the installation of pre-adapted plant lineages (Pillon et al., 2010). Adaptation to ultramafic substrate also drove the functional disharmony with for example an outstanding proportion of metal hyper-accumulator species (Jaffré et al., 2013; van der Ent et al., 2015; Jaffré et al., 2018). We bring further demonstration of the importance of this substrate on functional disharmony by showing that the monocaulous habit preferentially evolved on ultramafic soils (Chapter 5). Such constraining edaphic conditions are likely to favor the economic "few large leaves, no branches" strategy characterizing monocaulous plants. Effect of soil constraints on plant architecture has little been investigated but recent insights suggest that poor soil fertility reduces the structural development of trees (Levionnois et al., 2018b). In extreme cases, low soil fertility was observed to reduce the branched architecture of *Cecropia obtusa* into monocaulous trees, a phenomena called architectural pauperization (Barthélémy, 1988). In New Caledonia, some authors also suggested that constraining edaphic conditions linked to ultramafic substrate could be responsible for the frequency of tuft-trees in the island (Virot, 1956; Veillon, 1976). The frequency of ultramafic substrate in New Caledonia could then have contributed to the repeated evolution of monocauly in the archipelago through the reduction of growth and structural expression of branched species, ultimately leading to single stemmed plants. In accordance with this hypothesis, some species growing on ultramafic substrate exhibit few but regular branching (suggesting sequential branching) or a strictly monocaulous habit (e.g. *Cunonia macrophylla*), possibly depending on soil conditions.

If monocauly evolved principally on ultramafic, the proportion of species occurring on this substrate is not very different than for branched species (47% vs. 44% respectively, Chapter 5), suggesting further diversification of monocauly on non-ultramafic substrates. This does not seem to pertain to calcareous substrate since only two monocaulous species (*Acropogon calcicolus* and *Plerandra calcicola*) are restricted to this substrate and few monocaulous species occur in Loyalty Islands (less than ten and no endemics).

Herbivory **–** Absence of natural large browsers on islands is well known to allow the evolution of unarmed species, leading to insular naivety (Whittaker et al., 2017). Such process could be particularly striking in New Caledonia as there is no autochthonous large herbivorous species and no extinct browsing giant bird are known from the archipelago (*Sylviornis* was probably carnivorous or frugivorous, Mourer-Chauviré and Balouet, 2005; Worthy et al., 2016) contrary to other Pacific islands (e.g. Moanalos in Hawai, Olson and James, 1991; Moas in New

Zealand, Worthy and Holdaway, 2002). Two types of defense against herbivory are recognized: chemical and structural (Charles-Dominique et al., 2017). While the former has not been investigated for the New Caledonian flora (but hyper-accumulation of trace elements is suggested to evolve as a response to herbivory, Boyd, 2007; Pillon et al., 2014), the latter appears to be rare since very few indigenous species are armed with spines or thorns (*Carissa ovata*, *Maclura cochinchinensis*, *Capparis* spp., *Mezoneuron* spp.) and all are more or less specialized climbers (Bruy et al., 2018). Recent studies showed that structural defenses can also be achieved through particular architectural design: the more intrinsically branched is a plant, the more effective is the protection (Costes et al., 2013; Charles-Dominique et al., 2015; Charles-Dominique et al., 2017). In this context, monocauls with their single meristem and large leaves appeared to be disarmed against large herbivores. This insight is confirmed by IUCN redlist data showing that monocaulous species are more threatened by introduced herbivores than branched species (Chapter 5). Accordingly, monocaulous species of *Cyanea* (Campanulaceae) in Hawaii where browsing birds were present, have thorn-like prickles to protect the stem (Givnish, 1994).

As such, the absence of large herbivores in New Caledonia, largely present in other areas, released plants from a strong exogenous constraint and from selection against reduction of meristem redundancy, possibly allowing the specific evolution of the monocaulous habit in the archipelago.

8.2.4 Monocauly and species diversification

Evidence showed that evolutionary shift in growth habit often impacts diversification of clades (Gianoli, 2004; Roquet et al., 2013; Couvreur et al., 2015; Gianoli, 2015; Frenzke et al., 2016). In New Caledonia, we found a positive relationship between presence of monocauly in a genus and overall diversity of the genus (Chapter 5), but monocauly did not increase diversification rates more than other growth habits in the genus *Atractocarpus* (Chapter 6). More generally, genera with more than two monocaulous species are infrequent, and genera constituted by a majority of monocaulous species even more (Chapter 5). As such, while large monocaulous genera still have to be investigated (e.g. *Phyllanthus*, *Acropogon*, *Bocquillonia*), dramatic large radiations of monocaulous clades seem uncommon. It remains difficult to assess if this low number of monocaulous species per genera is associated with low speciation rate or with high extinction events, especially in the absence of calibrated phylogeny. Extinction could have been important in New Caledonia, if we considered the high incidence of phylogenetically isolated taxa (Pillon, 2012; Pillon et al., 2017). But the recent evolution of the habit in *Atractocarpus* and *Oxera* (between 2.4 and 0.6 Myr) rather suggests clades under diversification. Anyway, evidence suggests that monocauly probably did not increase diversification as a key innovation, i.e. by allowing the colonization of large and vacant niches involving rapid diversification of descendants (Heard and Hauser, 1995). We nevertheless suggest that, at least in some clades, the evolution of monocauly could have impacted diversification of clades through niche partitioning.

If large scale abiotic constraints drove the convergence toward monocauly in different lineages (see above), small scale biotic interaction between co-occurring species probably drove the divergence among growth habit. In the genus *Atractocarpus*, we identified a rapid diversification of architecture, and repeated evolution of monocauly, among closely related species that seem concomitant with speciation (Chapter 6). We hypothesized that competition between co-occurring species drove the divergence among growth habit through niche partitioning. For *Atractocarpus*, field observations further suggest that species with same growth habit are either rarely in sympatry or belong to different clades. As such, our case study could identify an example of adaptive radiation, i.e. “the rise of a diversity of ecological roles and associated adaptations within a lineage" (Givnish, 2016). Three of the four criteria of an adaptive radiation as defined by Schluter (2000) were satisfied: (i) common ancestry with the single colonization of the biota ca. 2.4 Myr ago; (ii) rapid speciation, *Atractocarpus* being the New Caledonian genera with the highest diversification rate currently known (1.17 species species^{-1} Myr^{-1}); and (iii) trait utility since growth habit was shown to be related to several ecologically important functional traits related to resources acquisition and use. The fourth criteria is the correlation between phenotype and environment and while the correlation between growth habit and ecological strategy suggests different niches, we did not investigate this aspect of adaptive radiation. Species occurring in other environments (dry forests and maquis) and their growth habits may have provided some additional support for the idea that divergent habitats lead to divergence in key functional traits via architectural evolution (Chapter 6). For instance, two species of *Atractocarpus* occurring respectively in maquis and dry forest seemed to express a very different architecture (3 axis categories) from those of rainforest (2 axis categories, Chapter 6). Unfortunately, environments were too degraded to accurately describe architecture of such species. More fundamentally, we were interested in shifts in growth habit in relation to functional diversification, the consideration of contrasting environments would have blurred the signal. We argue that further investigation linking environmental traits (e.g. vegetation structure, light availability, altitude, soils) and species distribution could accomplish to demonstrate that *Atractocarpus* represents one of the few cases of adaptive radiation in New Caledonia (see Pillon et al., 2017). We suspect that this adaptive radiation in association with growth habit involves reproductive strategy (fruit size and shape, flower shape) that appears to be variable in the genus (Mouly et al., *submitted*).

The genus *Bocquillonia*, for which no dated phylogenies are available (Chapter 4), could also exemplify another case of adaptive radiation involving growth habit diversification in relation to forest structure. In this genus, we showed that variation in plant size and branching intensity (here reiteration) led to different growth habits exploiting different strata of the rainforest, dry forest and maquis (Chapter 4, Figure 4.1).

8.3 Plant architecture as a key tool to depict plant evolution

8.3.1 Architectural and functional traits to define growth habits

Since Theophraste (372 B.C.), many classifications of plant growth habits have been proposed (reviewed in Du Rietz, 1931; Lacza and Fekete, 1969; Millan, 2016). Classes and their definitions largely differ among studies, authors disagreeing on the nature and hierarchy of characters to use. The main reason why no consensus has been found so far lies in the difficulty to propose universal classification that would rely on objective and functional criteria (Millan, 2016). One of the most used classifications (see Pérez-Harguindeguy et al., 2013) is that of Raunkiaer, that considers position of buds in plants (Raunkiaer, 1904). This definition was functionally meaningful, since based on strategies to survive winter in temperate regions, but cannot be generalized to the tropical regions. Most of the universal classifications proposed to date consider monocaulous plants in a more or less broad definition (e.g. Von Humboldt, 1808; Reiter, 1885; Warming, 1909; Du Rietz, 1931). These classifications are however often highly subjective. For instance, “Tuft-trees” in the well-known classification of (Warming, 1909) was defined as follows: “Shoots with short internodes ; leaves densely set on the end of the shoot, large, and few ; buds usually naked”. Almost all the used terms are subjective (“short”, “densely”, “large”, “few”, “usually”), and classification will consequently be largely influenced by observer.

The approach of Hallé et al. (1978), based on plant architecture, provides more objective criteria and can be generalized to most plants (Cremers, 1973, 1974; Jeannoda-Robinson, 1977;

Cremers and Edelin, 1995; Prosperi and Caballé, 2001; Hallé, 2004; Millan, 2016). Hallé et al. (1978) considered monocaulous as "trees with a single trunk or visible stem of the plant". This physiognomical definition was reinforced by three distinct structural types, namely the Holttum's, the Corner's, and the Chamberlain's architectural models, each defined by few qualitative morphological characters (see Chapter 2). But this strictly architectural approach also has limitations. (i) Hallé et al. (1978) considered morphological origins of structures (e.g. stem or leaf) rather than their functions (e.g. exploration or photosynthesis), making their classification sometimes inappropriate to a given ecological context. For example, architectural analysis of the genus *Atractocarpus* (Chapter 6) showed that some inflorescences (virtually no photosynthetic contribution, e.g. *A. longistipitatus*) could have exactly the same structural construction than a large photosynthetic branch (e.g. *A. artensis*). (ii) Architectural models are known to be stable states among an "architectural continuum" (Hallé et al., 1978; Barthélémy et al., 1989), i.e. an infinity of intermediate forms potentially exist. This phenomena was perfectly illustrated in the genus *Atractocarpus* where we showed a continuous transition between the Stone's model and the Corner's model, branches gradually becoming inflorescences (Chapter 6).

In this study we combined the architectural and functional approach to propose a definition more adapted to an ecological context; we defined monocauls as "self-supporting woody plants whose cardinal functions rely on a single visible stem". This definition was reinforced by the characterization of structural types that allow the use of objective morphological criteria. We recognize three structural types made of (i) a trunk (either monoaxial or pluriaxial), (ii) determinate growth structure highly specialized in photosynthesis and with an abscission point, (iii) axis or complex of axis highly specialized in reproduction and whose contribution to whole plant vegetative exploration and photosynthesis is negligible, and possibly (iv) opportunistic reiterates.

Finally, to resolve the problem of architectural continuum, we defined a functional branching index directly linking branching intensity and associated ecological functions (Chapter 6). This simple index, assessing the part of photosynthesis and exploration functions assumed by the different axis categories, ranges from 0 to 1 and is very easy to interpret. For example, species of *Atractocarpus* were considered as monocaulous when trunk assumes more than 80% of exploration functions and 95% of photosynthetic functions, i.e. when these functions are considered as “negligible” on lateral axis based on a *a priori* statistical analysis (significant grouping of the distribution of function).

Our definition of monocauly, based on a quantitative hierarchization of functions (here the branching index) and reinforced by non-ambiguous morphological criteria, proved to be relevant in our restricted ecological and evolutionary context. While this branching index seems difficult to use on some plant groups (e.g. with polyarchic architecture, Edelin, 1991), the general approach proposed here, merging architecture and functions, seems promising for the study of plant growth habit in an ecological and evolutionary context. It further shows that future directions in this field do not only rely on the use of big data, but rather on detailed studies aiming to improve our understanding of mechanisms responsible for plant forms and functions.

8.3.2 Heterochronic evolution

As far as we know, two developmental processes have been proposed for the evolution of monocauly: (i) evolution from herbaceous ancestors (e.g. Carlquist, 1974), through “proportionate giantism” and (ii) evolution from tree ancestors (D'Arcy, 1973), through “progenesis” and “neoteny” (see Chapter 3, Figure 3.1). Both processes involve heterochronic developmental pathways (i.e. a change in the relative timing of developmental events in one species relative to an ancestral species) on whole plant architecture. In this thesis, an additional evolutionary developmental process involved in the evolution of monocauly has been identified (Chapter 6).

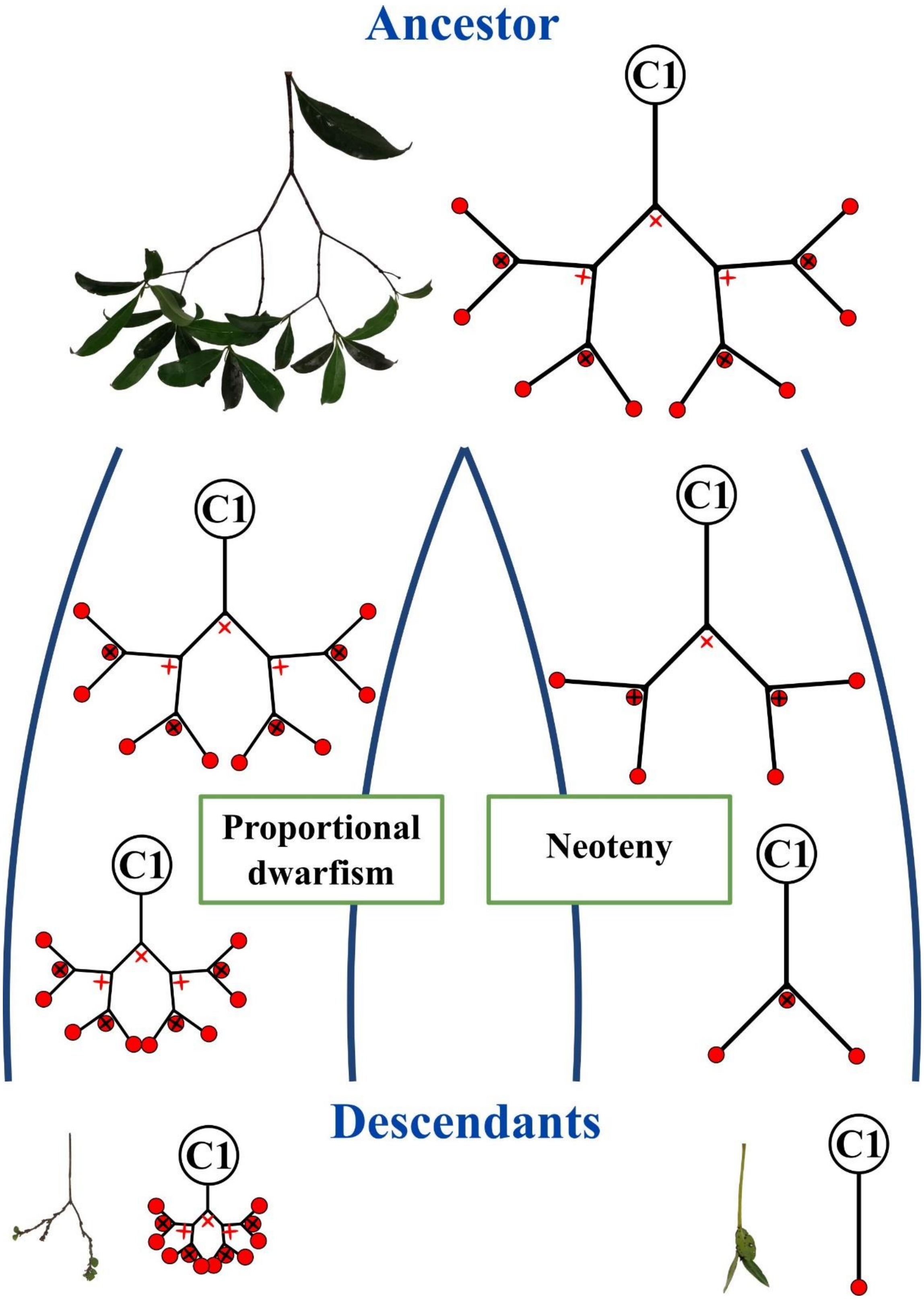


FIGURE 8.11 – Illustration of heterochronic processes occurring on axillary structures in *Atractocarpus* and leading to monocauly.

This process might also involve heterochrony, not on the whole plant architecture but on axillary structures (C2) only (Figure 8.11). (i) When branching is structurally reduced through the reduction of module number, the resulting axillary structure of the descendant is a truncated part of that of the ancestor, involving neoteny (Gould, 1977; Alberch et al., 1979; Smith, 2001). (ii) When branching is structurally reduced through module length, the resulting axillary structure of the descendant is the miniaturized copy of that of the ancestor, involving "proportional dwarfism" (Gould, 1977; Alberch et al., 1979; Smith, 2001). Note that some monocaulous species having few and short modules (e.g. *Atractocarpus confertus*) probably underwent both processes. As such, even if appearing in closely related taxa through a similar process (i.e. reduction of branches), developmental pathways leading to the evolution of growth habits could be much diversified and would need careful observation at lower integration levels.

We think that the evolution of monocauly through the reduction of branches in *Atractocarpus* is not an isolated case and probably occurred in other plant groups. We particularly recognize the genus *Tapeinosperma* (7 monocaulous species) where axillary structures range from long orthotropic branches (Scarrone's architectural model) to short determinate inflorescences on unbranched trunk (Corner's architectural model), with several intermediate states (Figure 8.12-A).

Evolution from herbaceous ancestors were hitherto illustrated for other geographic areas (e.g. Macaronesia, Böhle et al., 1996; Mort et al., 2007) but probably concerned few clades in New Caledonia (Chapter 5), of which we recognize the genus *Oxalis*. New Caledonian species actually range from creeping herbaceous species with several short rosettes of leaves, to creeping/semi-erect woody species with several short rosette of leaves, erect woody species with few large rosette of leaves, and monocaulous species (Figure 8.12-B). This pattern illustrates an interesting architectural gradient where anatomy, biomechanics and architecture seems intrinsically related.

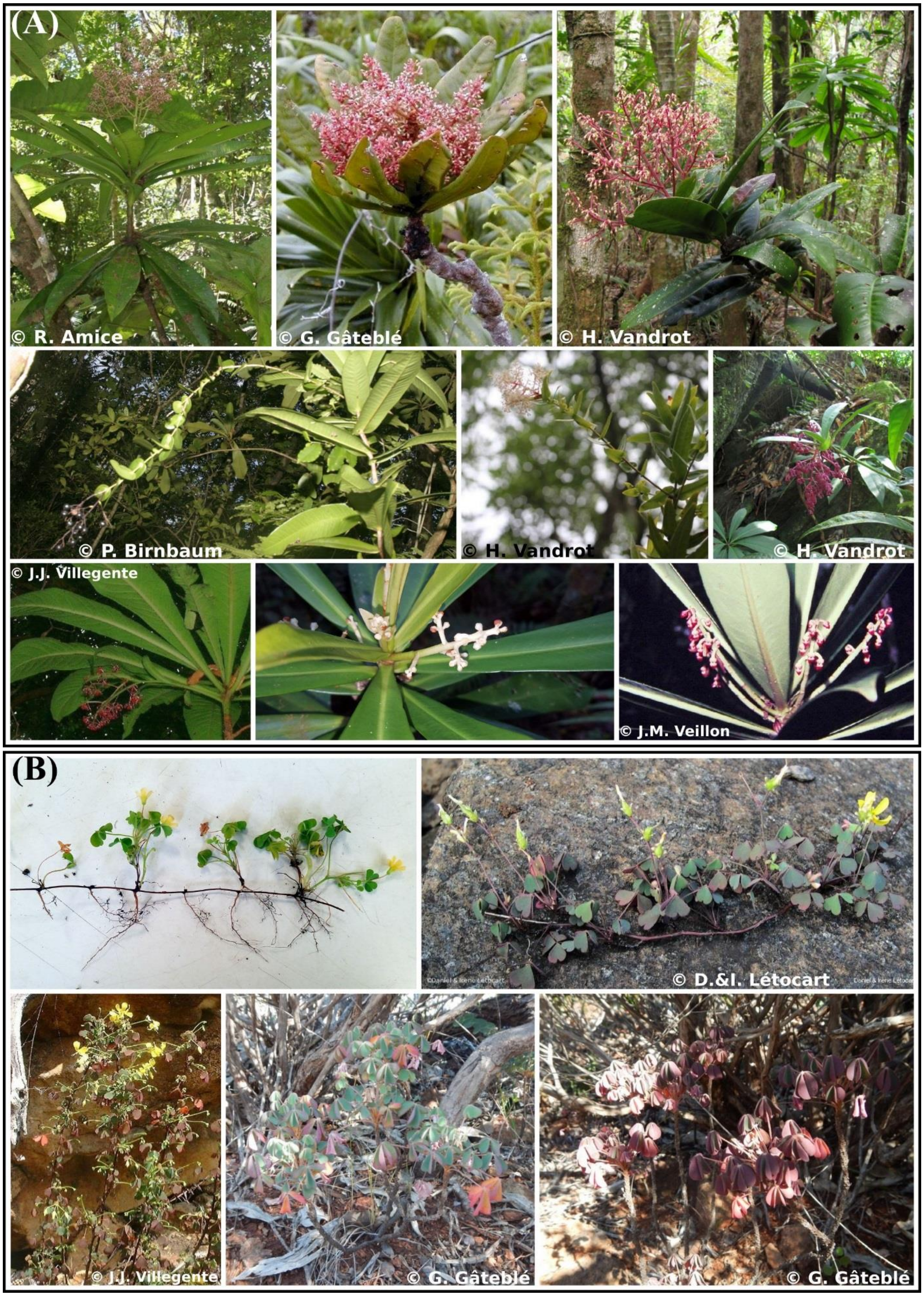


FIGURE 8.12 – Illustration of architectural gradient in **(A)** *Tapeinosperma* (Primulaceae): reduction of large branches toward determinate inflorescences (from top left to bottom right), and **(B)** *Oxalis* (Oxalidaceae): increasing woodiness and self-supporting while reducing branching (from top left to bottom right).

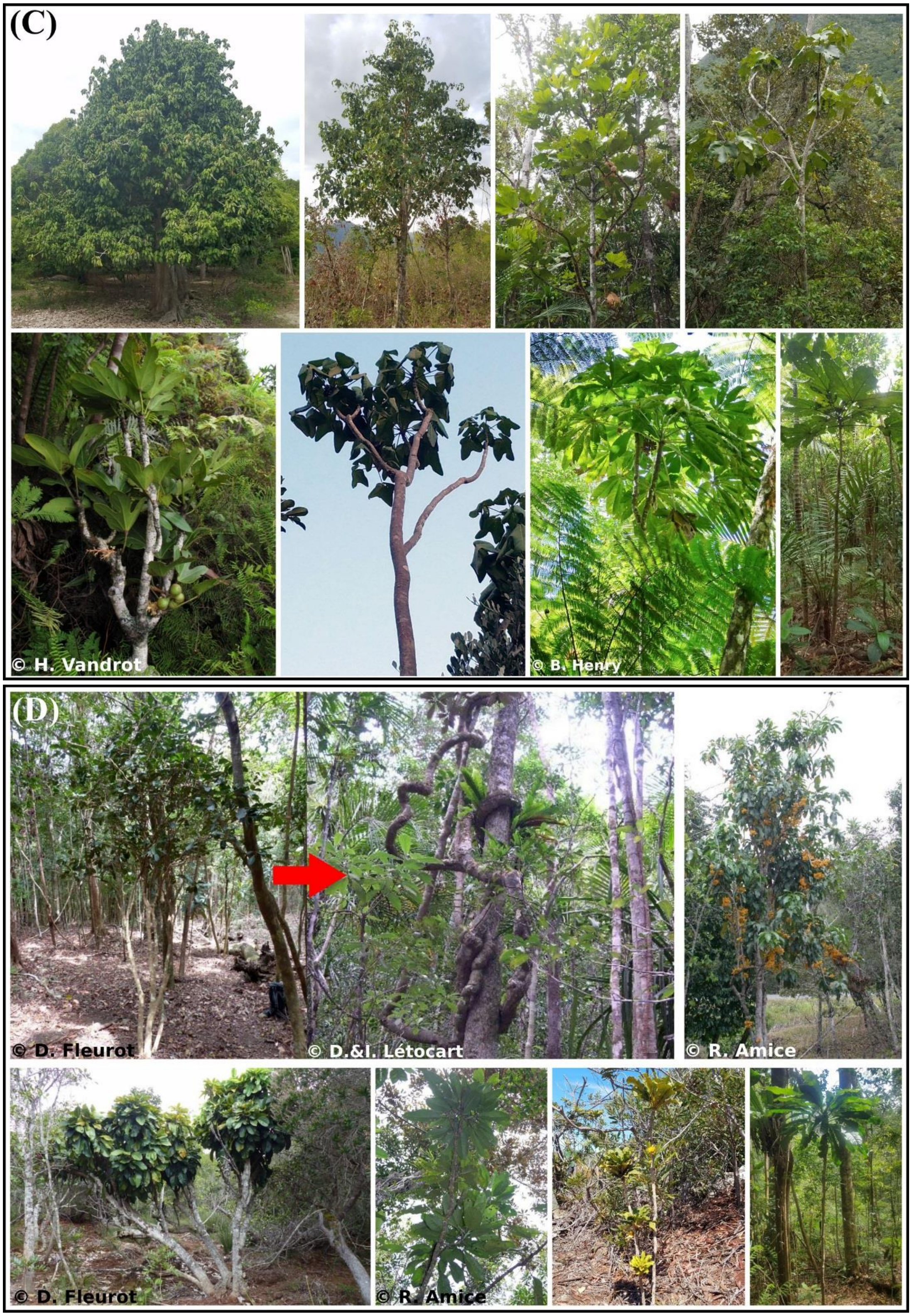


FIGURE 8.12 (continuation) – Illustration of architectural gradient in **(C)** *Acropogon* (Malvaceae): reducing reiteration frequency and predictability (from top left to bottom right), and **(D)** *Oxera* (Lamiaceae): increasing duration of juvenile self-supporting phase and reducing branching (from top left to bottom right).

Evolution of monocauly from canopy tree as suggested by D'Arcy (1973) was probably among the most frequent evolutionary pathways and the genus *Acropogon* (Malvaceae) seems an appropriate model to investigate this question. In this genus, architecture range from branched trees (Rauh's architectural model) – either flowering after or before the development of the first branches – to opportunistically reiterated monocauls or unreiterated monocauls (Corner's architectural model) (Figure 8.12-C).

Apart from this thesis, the only New Caledonian genus whose growth habit was investigated in a phylogenetic context is *Oxera* (Lamiaceae) where monocauly evolved from woody liana ancestors (Barrabé et al., 2018). We assume that this evolution could also involve heterochronic developmental process since architecture of extant climbing species is constructed by the frequent repetition of a single axis category (Champagnat's architectural model, Veillon, 1976) and species present quite a long juvenile self-supporting phase (Figure 8.12-D).

All these insights remain mainly speculative but suggest that architecture is a robust and perfectly fitted approach to assess heterochrony which has most probably been fundamental in the evolution of growth habit (Rowe and Speck, 2005; Wagner et al., 2012), at least as important as wood ontogeny (Olson, 2007; Carlquist, 2009). The New Caledonian flora, including several young clades with contrasting growth habits and intermediate states, might be well suited for investigating this promising research field.

8.3.3 The reiteration process: a gap that needs to be filled

Reiteration is defined as "a morphogenetic process through which the organism duplicates its own elementary architecture, i.e. its architectural unit" (Barthélémy and Caraglio, 2007). Reiteration, of which several modalities have been defined (see Chapter 2), is a key process in plant morphogenesis. For instance, sequential reiteration has been shown as fundamental in the expression of endogenous architecture of several plants, particularly in the development of tree crowns (Edelin, 1984; Barthélémy et al., 1991; Barthélémy and Caraglio, 2007). Opportunistic reiteration is one of the main adaptive processes by which a plant adapts its form after traumatism or increase in resource level (Oldeman, 1974; Barthélémy and Caraglio, 2007). In New Caledonia for example, all studied (non-monocot) monocaulous species showed the ability to reiterate at least after a traumatism. We assume that this process, inherent in most species, is particularly important for the monocaulous habit for which exploration and photosynthesis rely on a single trunk.

While the difference between sequential and opportunistic reiteration seems obvious in theory, the former being genetically determined (endogenous) and the second induced by environment (exogenous), it is not that apparent in the field. This represents the major difficulty we have not been able to solve in our definition of monocauly. We actually found several monocaulous species that could be such reiterated that they lost their monocaulous physiognomy, as illustrated by *Bocquillonia grandidens* (Chapter 4, Figure 4.1). Due to their sometimes slightly curved stem, the architecture of this species could have also been associated with the Champagnat's architectural model (Hallé et al., 1978), and therefore not considered as monocaulous. This illustrates a limit of architectural models to finely understand plant architecture and processes involved in their evolution. We actually found that different models such as the Corner's model (e.g. *Bocquillonia corneri*), the Champagnat's model (e.g. *Bocquillonia grandidens*) or the Tomlinson's model (e.g. *Bocquillonia* aff. *sessiliflora*) could be differentiated only on the basis of number and position of opportunistic reiterates, two features assumed to be rather exogenously than endogenously induced (Barthélémy and Caraglio, 2007).

This is particularly problematic when not only the physiognomy but also the ecological characteristics are lost, as in *Dysoxylum* aff. *roseum* (Meliaceae). This species has a long monocaulous phase in the rainforest understory where several flowering and fruiting occur (Figure 8.13). After a longer or shorter period, individuals produce new axes from dormant buds. These axes are morphologically and functionally identical to the primary trunk and their apparition is predictable neither in time nor in space (sometimes nearly not occurring): they are delayed opportunistic reiterates (see Chapter 2). In several cases, these reiterates become more and more numerous until the tree reaches the canopy and has a well-developed crown (Figure 8.13). As such, the inclusion of the opportunistic reiteration process in our definition involves the comparison of small understory monocaulous treelets with tall canopy well-branched trees. But the exclusion of this process is impossible as all of observed monocauls in New Caledonia have the ability to reiterate. A criteria/threshold based on a number of reiteration could have been a solution but unsatisfying from our point of view since the process depends on environmental conditions and is consequently highly variable between individuals for a given species.

Nevertheless, the maximal number of reiterates supported is not equal between taxa, some species or genus having a greater propensity for opportunistic reiteration. This shows that the process is not totally independent from genetic background of plant individual and could be heritable. As such, further investigations are needed on the difference between sequential and opportunistic reiterations that sometimes seem to be two extremes of the same gradient. Besides, fine architectural study in a phylogenetic context (as in Chapter 6) would bring interesting information about the importance of reiteration process in the evolution of growth habit (see *Acropogon*, Figure 8.12-C). The simple structure of monocaulous plants makes them particularly suited to investigate this question.

8.3.4 Constrained evolution of plant architecture

Convergent evolution is considered as a major evidence of evolutionary constraint, i.e. that

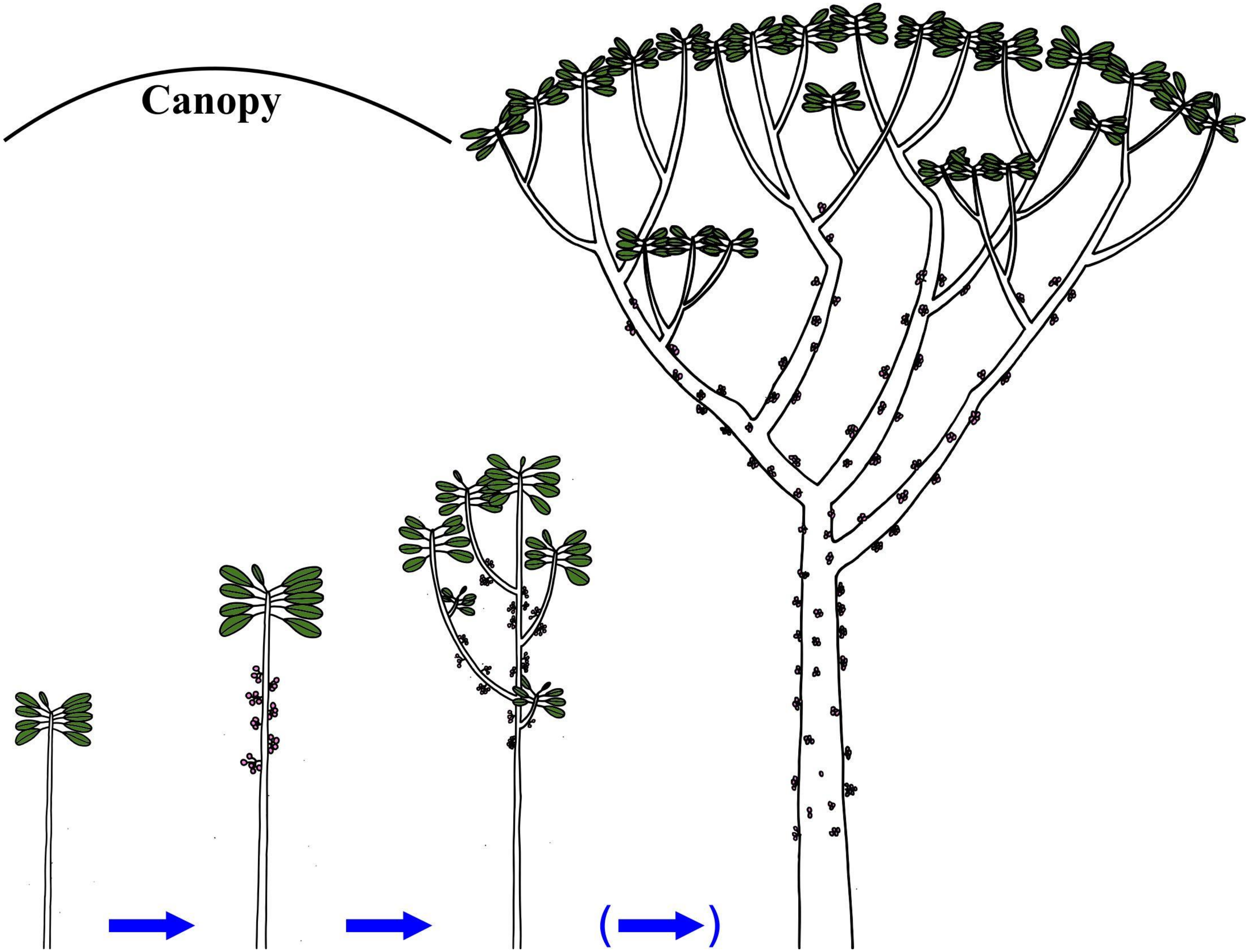


FIGURE 8.13 – Developmental sequence of *Dysoxylum* aff. *roseum*, a monocaulous treelet that could become a canopy tree by means of opportunistic reiteration. The fourth stage does not always occurs.

evolutionary pathways are constrained by a limited set of functional and developmental possibilities (McGhee, 2011). We showed that the monocaulous habit is coherent in terms of functional properties but is achieved in different, though limited, structural ways. We recognize three different structural types in New Caledonia in agreement with our functional definition of monocauly (Chapter 2). Some theoretical structural types fitting this definition were however lacking, such as the combination of sympodial trunk and phyllomorphic branches. This restricted diversity of structural types is more obvious for architectural models, of which 23 have been found in nature among a high number of theoretical forms (Hallé and Oldeman, 1970; Hallé et al., 1978). Such patterns suggest strong genetic and/or environmental constraints in the evolution of plant architecture (Monro and Poore, 2009). In the same vein, correlated evolution of some architectural trait attributes seems impossible, reflecting genetic constraints or implying that resulting architecture are maladapted (Chomicki et al., 2017). As such, we found some association between some monocaulous and branched architectural models, even if it needs to be tested with the completeness of architectural data for branched species. Most of genera achieving the Corner's, the Chamberlain and the Cook's models also achieve respectively the Rauh's, the Leeuwenberg's and the Roux's model (Chapter 5). These theoretical preferential evolutionary pathways are coherent with the non-random distribution of monocauly through the phylogeny (Chapter 5), often interpreted as evidence for prerequisites (Boucher et al., 2016). *Atractocarpus* for instance, as parts of the Gardenieae, is susceptible to present some evolutionary facilities in the branch reduction. Actually, the phenomena occurs at least two times in the genus (Chapter 6), but also in related genera such as *Sukunia* (Chapter 6), *Pentagonia*, *Schumanniophyton, Duroia* or *Rothmannia* (Hallé, 1967). In *Randia* and affine genera, which some New Caledonian *Atractocarpus* was for long considered a part of (Mouly et al., *submitted*), this variation in branch length was also noted and considered of taxonomical importance (Tirvengadum and Sastre, 1979).

Nevertheless, if transition toward monocauly was probably facilitated by some prerequisites and preferentially evolved in some lineages, the evolution of this habit does not seem strongly constrained. It evolved, at least, from treelets (Chapter 6), herbs (e.g. Böhle et al., 1996), lianas (Barrabé et al., 2018) and probably trees (D'Arcy, 1973; Barthélémy, 1988). In our case study, we illustrated a transition from the Stone's model toward the Corner's model through a reduction from branches to inflorescences (Chapter 6). However, such process does not involve special architectural prerequisites and could occur in most of the described architectural models. As such, while evolutionary constraints seem important in the evolution of growth habit (Rowe and Speck, 2005; Monro and Poore, 2009; Wagner, 2010; Wagner et al., 2012), this does not seem critically important for the evolution of monocauly, probably because of the simplicity of the form. Given that heterochronic processes is probably central in the evolution of growth habit (see above) and that the large majority of woody plants pass through a monocaulous phase during their ontogeny, we argue that transition toward monocauly could occur in many plant groups. Juvenile monocauly can be considered as a developmental enabler (*sensu* Donoghue, 2005), that probably permitted the evolution of monocauly independently in several lineages. This repeated evolution might have been particularly facilitated in New Caledonia given several environmental and historical contingencies (see section 8.2.3). The diversity of evolutionary scenario that can lead to monocauly (see above) actually suggests a strong environmental forcing in several clades, each dealing with its own architectural background. The evolution of the monocaulous habit is however less advantageous outside of rainforests, emphasizing the role of environmental context in the diversification or iterative evolution of a trait attributes.

In *Atractocarpus,* evolution of growth habit was gradual and did not evolve by saltation as sometimes proposed for architectural evolution (Bateman and DiMichele, 1994; Bateman, 1999).

This reflects that profound change in the whole plant form does not necessarily involve deep changes at lower integration levels. Minute but directional quantitative variations from one generation to the next could rapidly (less than 2 Myr in *Atractocarpus*, Chapter 6) lead to very different growth habits. Extinction of intermediate states could easily mask such a pattern (Bateman and DiMichele, 1994). Whether evolution of plant architecture has to be gradual and if architecture presents adaptive "peaks" in the course of plant evolution is a fascinating question whose exploration will bring more insights into the evolution of plant forms.

8.4 Conservation of the flora

New Caledonian flora, as one of the world's hotspots for biodiversity conservation (Myers, 1988; Mittermeier et al., 2004), is known to be highly threatened (Jaffré et al., 1998; Lowry, 1998; Jaffré, 2005; Jaffré et al., 2010; Wulff et al., 2013; Ibanez et al., 2017b; Ibanez et al., 2018b). This threat seems even greater for monocaulous flora according to IUCN redlist criteria (Chapter 5). We actually showed that proportion of EN and CR species was nearly significantly higher than for other woody non-monocot species (41% and 32.5% respectively, Chapter 5). Overall, 17.5%, 23.8% and 9.5% of evaluated species were respectively in the CR, EN and VU classes, leading to more than half of the evaluated monocaulous species being considered as threatened.

Typical threats of the New Caledonian flora such as bushfire (Figure 8.14-A) or mining activity strongly affect monocaulous species (51% and 43% of species concerned, respectively). Introduced herbivores (deer, pig and rat) were identified as impacting monocauls significantly more than branched species (Chapter 5). We related this vulnerability to the single meristem and large leaves characterizing the monocaulous habit that make a browsing event highly damaging (see Charles-Dominique et al., 2017), despite various reiteration capacities. This should be particularly true for deer *Rusa timorensis*, the most threatening herbivore for New Caledonian flora (de Garine-Wichatitsky et al., 2005; IUCN, 2017), that could rapidly remove a large portion of leaf area and even apical meristems of monocaulous plants (Figure 8.14-B). Introduced rats, present in the most isolated forests (Rouys and Theuerkauf, 2003; Duron, 2016), could also have a dramatic impact on monocauls by eating apical meristems as observed on several individual of *Meryta balansae* (Figure 8.14-B). Among the three introduced rat species, this most likely concerns the black rat (*Rattus rattus*) rather than the Polynesian rat (*Rattus exulans*) or the brown rat (*Rattus norvegicus*), the second being a poor climber and the third being absent from wild environments (Rouys and Theuerkauf, 2003; Munzinger and Gâteblé, 2017; Vidal, comm. pers.). Impact of feral pig (*Sus scrofa*) occurs mainly by soil foraging involving predation on seedlings, roots or seeds (Caley, 1997). As such, this introduced omnivorous is not expected to impact the monocauls more than the branched species, but the species mainly forages in rainforest understory (Rouys and Theuerkauf, 2003), where monocauls preferentially occur. Monocauls represent an extreme case of insular naivety that seems largely expressed in New Caledonia and more generally in islands. Despite this, the impact of introduced herbivores on New Caledonian flora remains difficult to quantify (de Garine-Wichatitsky et al., 2005) and IUCN criteria probably underestimate the threats. This calls for further investigations into the impact of introduced herbivores on native vegetation and additionally highlights the need for concrete solutions to limit their impact.

Another probable threat impacting monocaulous species, although difficult to precisely estimate, is the effect of climate change. On one hand, the predicted increase in tropical cyclone activity (Emanuel, 2013) could favor the unbranched architecture, potentially less sensitive to falling debris and domino effect. On the other hand, the predicted increase in intensity and duration of drought events (Meehl and Tebaldi, 2004; Cavarero et al., 2012; IPCC, 2014; Whan et al., 2014), could impact preferentially drought sensitive species such as monocauls. Drought-induced

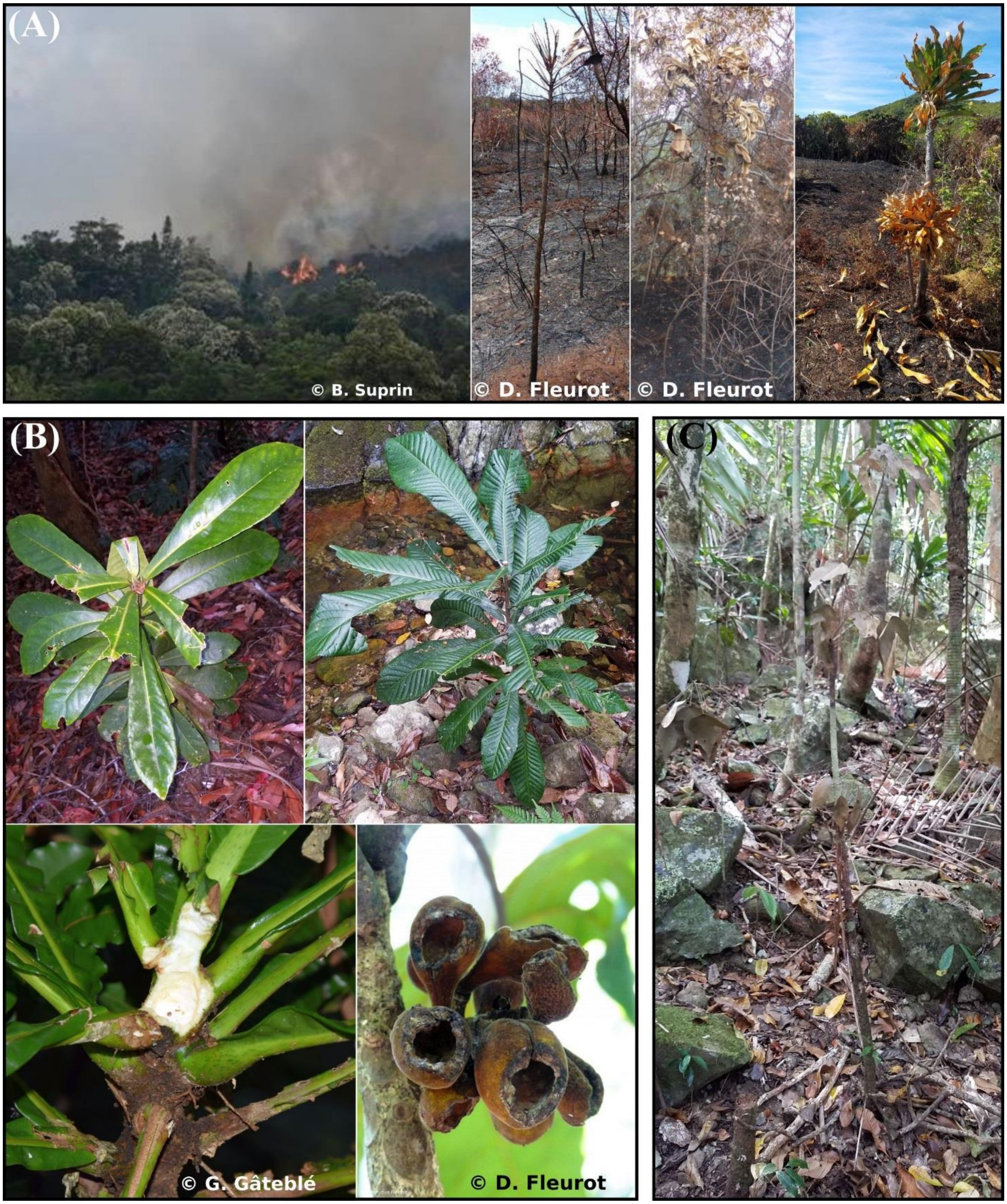


FIGURE 8.14 – Illustration of major threats for New Caledonian monocaulous flora. **(A)** Bushfires. **(B)** Introduced herbivores: deer that remove large portion of leaves and apical meristems, and rats that eat apical meristem and seeds before maturity. **(C)** Drought events: here *Acropogon schumannianus* (Malvaceae), the only plant dried in a rainforest community.

mortalities are increasingly observed, even if not documented for New Caledonia in recent reviews (Allen et al., 2015; Hartmann et al., 2015). During this study, we noted two drought-induced mortality events for monocaulous species occurring during the drastic dry season of 2017 (August in *Diahoué* and October at *Katalupaik*, respectively). These events, involving respectively three individuals of *Phelline dumbeensis* (Phellinaceae, not shown) and one individual of *Acropogon schumannianus* (Malvaceae, Figure 8.14-C) from rainforest understory were remarkable since co-occurring species seemed less or not affected. These observations need further quantification but somehow confirm the drought vulnerability of some monocaulous species, which appear as good indicators of drought events as suggested for basal angiosperms in a previous study (Trueba, 2016).

As such monocaulous species are particularly threatened and several monocaulous species could be among the firsts to disappear in response to increasing pressures. These threats are even likely to be underestimated giving the high proportion of monocaulous species in the "Data Deficient" IUCN class (10%, Chapter 5). Their extinction would not be anecdotal given their high contribution to species richness and abundance in rainforest (see section 8.1). This abundance, along with particular functional trait values, suggests that monocaulous plants are an important component of rainforest understories where they probably play a particular role (e.g. litter-trapping, Lachenaud and Jongkind, 2013; Zona and Christenhusz, 2015). As such, conservation and study of this original growth habit, which is part of the New Caledonian biological heritage, seem of prime importance.

8.5 Out of New Caledonia: monocaulies rather than monocauly?

Monocaulous species investigated in this thesis tend to share many functional features (see section 8.2). More generally, their functional and life history traits (in comparison with branched relatives) were largely consistent with hypotheses proposed in literature (Figure 8.2). We however

FIGURE 8.15 – Examples of monocaulous species from other regions with other evolutionary history and/or habitats. **(A)** *Argyroxiphium sandwicense* (Asteraceae), **(B)** *Dendrosenecio keniodendron* (Asteraceae), **(C)** *Lobelia deckenii* (Campanulaceae), **(D)** *Espeletia killipii* (Asteraceae), **(E)** *Lobelia gloria-montis* (Campanulaceae), **(F)** *Cyanea shipmanii* (Campanulaceae), **(G)** *Plantago princeps* (Plantaginaceae), **(H)** *Wilkesia gymnoxiphium* (Asteraceae), **(I)** *Biophytum reinwardtii* (Oxalidaceae), **(J)** *Brighamia rockii* (Campanulaceae), **(K)** *Aeonium urbicum* (Crassulaceae), **(L)** *Pachypodium namaquanum* (Apocynaceae), **(M)** *Echium pininana* (Boraginaceae), **(N)** *Brassica oleracea* (Brassicaceae), **(O)** *Melanoselinum decipiens* (Apiaceae), **(P)** *Sonchus congestus* (Asteraceae).

found major differences with other types of monocauly described elsewhere. First, macro-anatomy is different as a large part of the stem section was made of wood with little parenchymatous tissues, and thin cortex and pith. Comparisons are complex due to variation in ontogeny and stem location between studies, but the woody monocauly of New Caledonian species can be confidently differentiated from other anatomical models that mainly concerned secondary woody pachycauls (rosette-trees/shrubs) containing true monocauls (e.g. Cotton, 1944; Carlquist, 1974; Mabberley, 1974a; Aldridge, 1978; Aldridge, 1981; Meinzer and Goldstein, 1986; Mosbrugger, 1990). Most of these species are not found in rainforest understories but rather in dry (e.g. Cotton, 1944; Mabberley, 1974a; Aldridge, 1978; Aldridge, 1981) or tropical alpine environments (e.g. Hedberg and Hedberg, 1979; Meinzer and Goldstein, 1986; Givnish, 2016) (Figure 8.15). (i) For monocaulous species living in dry environment, thick pith and cortex together with parenchymatous wood probably relate to water storage, an adaptation unnecessary in rainforest understory. These species are also smaller than rainforest monocauls and seem characterized by small size vessels (Mosbrugger, 1990), probably to limit embolism risks. (ii) For species living in tropical alpine environments with drastic diurnal variations in temperature, the unbranched trunk would be a way to increases the vertical growth and bring the meristem more rapidly away from the ground surface; and the dense rosettes of leaves protect the unique meristem from frost (Givnish, 2016). In these conditions, large pith allows the storage and rapid remobilisation of water for photosynthesis when ground water is frozen and inaccessible (Meinzer and Goldstein, 1986). Leaves of these monocaulous species are also long but often narrow to resist high insolation (Cotton, 1944), pubescent to resist frost, and marcescent to protect the stem after their death (Givnish, 2016). In New Caledonia, large leaves are grouped in distal parts of the stem but do not always form dense rosette and no case of marcescence nor extreme pubescence was observed.

As such, apart from the tropical rainforests, where monocauly largely occurs (Hallé and Hallé, 1965; Richards, 1966; D'Arcy, 1973; Hallé, 1974; Hallé et al., 1978), species in agreement with our definition of monocauly are also present in other contrasting habitats. They are nevertheless restricted to tropical and subtropical areas since temperate climate with annual seasonality is probably too constraining for their few growing meristem (Corner, 1949). Interestingly, there seems to be a correlation between evolutionary history and functional properties of monocaulous plants, reflecting different habitat preferences. Most species from dry and alpine habitat are secondary woody monocauls (e.g. *Echium*, *Aeonium*, *Dendrosenecio*, *Lobelia*, *Argyroxiphium*) while species from rainforest could have rather evolved from woody ancestor (e.g. *Atractocarpus*, *Oxera*, *Pittosporum*, *Tapeinosperma*), even if phylogenetic insights are lacking for other regions. Interestingly, the two New Caledonian genera that potentially experienced secondary woodiness (*Oxalis* and *Scaevola*) contain monocaulous species that are restricted to maquis. This suggests that different selective pressures drove the evolution of monocauly and that their importance for diversification of growth habit largely depends on prerequisite morpho-anatomical features. In this context, it will be interesting to investigate functional characteristics of secondary woody monocauls that secondary gain rainforest (e.g. Hawaian lobeliads, Givnish et al., 2009). More generally, other studies are necessary to disentangle effect of growth habit, environment and prerequisites on plant functional diversification. These studies should use a trans-disciplinary approach including architectural characterization to differentiate true monocauly from pachycauly that are often confounded in literature.

8.6 Conclusion and perspectives

In this study, we used a transversal approach merging plant architecture, taxonomy, phylogenies and functional ecology to characterize and illustrate the evolutionary history of monocaulous species in New Caledonia. Through an original approach of growth habit we defined monocauls as “self-supporting woody plants whose cardinal functions rely on a single visible stem”, i.e. made of (i) a trunk (either monoaxial or pluriaxial), (ii) determinate growth structure highly specialized in photosynthesis and with an abscission point, (iii) axis or complex of axis highly specialized in reproduction and whose contribution to whole plant vegetative exploration and photosynthesis is negligible, and possibly (iv) opportunistic reiterates. This definition proved to be adapted for evolutionary and ecological studies in New Caledonia but remains to be tested in other contexts. Furthermore, the reiteration process showed to be problematic for defining the monocaulous habit, particularly because the differences between opportunistic and sequential reiterations is difficult to assess. In-depth and detailed investigations of these processes in plant groups with a variation in reiterative strategies might provide further insights to refine the definition of monocauly, and perhaps more generally to refine our understanding of reiteration processes in plant diversification. The genus *Acropogon* would be a suitable model, as growth habit diversity in the genus is mainly achieved through variations in reiteration frequency that range from highly predictable to almost never occurring.

Based on this definition of monocauly, we demonstrated that monocauls represent 5.5% of the New Caledonian vascular flora, and that the monocaulous habit appeared more than 31 times in the archipelago, illustrating one of the most striking cases of convergent evolution on islands. We identified four possible factors responsible for this strong convergence, namely the frequency and intensity of cyclones, late quaternary climatic changes, nutrient poor ultramafic substrates and the lack of native browsers. Lists of monocaulous species for other areas with contrasting history would provide comparative data to test such hypotheses. Dated phylogenies are needed to confront the apparition of monocauly with recent climatic events. Currently available phylogenies for this purpose are unfortunately poor and concern *Atractocarpus* (Mouly et al., *submitted*), *Beauprea* (He et al., 2016), *Pycnandra* (Swenson et al., 2015), *Melicope*/*Dutaillyeae* (Appelhans et al., 2014), *Plerandra* (Plunkett and Lowry, 2012) and *Oxera* (Barrabé et al., 2018). Other monocaulous genera are currently under study and phylogenies are expected to be available soon for *Pittosporum* (Gemmill, unpublished data), *Tapeinosperma*/*Mangenotiella* (Gemmill, unpublished data), and *Cupaniopsis* (Buerki et al. unpublished data). These nine genera will offer a substantial basis to study in detail the contextual evolution of monocauly.

Monocauly probably mainly evolved from woody ancestors through heterochronic processes and can contribute to the diversification of New Caledonian lineages through niche partitioning. These hypotheses have yet to be tested in other plant groups considering fine environmental data (e.g. forest structure) which was lacking in this study. New Caledonian flora holds an interesting set of young lineages with potentially ongoing diversification, and in which evolutionary process are easy to capture, as shown in *Atractocarpus*. *Bocquillonia*, one of the richest monocaulous genera that offers remarkable diversity in growth habit and environments, arises as particularly promising to study architectural transitions and their relation to species diversification.

New Caledonian monocauls are characterized by a complex set of interrelated traits that point toward a resource conservation strategy suited and constrained for dense, humid and shady understory. Most species actually occurred in rainforest and on ultramafic substrate where they preferentially evolved. Despite this apparent homogeneity in form and function, our study brought only incomplete insights on only one kind of monocauly and therefore calls for further research on different plant groups in various geographical areas and environments. We effectively demonstrated that monocaulous plants are more than anecdotic botanical curiosities and that their thorough examination could bring up innovative insights about plant ecology and evolution.

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Appendices

Appendix 1 – List of monocaulous species for New Caledonia.

Family	**Species**	**Architectural model**
Anacardiaceae	*Euroschinus aoupiniensis* M.Hoff	Chamberlain
Anacardiaceae	*Euroschinus rubromarginatus* Baker f.	Chamberlain
Anacardiaceae	*Euroschinus verrucosus* Engl.	Chamberlain
Araliaceae	*Meryta balansae* Baill.	Chamberlain
Araliaceae	*Meryta coriacea* Pancher ex Baill.	Chamberlain
Araliaceae	*Meryta heleneae* Lowry, ined.	Chamberlain
Araliaceae	*Meryta koniamboensis* Lowry & F.Tronchet, ined.	Chamberlain
Araliaceae	*Meryta lecardii* (R.Vig.) Lowry & F.Tronchet, ined.	Chamberlain
Araliaceae	*Meryta oxylaena* Baill.	Chamberlain
Araliaceae	*Meryta pachycarpa* Baill.	Chamberlain
Araliaceae	*Meryta schizolaena* Baill.	Chamberlain
Araliaceae	*Meryta sonchifolia* (Linden) Linden & André	Chamberlain
Araliaceae	*Plerandra calcicola* Lowry & G.M.Plunkett, ined.	Chamberlain
Araliaceae	*Plerandra leptophylla* (Veitch ex T.Moore) Lowry, G.M.Plunkett & Frodin	Chamberlain
Araliaceae	*Plerandra letocartiorum* Lowry & G.M.Plunkett, ined.	Chamberlain
Araliaceae	*Plerandra osyana* (Veitch ex Regel) Lowry, G.M.Plunkett & Frodin	Chamberlain
Araliaceae	*Plerandra pouemboutensis* Lowry & G.M.Plunkett, ined.	Chamberlain
Araliaceae	*Polyscias balansae* (Baill.) Harms	Chamberlain
Araliaceae	*Polyscias calophylla* Guillaumin ex Lowry & G.M.Plunkett, ined.	Chamberlain
Araliaceae	*Polyscias mackeei* Lowry & G.M.Plunkett	Chamberlain
Araliaceae	*Polyscias munzingeri* Lowry & G.M.Plunkett, ined.	Chamberlain
Araliaceae	*Polyscias otopyrena* (Baill.) Lowry & G.M.Plunkett	Chamberlain
Araliaceae	*Polyscias pancheri* (Baill.) Harms	Chamberlain
Argophyllaceae	*Argophyllum acinetochromum* Guillaumin	Corner
Argophyllaceae	*Argophyllum ellipticum* Labill.	Corner
Balanopaceae	*Balanops pancheri* Baill.	Chamberlain
Celastraceae	*Salaciopsis megaphylla* (J.Poiss. ex Guillaumin) Loes.	Corner
Cunoniaceae	*Cunonia macrophylla* Brongn. & Gris	Corner
Cunoniaceae	*Cunonia schinziana* Däniker	Corner
Elaeocarpaceae	*Sloanea billardierei* (Vieill.) A.C.Sm.	Corner
Elaeocarpaceae	*Sloanea magnifolia* Tirel	Corner

Elaeocarpaceae	*Sloanea montana* (Labill.) A.C.Sm.	Corner
Elaeocarpaceae	*Sloanea raynaliana* Tirel	Corner
Euphorbiaceae	*Bocquillonia castaneifolia* Guillaumin	Corner
Euphorbiaceae	*Bocquillonia corneri* Bruy, Barrabé & Munzinger, ined.	Corner
Euphorbiaceae	*Bocquillonia goniorrhachis* AiryShaw	Corner
Euphorbiaceae	*Bocquillonia grandidens* Baill.	Corner
Euphorbiaceae	*Bocquillonia longipes* McPherson	Corner
Euphorbiaceae	*Bocquillonia lucidula* AiryShaw	Corner
Euphorbiaceae	*Bocquillonia nervosa* AiryShaw	Corner
Euphorbiaceae	*Bocquillonia phenacostigma* AiryShaw	Corner
Euphorbiaceae	*Bocquillonia sessiliflora* Baill.	Corner
Euphorbiaceae	*Bocquillonia spicata* Baill.	Corner
Euphorbiaceae	*Cleidion lasiophyllum* Pax & K.Hoffm.	Corner
Euphorbiaceae	*Cleidion macrophyllum* Baill.	Corner
Fabaceae	*Sophora jabandao* Montrouz.	Chamberlain
Goodeniaceae	*Scaevola beckii* Zahlbr.	Corner
Lamiaceae	*Oxera baladica* Vieill.	Corner
Lamiaceae	*Oxera comptonii* S.Moore	Corner
Lamiaceae	*Oxera doubetiae* Gateblé, ined.	Corner
Lamiaceae	*Oxera garoense* Gateblé, ined.	Corner
Lamiaceae	*Oxera ounemoa* Gateblé, ined.	Corner
Lamiaceae	*Oxera papineaui* Gateblé, ined.	Corner
Lamiaceae	*Oxera rugosa* Guillaumin	Corner
Lamiaceae	*Oxera sessilifolia* Dubard	Corner
Lauraceae	*Litsea ripidion* Guillaumin	Corner
Linaceae	*Hugonia racemosa* Schltr.	Corner
Malvaceae	*Acropogon austrocaledonicus* (Hook.f.) Morat	Corner
Malvaceae	*Acropogon bosseri* Morat & Chalopin	Corner
Malvaceae	*Acropogon calcicolus* Morat & Chalopin	Corner
Malvaceae	*Acropogon chalopiniae* Morat	Corner
Malvaceae	*Acropogon domatifer* Morat	Corner
Malvaceae	*Acropogon fatsioides* Schltr.	Corner
Malvaceae	*Acropogon francii* (Guillaumin) Morat	Corner
Malvaceae	*Acropogon grandiflorus* Morat & Chalopin	Corner
Malvaceae	*Acropogon jaffrei* Morat & Chalopin	Corner
Malvaceae	*Acropogon megaphyllus* (Bureau & J.Poiss. ex Guillaumin) Morat	Corner
Malvaceae	*Acropogon merytifolius* Morat & Chalopin	Corner
Malvaceae	*Acropogon moratianus* Callm., Munzinger & Lowry	Corner
Malvaceae	*Acropogon paagoumenensis* Morat & Chalopin	Corner
Malvaceae	*Acropogon pilosus* Morat & Chalopin	Corner

Malvaceae	*Acropogon sageniifolius* Schltr.	Corner
Malvaceae	*Acropogon schumannianus* Schltr.	Corner
Meliaceae	*Dysoxylum kouiriense* Virot	Corner
Meliaceae	*Dysoxylum macranthum* C.DC.	Corner
Meliaceae	*Dysoxylum macrostachyum* C.DC.	Corner
Meliaceae	*Dysoxylum roseum* C.DC.	Corner
Meliaceae	*Dysoxylum rufescens* Vieill. ex Pancher & Sebert	Corner
Moraceae	*Ficus asperula* Bureau	Corner
Moraceae	*Ficus auriculigera* Bureau	Corner
Moraceae	*Ficus otophoroides* Corner	Corner
Myodocarpaceae	*Delarbrea longicarpa* R.Vig.	Chamberlain
Myodocarpaceae	*Delarbrea montana* R. Vig.	Chamberlain
Myodocarpaceae	*Delarbrea paradoxa* Vieill.	Chamberlain
Myrtaceae	*Syzygium acre* (Pancher ex Guillaumin) J.W.Dawson	Corner
Myrtaceae	*Syzygium toninense* (Baker f.) J.W.Dawson	Corner
Oxalidaceae	*Oxalis balansae* Guillaumin	Corner
Phellinaceae	*Phelline comosa* Labill.	Corner
Phellinaceae	*Phelline dumbeensis* Guillaumin	Corner
Phyllanthaceae	*Phyllanthus aoupinieensis* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus artensis* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus baladensis* Baill.	Cook
Phyllanthaceae	*Phyllanthus baraouaensis* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus boguenensis* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus bupleuroides* Baill.	Cook
Phyllanthaceae	*Phyllanthus carlottae* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus casearoides* S.Moore	Cook
Phyllanthaceae	*Phyllanthus chamaecerasus* Baill.	Cook
Phyllanthaceae	*Phyllanthus comptonii* S.Moore	Cook
Phyllanthaceae	*Phyllanthus conjugatus* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus dorotheae* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus dracunculoides* Baill.	Cook
Phyllanthaceae	*Phyllanthus favieri* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus francii* Guillaumin	Cook
Phyllanthaceae	*Phyllanthus golonensis* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus guillauminii* Däniker	Cook
Phyllanthaceae	*Phyllanthus jaffrei* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus ligustrifolius* S. Moore	Cook
Phyllanthaceae	*Phyllanthus loranthoides* Baill.	Cook
Phyllanthaceae	*Phyllanthus macrochorion* Baill.	Cook
Phyllanthaceae	*Phyllanthus mangenotii* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus margaretae* M.Schmid	Cook

Phyllanthaceae	*Phyllanthus moorei* M. Schmid	Cook
Phyllanthaceae	*Phyllanthus moratii* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus pancherianus* Baill.	Cook
Phyllanthaceae	*Phyllanthus parangoyensis* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus pronyensis* Guillaumin	Cook
Phyllanthaceae	*Phyllanthus pseudotrichopodus* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus pterocladus* S.Moore	Cook
Phyllanthaceae	*Phyllanthus quintuplinervis* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus salicifolius* Baill.	Cook
Phyllanthaceae	*Phyllanthus sarasinii* Guillaumin	Cook
Phyllanthaceae	*Phyllanthus serpentinus* S.Moore	Cook
Phyllanthaceae	*Phyllanthus sylvincola* S.Moore	Cook
Phyllanthaceae	*Phyllanthus tireliae* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus tixieri* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus torrentium* Müll.Arg.	Cook
Phyllanthaceae	*Phyllanthus trichopodus* Guillaumin	Cook
Phyllanthaceae	*Phyllanthus tritepalus* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus valeriae* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus veillonii* M.Schmid	Cook
Phyllanthaceae	*Phyllanthus vespertilio* Baill.	Cook
Pittosporaceae	*Pittosporum artense* Guillaumin	Corner
Pittosporaceae	*Pittosporum leratii* Guillaumin	Corner
Pittosporaceae	*Pittosporum morierei* Vieill. ex Guillaumin	Chamberlain
Pittosporaceae	*Pittosporum muricatum* Tirel & Veillon	Chamberlain
Pittosporaceae	*Pittosporum paniculatum* Brongn. & Gris	Chamberlain
Pittosporaceae	*Pittosporum pronyense* Guillaumin	Chamberlain
Primulaceae	*Mangenotiella stellata* M.Schmid	Corner
Primulaceae	*Myrsine grandifolia* (S.Moore) Ricketson & Pipoly	Corner
Primulaceae	*Tapeinosperma amplexicaule* Mez	Corner
Primulaceae	*Tapeinosperma ateouense* M.Schmid	Corner
Primulaceae	*Tapeinosperma canalense* Guillaumin	Corner
Primulaceae	*Tapeinosperma ellipticum* Mez	Corner
Primulaceae	*Tapeinosperma gracile* Mez	Corner
Primulaceae	*Tapeinosperma grandiflorum* Guillaumin	Corner
Primulaceae	*Tapeinosperma sessilifolium* Mez	Corner
Proteaceae	*Beauprea balansae* Brongn. & Gris	Chamberlain
Proteaceae	*Beauprea filipes* Schltr.	Chamberlain
Proteaceae	*Beauprea penariensis* Guillaumin	Corner
Proteaceae	*Virotia angustifolia* (Virot) P.H.Weston & A.R.Mast	Corner
Proteaceae	*Virotia rousselii* (Vieill.) P.H.Weston & A.R.Mast	Corner

Proteaceae	*Virotia vieillardii* (Brongn. & Gris) P.H.Weston & A.R.Mast	Corner
Rubiaceae	*Atractocarpus baladicus* (Montrouz. ex Guillaumin & Beauvis.) Mouly, comb. nov.	Corner
Rubiaceae	*Atractocarpus bracteatus* Schltr. & K.Krause	Corner
Rubiaceae	*Atractocarpus colnettianus* (Guillaumin) Mouly, comb. nov.	Corner
Rubiaceae	*Atractocarpus confertus* (Guillaumin) Mouly, comb. nov.	Corner
Rubiaceae	*Atractocarpus heterophyllus* (Montrouz.) Guillaumin & Beauvis.	Corner
Rubiaceae	*Atractocarpus longistipitatus* Baill. ex Guillaumin	Corner
Rubiaceae	*Atractocarpus pterocarpon* (Guillaumin) Puttock	Corner
Rubiaceae	*Atractocarpus vaginatus* Baill. ex Guillaumin	Corner
Rubiaceae	*Ixora aoupinieensis* Hoang & Mouly	Corner
Rubiaceae	*Ixora cauliflora* Montr. & Baker f.	Corner
Rubiaceae	*Ixora margaretae* (N.Hallé) Mouly & B.Bremer	Corner
Rutaceae	*Dutaillyea trifoliolata* Baill.	Corner
Rutaceae	*Melicope lasioneura* (Baill.) Baill. ex Guillaumin	Corner
Rutaceae	*Zanthoxylum albiflorum* Baker f.	Chamberlain
Salicaceae	*Casearia coriifolia* Lescot & Sleumer	Cook
Salicaceae	*Casearia puberula* Guillaumin	Cook
Salicaceae	*Casearia silvana* Schltr.	Cook
Salicaceae	*Xylosma gigantifolium* Sleumer	Cook
Sapindaceae	*Cupaniopsis azantha* Radlk.	Corner
Sapindaceae	*Cupaniopsis glomeriflora* Radlk.	Corner
Sapindaceae	*Cupaniopsis grandiflora* Adema	Corner
Sapindaceae	*Cupaniopsis inoplaea* Radlk.	Corner
Sapindaceae	*Cupaniopsis oedipoda* Radlk.	Corner
Sapotaceae	*Pycnandra kaalaensis* Aubrév.	Corner
Sapotaceae	*Pycnandra longipetiolata* Swenson & Munzinger	Corner
Sapotaceae	*Pycnandra ouaiemensis* Swenson & Munzinger	Corner
Sapotaceae	*Pycnandra paniensis* Aubrév.	Corner
Sapotaceae	*Pycnandra vieillardii* (Baill.) Vink	Corner
Symplocaceae	*Symplocos neocaledonica* (Vieill.) Noot.	Corner

Appendix 2 – Mean value and standard deviation of traits values for each sampled *Atractocarpus* species (Chapter 6)

Taxon	Voucher	Site	GPS point (DD)	Photosynthetic BI	Exploration BI	Fruit volume (cm^3)	SR	Total LA (cm^2)	Mean LA (cm^2)	Leaf number	IN length (cm)	IN diameter (cm)	SLA (cm².g^{-1})	SWD (g.cm^{-3})	SSD (g.cm^{-3})	HV	% Pith	% Wood	% Cortex
Atractocarpus sp. nov. 1 Mouly, ined	Bruy 964	Diahoué	164.6894 - 20.4851	0,92 ± 0,02	0,81 ± 0,08	53,5 ± 31,3	101 ± 17	18817 ± 4392	154,8 ± 22,3	243,6 ± 125,2	5,1 ± 1,13	0,73 ± 0,03	75,9 ± 4,1	0,71 ± 0,11	0,49 ± 0,04	1475 ± 259	0,24 ± 0,08	0,35 ± 0,1	0,41 ± 0,07
Atractocarpus aragoensis Guillaumin	Bruy 615	Pic Vincent	165.7737 - 21.6031	0,29 ± 0,19	0,49 ± 0,15	13,6 ± 6,6	121 ± 32	1477 ± 1175	84,3 ± 29,1	74 ± 39,2	2,37 ± 0,74	0,36 ± 0,04	107,8 ± 6,7	0,65 ± 0,09	0,5 ± 0,07	888 ± 430	0,24 ± 0,05	0,3 ± 0,05	0,46 ± 0,01
Atractocarpus artensis (Montrouz.) Mouly	Bruy 922	Creek bambou	164.3410 - 20.4607	0,82 ± 0,04	0,73 ± 0,14	109,6 ± 13,2	110 ± 29	10396 ± 6387	164,1 ± 19,9	219,4 ± 211,7	6,72 ± 2,99	0,68 ± 0,12	98 ± 10,9	0,7 ± 0,09	0,49 ± 0,09	1710 ± 773	0,3 ± 0,07	0,31 ± 0,15	0,39 ± 0,1
Atractocarpus sp. nov. 2 Mouly, ined	Bruy 889	Dogny	165.8778 - 21.6217	0,84 ± 0,07	0,67 ± 0,13	11,1 ± 1,6	133 ± 32	3770 ± 2558	53,6 ± 12,9	154 ± 89,5	4,03 ± 1,64	0,45 ± 0,05	91,1 ± 6,6	0,71 ± 0,05	0,5 ± 0,05	501 ± 276	0,28 ± 0,06	0,3 ± 0,07	0,42 ± 0,04
Atractocarpus baladicus (Montrouz. ex Guillaumin & Beauvis.) Mouly	Bruy 650	Tchamba	165.2315 - 21.0178	0,01 ± 0,01	0,13 ± 0,07	120,7 ± 61,3	117 ± 17	4619 ± 537	305,6 ± 30,9	21,8 ± 4,9	3,91 ± 1,04	0,81 ± 0,11	69,7 ± 6,8	0,82 ± 0,04	0,5 ± 0,05	4548 ± 517	0,22 ± 0,1	0,41 ± 0,14	0,37 ± 0,05
Atractocarpus bracteatus Schltr. & K.Krause	Bruy 133	Plaine des lacs	166.9035 - 22.2751	0,02 ± 0,01	0,11 ± 0,03	218,6 ± 53,2	164 ± 25	4188 ± 1755	144,5 ± 35,5	42,2 ± 8,2	2,46 ± 0,59	0,62 ± 0,04	60,2 ± 2,8	0,77 ± 0,06	0,56 ± 0,05	4104 ± 1748	0,17 ± 0,03	0,37 ± 0,09	0,46 ± 0,07
Atractocarpus brandzeanus (Baill.) Mouly	Bruy 920	Paagoumene	164.1931 - 20.4908	0,46 ± 0,19	0,4 ± 0,2	29 ± 9,4	106 ± 25	2299 ± 1116	103 ± 30,5	49 ± 33,5	3,32 ± 1,16	0,47 ± 0,06	83,8 ± 14,4	0,81 ± 0,04	0,52 ± 0,08	1107 ± 312	0,27 ± 0,03	0,26 ± 0,09	0,47 ± 0,08

Atractocarpus sp. nov. 12 Mouly, ined.	Bruy 1042	Nodela	165.3531 - 21.4392	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Atractocarpus colnettianus (Guillaumin) Mouly	Bruy 154	Roche Ouaième	164.8630 - 20.6401	0,02 ± 0,01	0,15 ± 0,09	156,1 ± 109,9	112 ± 39	3791 ± 770	196,2 ± 64,2	32,6 ± 8,4	1,87 ± 0,46	1,09 ± 0,17	41,8 ± 2,7	0,7 ± 0,08	0,43 ± 0,02	3709 ± 739	0,18 ± 0,02	0,3 ± 0,01	0,52 ± 0,03
Atractocarpus confertus (Guillaumin) Mouly	Veillon 5733	Demazure	166.6251 - 22.1962	0,01 ± 0,01	0,02 ± 0,01	44,8 ± 8	106 ± 18	16393 ± 5504	922,5 ± 151,5	24,4 ± 6,1	2,46 ± 0,48	1,3 ± 0,12	64,2 ± 5,6	0,7 ± 0,02	0,48 ± 0,03	16314 ± 5514	0,33 ± 0,03	0,28 ± 0,03	0,39 ± 0,03
Atractocarpus sp. nov. 8 Mouly, ined.	Bruy 953	Tchamba	165.2315 - 21.0178	0,68 ± 0,06	0,66 ± 0,07	9,4 ± 0,7	117 ± 17	5245 ± 3215	120,4 ± 24,3	99 ± 33,3	3,96 ± 0,62	0,45 ± 0,08	139,9 ± 18	0,77 ± 0,04	0,52 ± 0,05	1505 ± 485	0,3 ± 0,07	0,32 ± 0,06	0,38 ± 0,03
Atractocarpus heterophyllus (Montrouz.) Guillaumin & Beauvis.	Bruy 632	Paagoumene	164.1931 - 20.4908	0,12 ± 0,06	0,22 ± 0,09	147,2 ± 36,3	131 ± 30	2349 ± 1368	140,3 ± 47,5	30,2 ± 13,8	2,5 ± 0,63	0,59 ± 0,07	54,1 ± 7,4	0,67 ± 0,07	0,55 ± 0,01	2035 ± 1169	0,21 ± 0,03	0,29 ± 0,08	0,5 ± 0,06
Atractocarpus sp. nov. 13 Mouly, ined.	Barrabé 1513	Barautê	165.2303 - 20.9798	0,89 ± 0,03	0,85 ± 0,04	7,4 ± 0,8	114 ± 15	3743 ± 1773	49,9 ± 4,2	181 ± 114,2	4,57 ± 3	0,47 ± 0,04	99,6 ± 15,4	0,75 ± 0,06	0,5 ± 0,06	388 ± 74	0,34 ± 0,07	0,26 ± 0,09	0,41 ± 0,09
Atractocarpus longistipitatus Baill. ex Guillaumin	Bruy 612	Monts Koghis	165.5086 - 22.178507	0,0 ± 0,0	0,3 ± 0,12	15,4 ± 3,2	151 ± 39	6417 ± 2650	361,3 ± 110,1	52,2 ± 19,8	1,88 ± 0,7	0,74 ± 0,07	94,3 ± 15,4	0,76 ± 0,04	0,57 ± 0,03	6395 ± 2636	0,15 ± 0,05	0,38 ± 0,08	0,47 ± 0,07
Atractocarpus mollis (Schltr.) Mouly	Bruy 683	Ponandou	165.2173 - 20.8171	0,89 ± 0,05	0,74 ± 0,08	8,6 ± 1,1	102 ± 32	8543 ± 5432	86,3 ± 17,3	191,4 ± 48	1,89 ± 0,88	0,4 ± 0,04	159,3 ± 17,3	0,82 ± 0,04	0,45 ± 0,03	787 ± 217	0,25 ± 0,08	0,24 ± 0,05	0,51 ± 0,05
Atractocarpus sp. nov. 6 Mouly, ined.	Bruy 1012	Mont Mou	166.3349 - 22.0751	0,6 ± 0,11	0,82 ± 0,06	NA	88 ± 23	5252 ± 2014	190,1 ± 30,3	115,6 ± 39,7	2,64 ± 1,05	0,71 ± 0,05	70,6 ± 9,5	0,72 ± 0,13	0,53 ± 0,07	2174 ± 1137	0,26 ± 0,06	0,25 ± 0,12	0,49 ± 0,08

Atractocarpus ngoyensis (Schltr.) Mouly	Bruy 139	Plaine des lacs	166.9035 - 22.2751	0,4 ± 0,13	0,49 ± 0,16	169,4 ± 39,1	140 ± 13	6580 ± 2245	228,9 ± 36,9	85 ± 47	3,64 ± 1,63	0,77 ± 0,1	70,7 ± 7,8	0,81 ± 0,04	0,58 ± 0,16	3740 ± 758	0,2 ± 0,06	0,38 ± 0,06	0,42 ± 0,04
Atractocarpus nigricans (Schltr.) Mouly	Bruy 662	Roche Ouaième	164.8630 - 20.6401	0,86 ± 0,07	0,66 ± 0,16	17,3 ± 4,3	115 ± 13	6714 ± 3161	135,3 ± 31,8	79,4 ± 42,6	4,79 ± 3,41	0,63 ± 0,05	92,4 ± 5	0,73 ± 0,11	0,43 ± 0,04	792 ± 190	0,29 ± 0,06	0,2 ± 0,07	0,51 ± 0,04
Atractocarpus sp. nov. 4 Mouly, ined.	Bruy 929	Mandjelia	164.5421 - 20.4038	0,69 ± 0,11	0,68 ± 0,06	3,9 ± 0,6	144 ± 37	1294 ± 200	36,9 ± 7,5	85,2 ± 33	2,39 ± 1,56	0,35 ± 0,01	82,6 ± 3,7	0,79 ± 0,05	0,51 ± 0,04	409 ± 156	0,25 ± 0,07	0,26 ± 0,06	0,5 ± 0,03
Atractocarpus sp. nov. 10 Mouly, ined.	Bruy 944	Pwaala	164.5087 - 20.3750	0,92 ± 0,04	0,85 ± 0,02	11,2 ± 6,6	101 ± 16	10925 ± 3546	95,5 ± 34	148 ± 60,4	1,96 ± 0,61	0,45 ± 0,05	157,4 ± 7,6	0,79 ± 0,02	0,53 ± 0,03	833 ± 411	0,26 ± 0,03	0,3 ± 0,03	0,44 ± 0,04
Atractocarpus sp. nov. 3 Mouly ined.	Barrabé 699	Aoupinié	165.2769 - 21.1780	0,87 ± 0,07	0,84 ± 0,06	10,5 ± 3,3	122 ± 22	9511 ± 3455	142,2 ± 44,1	140 ± 62,8	5,25 ± 2,39	0,7 ± 0,1	172,1 ± 36,6	0,68 ± 0,09	0,42 ± 0,05	1126 ± 585	0,34 ± 0,08	0,27 ± 0,12	0,39 ± 0,06
Atractocarpus pseudoterminalis (Guillaumin) Mouly	Bruy 162	Plaine des lacs	166.9035 - 22.2751	0,78 ± 0,12	0,76 ± 0,14	13,5 ± 4,1	160 ± 13	2933 ± 1461	44,4 ± 7,6	186,2 ± 138,1	3,46 ± 1,28	0,32 ± 0,01	88,9 ± 5,5	0,81 ± 0,03	0,58 ± 0,04	517 ± 49	0,21 ± 0,07	0,37 ± 0,11	0,42 ± 0,06
Atractocarpus pterocarpon (Guillaumin) Puttock	McPherson 3003	Plaine des lacs	166.9035 - 22.2751	0,01 ± 0,01	0,26 ± 0,11	30,4 ± 11,6	127 ± 28	2321 ± 701	189 ± 22,5	38,8 ± 21,6	2,57 ± 1,02	0,6 ± 0,05	76,3 ± 4,3	0,75 ± 0,06	0,5 ± 0,02	2304 ± 698	0,19 ± 0,03	0,25 ± 0,05	0,55 ± 0,02
Atractocarpus sp. nov. 7 Mouly, ined.	Hattermann 01	Mont Do	166.0008 - 21.7536	0,48 ± 0,08	0,4 ± 0,11	33,8 ± 17,2	177 ± 31	1610 ± 581	63,5 ± 10	46 ± 18,5	3,37 ± 1,77	0,58 ± 0,12	63,2 ± 12,2	0,72 ± 0,08	0,48 ± 0,05	842 ± 351	0,22 ± 0,05	0,33 ± 0,09	0,45 ± 0,07
Atractocarpus sessilifolius Guillaumin	Bruy 645	Tchamba	165.2315 - 21.0178	0,15 ± 0,14	0,53 ± 0,13	6,5 ± 5,6	98 ± 16	1872 ± 738	113,7 ± 36	80,4 ± 25,7	1,99 ± 1,3	0,45 ± 0,08	67,4 ± 10,8	0,8 ± 0,03	0,59 ± 0,03	1641 ± 828	0,1 ± 0,06	0,37 ± 0,04	0,53 ± 0,06

Atractocarpus sezitat (Guillaumin) Mouly	Bruy 900	Roche d'Adio	165.2422 -21.2405	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Atractocarpus vaginatus Guillaumin	Bruy 621	Sarramea	165.8072 -21.6658	0,09 ± 0,1	0,07 ± 0,03	360,7 ± 110,9	128 ± 16	3754 ± 1003	229,7 ± 26,8	24 ± 7,3	6,58 ± 1,13	0,82 ± 0,08	40,7 ± 5,3	0,82 ± 0,15	0,59 ± 0,23	3356 ± 718	0,19 ± 0,04	0,35 ± 0,04	0,46 ± 0,03

BI: branching index, SR: slenderness ratio, LA: leaf area, IN: internode, SLA: specific leaf area, SWD: specific wood density, SSD: specific stem density, HV: Huber value

Appendix 3 – Correlation table (method of Spearman) for 32 morpho-anatomical traits measured on twenty species (Chapter 7).

	S_{area}	SR	T	SDMC	SSD	WSD	leaf nb	LA
SR	**-0.63*** **							
T	**0.54*** **	**-0.99*** **						
SDMC	**-0.26** **	0.11	-0.06					
SSD	**-0.27** **	0.11	-0.06	**0.97*** **				
WSD	**-0.48*** **	**0.27** **	**-0.21* **	**0.73*** **	**0.75*** **			
Leaf nb	**0.51*** **	**-0.20* **	0.16	0.1	0.07	-0.04		
LA	**0.74*** **	**-0.43*** **	**0.35*** **	-0.1	-0.12	**-0.31** **	**0.32** **	
LA_{total}	**0.82*** **	**-0.39*** **	**0.31** **	-0.07	-0.09	**-0.26** **	**0.71*** **	**0.86*** **
P_{area}	**0.92*** **	**-0.67*** **	**0.60*** **	**-0.39*** **	**-0.40*** **	**-0.54*** **	**0.35*** **	**0.67*** **
$Pith_p$	**0.35*** **	**-0.42*** **	**0.40*** **	**-0.48*** **	**-0.47*** **	**-0.32** **	-0.03	**0.24* **
$Xylem_p$	-0.12	**0.30** **	**-0.31** **	**0.46*** **	**0.44*** **	**0.29** **	**0.25* **	0.14
$Phloem_p$	**-0.52*** **	**0.48*** **	**-0.45*** **	**0.42*** **	**0.40*** **	**0.36*** **	-0.13	**-0.24* **
$Cortex_p$	-0.05	-0.05	0.06	-0.19	-0.16	-0.07	-0.13	**-0.27** **
HV	0.02	-0.06	0.06	0.16	0.16	-0.03	**-0.25* **	**-0.23* **
RT	0.15	-0.08	0.06	**-0.39*** **	**-0.36*** **	**-0.34*** **	-0.09	-0.06
V_d	**0.63*** **	**-0.24* **	0.18	-0.12	-0.15	**-0.31** **	**0.44*** **	**0.64*** **
Dm	**0.62*** **	**-0.26* **	0.19	-0.17	**-0.20* **	**-0.34*** **	**0.38*** **	**0.64*** **
K_{th}	**0.63*** **	**-0.26** **	**0.20* **	-0.13	-0.16	**-0.32** **	**0.41*** **	**0.64*** **
$K_{s\text{-}th}$	**0.85*** **	**-0.42*** **	**0.34*** **	-0.13	-0.16	**-0.37*** **	**0.58*** **	**0.81*** **
FD	**-0.55*** **	**0.27** **	**-0.21* **	**0.29** **	**0.28** **	**0.30** **	**-0.39*** **	**-0.26*** **
RF	-0.16	0.09	-0.09	-0.02	-0.01	0.16	-0.06	0.03
VD	**-0.54*** **	0.18	-0.12	0.09	0.10	**0.28** **	**-0.32** **	**-0.54** **
SLA	**-0.30** **	**0.33*** **	**-0.33*** **	**-0.45*** **	**-0.43*** **	-0.18	**-0.40*** **	**-0.20*** **
LDMC	**-0.29** **	0.04	-0.01	**0.47*** **	**0.45*** **	**0.34*** **	0.09	-0.20
PL	0.15	0.1	-0.14	**-0.47*** **	**-0.46*** **	**-0.24* **	-0.19	0.24
LT	**0.43** **	-0.10	0.04	-0.12	-0.14	-0.06	**0.38** **	0.23
PSR	0.16	-0.05	0.03	-0.17	-0.18	-0.18	0.26	-0.01
SD	**-0.35* **	**0.36* **	**-0.35* **	0.23	0.19	0.20	**-0.43** **	-0.09

**: $P<0.05$, **: $P<0.01$, ***: $P<0.001$*

	LA_{total}	P_{area}	$Pith_p$	$Xylem_p$	$Phloem_p$	$Cortex_p$	HV	RT	V_d	K_{th}
P_{area}	**0.69*****									
$Pith_p$	0.16	**0.66*****								
$Xylem_p$	**0.21***	**-0.34*****	**-0.64*****							
$Phloem_p$	**-0.24***	**-0.62*****	**-0.57*****	**0.45*****						
$Cortex_p$	**-0.25***	-0.06	0.00	**-0.68*****	**-0.29****					
HV	**-0.29****	-0.09	**-0.40*****	**0.24***	0.08	-0.03				
RT	-0.09	0.16	0.11	**-0.35*****	**-0.36*****	**0.40*****	0.13			
V_d	**0.69*****	**0.56*****	0.10	**0.22***	**-0.28****	**-0.28****	-0.04	-0.03		
Dm	**0.66*****	**0.57*****	0.16	0.18	**-0.26****	**-0.31****	-0.06	-0.04	**0.96*****	
K_{th}	**0.68*****	**0.57*****	0.13	**0.21***	**-0.27****	**-0.30****	-0.05	-0.05	**0.99*****	**0.98*****
K_{s-th}	**0.88*****	**0.72*****	0.14	**0.21***	**-0.32****	**-0.27****	-0.04	-0.01	**0.87*****	**0.85*****
FD	**-0.41*****	**-0.45*****	-0.11	**0.30****	**0.40*****	**-0.41*****	0.02	**-0.42*****	**-0.30****	**-0.23***
RF	0.02	-0.07	0.19	0.03	0.10	**-0.22***	**-0.36*****	**-0.47*****	-0.19	-0.08
VD	**-0.59*****	**-0.48*****	-0.09	**-0.30****	0.19	**0.39*****	-0.09	0.14	**-0.70*****	**-0.71*****
SLA	**-0.30****	**-0.24***	0.01	-0.03	-0.08	-0.00	-0.08	**0.28****	**-0.20***	-0.18
LDMC	-0.17	**-0.29****	-0.18	0.12	**0.47*****	-0.11	0.02	**-0.51*****	**-0.23***	-0.19
PL	0.13	0.17	0.16	-0.08	**-0.22***	-0.01	-0.16	0.01	0.20	**0.21***
LT	**0.38****	**0.43****	0.18	-0.16	**-0.56*****	**0.32***	-0.14	**0.43****	**0.40****	**0.30***
PSR	0.15	0.11	-0.11	0.23	-0.27	-0.06	0.19	-0.21	0.26	0.25
SD	-0.26	**-0.31***	-0.09	0.11	**0.50*****	-0.24	-0.02	-0.15	-0.19	-0.16

*: $P<0.05$, **: $P<0.01$, ***: $P<0.001$

	K_{th}	$K_{s\text{-}th}$	FD	RF	VD	SLA	LDMC	PL	LT	PSR
$K_{s\text{-}th}$	**0.86***									
FD	**-0.26****	**-0.41*****								
RF	-0.13	-0.11	**0.40*****							
VD	**-0.71*****	**-0.59*****	0.19	0.11						
SLA	-0.20	**-0.30****	0.05	0.10	0.08					
LDMC	**-0.21***	**-0.23***	**0.34*****	**0.35*****	0.18	**-0.58*****				
PL	**0.20***	0.17	-0.06	0.06	-0.14	**0.35*****	**-0.42*****			
LT	**0.36****	**0.39****	**-0.62*****	**-0.53*****	-0.24	**-0.30***	**-0.62*****	0.12		
PSR	0.26	0.26	-0.11	0.03	-0.27	0.26	-0.21	**0.41****	0.17	
SD	-0.18	-0.27	**0.34***	0.09	0.06	-0.27	**0.29***	-0.26	-0.11	**-0.60*****

*: $P<0.05$, **: $P<0.01$, ***: $P<0.001$

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Appendix 4 - 9th International Plant Biomechanics Conference - Montreal, August 9-14, 2018

Foliar support and allocating patterns across three leaf types in the Araliaceae of New Caledonia

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Background

The **economy of light harvesting** opposes the photosynthetically active lamina to the petiole, whose primary function is to mechanically and hydraulically sustain the lamina (Niinemets and Kull, 1999)[1].

Leaf **biomass partitioning** between the lamina and its support impacts foliar productivity (Niinemets et *al*., 2006)[2] and thus, plant strategies and ecosystem functioning.

The **ecological and adaptative significance of leaf type** (simple *vs* compound) is still under debate (Warman et *al*., 2011 ; Nicotra et *al*. 2011)[3,4].

How does leaf type affect the balance between leaf traits related to support and light interception?

Material and methods

Comparing 3 leaf types in 3 genera in the Araliaceae family: **simple** (*Meryta*), **palmately compound** (*Plerandra*) and **pinnately compound** (*Polyscias*).

We harvested 270 mature leaves from 18 taxa endemic from New Caledonia (6 in each genus)

→ A set of **leaf traits** from fresh and dry weight of lamina and petiole, lamina area and partitioning into leaflets

+ Petiole bending tests and transverse anatomical sections for a subsample of 3 taxa

1 – Foliar support allometries

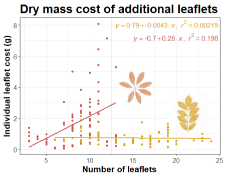
How does leaf dry mass (DM, as a proxy for leaf support investment) scale with leaf area (LA)? We tested the log-log relationships with a Standardized Major Axis (SMA) analysis:

$LA=\beta.(DM)^{\alpha}$

	α	95% C.I.	r^2	allometry
Meryta	**0.936**	0.866 - 1.012	86%	isometry ($\alpha = 1$)
Plerandra	**0.896**	0.857 - 0.937	95%	negative allometry ($\alpha < 1$)
Polyscias	**1.165**	1.044 - 1.299	73%	positive allometry ($\alpha > 1$)

The cost for expanding leaf area is constant for *Meryta*, while it increases for *Plerandra* ("diminishing returns") and decreases for *Polyscias*.

- increasing leaflet cost for additional leaflets in *Plerandra* (r^2 = 20%)
- constant leaflet cost in *Polyscias* (r^2 = 0%)


Dry mass cost of additional leaflets

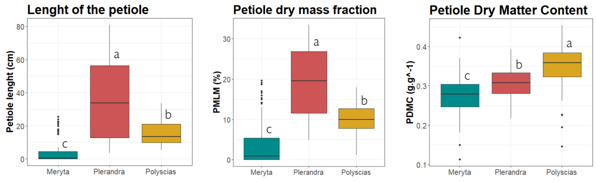
2 – Petiole structural investments

The three leaf types diverge in their **petiole-to-lamina allocating patterns**.

- *Meryta*'s simple leaves have short petioles (4 cm), accounting for 4% of the dry mass

- *Plerandra*'s palmate leaves have longer petioles (35 cm), representing 20% of leaf dry mass.

- *Polyscias*' pinnate leaves have petioles of intermediate dimensions (15 cm, dry mass fraction 10%), but higher dry matter content (dry mass to fresh mass)


Lenght of the petiole
Petiole dry mass fraction
Petiole Dry Matter Content

N = 90x3

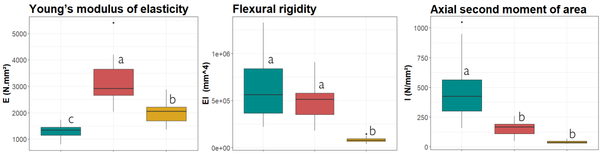
Tukey's comparison of means ($p < 0.05$)

3 – Biomechanical properties of the petiole

Petioles of compound leaves have higher Young's modulus (**E**) than the simple leaf, suggesting higher tissue density, especially in *Plerandra osyana* subsp. *osyana*.

The simple leaved *Meryta balansae* however exhibits similar flexural rigidity (**EI**) to the latter, through an increase in petiole diameter (**I**, axial second moment of area) rather than through tissue mechanical properties (E).

$$(EI = E \times I)$$

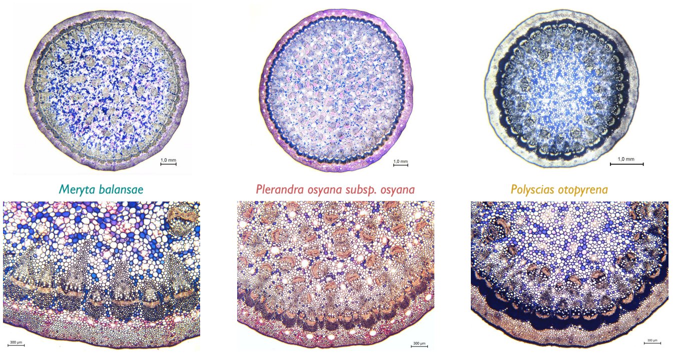

Young's modulus of elasticity
Flexural rigidity
Axial second moment of area

Meryta balansae Baill.
Plerandra osyana (Veitch ex Regel) Lowry, G.M. Plunkett & Frodin subsp. *osyana*
Polyscias otopyrena (Baill.) Lowry & G.M. Plunkett

N = 15x3

Tukey's comparison of means ($p < 0.05$)

4 – Anatomical organization of the petiole



Meryta balansae

Plerandra osyana subsp. osyana

Polyscias otopyrena

Reinforcement by thick-walled **collenchyma** and **sclerenchyma** (fiber caps)

Lignification of the "pith", containing **medullary bundles**, an unusual feature in dicotyledons, distributed: randomly (*Meryta balansae*), in a second ring inversely orientated (*Polyscias otopyrena*) or both (*Plerandra osyana* subsp. *osyana*)

Discussion

***Meryta*'s simple leaves** have short petioles, inducing self shading and little possibility for reorientation under wind drag force - a reduced constraint in rainforest understories

***Plerandra*'s palmate leaves** maximize light interception and reduce the wind drag force by long petioles, which may compensate for costly investment into support

***Polyscias*' pinnate leaves** have leaflet weights distributed along a rachis prolongating the petiole, allowing lamina expansion at reduced cost: a flexible model

Main findings & perspectives

- **Diverging allocating patterns** between leaf support and photosynthetic lamina across 3 leaf types in the Araliaceae of New Caledonia, underlying different foliar strategies

- **Palmate *vs* pinnate** compound leaves: we should not just oppose "simple" to "compound" leaves

To be tested next:

- **Biochemical** composition (nitrogen and phosphorus content) for a glimpse into metabolic activity
- **Phylogenetic** approach to better understand the **adaptative radiation** of leaf type among the Araliaceae

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1 - Niinemets Ü. and Kull O. 1999. Biomass investment in leaf lamina versus lamina support in relation to growth irradiance and leaf size in temperate deciduous trees. *Tree Physiology.* 19(6), p. 349–358.
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3 - Warman L., Moles A.T., and Edwards W. 2011. Not so simple after all: searching for ecological advantages of compound leaves. *Oikos.* 120(6), p. 813–821.
4 - Nicotra A.B., Leigh A., Boyce C.K., Jones C.S., Niklas K.J., Royer D.L., and Tsukaya H. 2011. The evolution and functional significance of leaf shape in the angiosperms. *Functional Plant Biology.* 38(7), p. 535–552.

Résumé en français – Diversité, Ecologie et Evolution des plantes monocaules de Nouvelle-Calédonie

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Chapitre 1 – Introduction générale

Les caractéristiques biogéographiques des îles font d’elles des modèles de choix pour l’étude des processus écologiques et évolutifs. Ainsi, nombreuses sont les grandes théories qui ont été inspirées par les systèmes insulaires puis généralisées aux régions continentales. Pour les années à venir, les approches combinant traits fonctionnels et phylogénies moléculaires semblent particulièrement prometteuses pour développer de nouveaux concepts. Parmi les différents systèmes insulaires, la Nouvelle-Calédonie, en tant que « vieille île Darwinienne », apparait être un modèle particulièrement intéressant. Malgré l’originalité exceptionnelle de sa flore aucun grand cas de convergence évolutive, pourtant commun dans les îles, n’a été mis en évidence dans cet archipel.

L’une des caractéristiques principales des systèmes insulaires est leur disharmonie taxonomique (la représentation inégale des lignées) et fonctionnelle (la représentation inégale des fonctions) par rapport aux régions adjacentes. La surreprésentation d’un caractère sur une île peut être due à (i) l’établissement préférentiel des espèces présentant ce caractère, (ii) l’évolution répétée du caractère sur l’île et/ou (iii) la diversification sur l’île des espèces présentant ce caractère. Parmi les mécanismes responsables de la disharmonie des flores, l’un des plus importants est la convergence évolutive, c’est-à-dire l’évolution d’un même caractère sous des pressions écologiques similaires mais non-hérité d’un ancêtre commun.

Les cas les plus marquants de convergence évolutive concernent les formes de croissance, c’est-à-dire l’apparence physionomique générale des plantes (par exemple les arbres en rosette ou les lianes). La diversification des formes de croissance, dont les interactions avec l’environnement sont particulièrement marquées, joue un rôle prépondérant dans l’accroissement de la richesse en espèces. Les formes de croissance résultent d’une combinaison de nombreux traits morphologiques, anatomiques, physiologiques et autres. L’un des exemples les mieux connus parmi ces associations de traits est représenté par les lois de Corner qui décrivent une corrélation négative entre le degré de ramification d’une part et la taille des feuilles, des fruits et des inflorescences d’autre part.

L’architecture des plantes est une discipline de la botanique qui s’intéresse à l’origine et à l’arrangement spatial des structures végétales ainsi qu’à leur évolution au cours de l’ontogénie. En ce sens, il s’agit d’une approche intégrative qui offre des perspectives multiples pour la compréhension des relations entre structure, fonction et environnement des plantes, et leur évolution.

Les travaux en architecture végétale ont montré que les fonctions des plantes sont réparties dans différents compartiments. Par exemple, le tronc des arbres assure principalement une fonction d’exploration et de support tandis que les branches et rameaux sont en comparaison plus spécialisés dans la photosynthèse et la reproduction. Mais parmi la diversité des architectures connues chez les végétaux, les plantes dites monocaules sont réduites à une extrême simplicité, n’étant constituées que d’un tronc unique. Cette forme de croissance ligneuse est souvent caractérisée par de très grandes feuilles disposées à l’extrémité du tronc. Probablement en raison de leur simplicité, de leur allure originale et des contraintes développementales évidentes liées à la restriction des méristèmes, les plantes monocaules ont toujours suscité la curiosité des botanistes. La monocaulie est aussi au cœur de grandes théories écologiques et évolutives, telles que les lois de Corner, dont elle illustre l'extrême d'un continuum (absence de la ramification, grandes feuilles, tige épaisse, gros fruits et inflorescences complexes). Malgré cela, les avantages adaptatifs et l'histoire évolutive des plantes monocaules restent très mal connus. Cette lacune est d'autant plus prégnante qu'elles sont présentes dans toutes les forêts tropicales humides, et particulièrement diversifiées dans certaines régions, comme en Nouvelle-Calédonie.

Nous partons de l'hypothèse que la forte représentation de la forme de croissance monocaule en Nouvelle-Calédonie pourrait représenter un cas de convergence évolutive pour l'archipel, le premier qui serait ainsi mis en évidence. Il en découlerait que la Nouvelle-Calédonie arbore des conditions environnementales favorables, et/ou non limitantes, pour l'évolution de cette forme de croissance. Le but de ce travail de thèse est de caractériser la diversité, l'écologie et l'évolution des espèces monocaules en Nouvelle-Calédonie. Plus précisément, nous tenterons à travers plusieurs chapitres, de répondre aux questions suivantes :

- Qu'est-ce que la monocaulie ? Combien y-a-t-il d'espèces monocaules en Nouvelle-Calédonie ?
- Combien de fois la monocaulie a-t-elle évoluée ? Peut-on identifier des traits d'histoire de vie ou environnementaux évolutivement corrélés à la monocaulie ? Représentent-ils des prérequis ou des contingences environnementales facilitant cette évolution ?
- Peut-on utiliser l'approche architecturale pour comprendre l'évolution de la monocaulie dans une phylogénie résolue à l'espèce ? Quelles sont les implications écologiques et fonctionnelles

d’un changement de forme de croissance ? La monocaulie est-elle impliquée dans la diversification des lignées en Nouvelle-Calédonie ?

- Quels sont les traits morpho-anatomiques associés à la forme de croissance monocaule ? Est-ce qu’ils peuvent nous permettre de mieux comprendre les lois de Corner ?
- Quelles hypothèses peuvent expliquer la convergence évolutive vers la monocaulie en Nouvelle-Calédonie ?

Chapitre 2 – Méthodologie générale

Le site d’étude : l’archipel néo-calédonien

La Nouvelle-Calédonie est un archipel océanique situé dans le Sud-Ouest de l’océan Pacifique. La majeure partie de sa superficie consiste en une île allongée (la Grande Terre) d’environ 16500 km² et parcourue sur toute sa longueur par une chaine montagneuse culminant à 1628 mètres d’altitude. Le climat est subtropical avec des précipitations moyennes annuelles variant selon les régions et les années (entre 800 mm/an et plus de 4000 mm/an). Une saison sèche s’étend d’août à novembre et les températures sont supposées ne descendre en dessous de zéro que très rarement (moyenne annuelle variant de 20 à 25 °C). La Nouvelle-Calédonie est fréquemment sujette à des cyclones qui peuvent être très intenses. Trois principaux substrats géologiques sont communément reconnus en Nouvelle-Calédonie : le substrat ultramafique (environ 1/3 de la Grande Terre) qui est très contraignant pour la croissance des plantes, le substrat volcano-sédimentaire (environ 2/3 de la Grande Terre) qui est très variable en composition et origine, et le substrat calcaire qui est rare sur la Grande Terre.

La Nouvelle-Calédonie est un fragment du Gondwana qui s’est séparé il y a environ 120-80 Ma puis a été immergé entre -62 et -35 Ma. Durant cette immersion l’île a été recouverte d’une partie de croute océanique, évènement à l’origine du substrat ultramafique, qui s’est ensuite érodé après l’émergence de l’île pour laisser apparaitre les autres substrats connus aujourd’hui. Les données paléoclimatiques suggèrent que la Nouvelle-Calédonie a connu des périodes d’aridification il y a quelques millions d’années (-6,5 Ma et -2,5 Ma) et plus récemment (-22000 et -12000 ans). Ces évènements sont supposés avoir été moins sévères que pour le reste du Pacifique, permettant la persistance des forêts denses humides sous forme de refuges alors qu’elles déclinaient dans les régions adjacentes comme l’Australie.

La flore de Nouvelle-Calédonie est extrêmement diversifiée (environ 3400 espèces vasculaires) et originale (75% d’endémisme). Elle présente notamment une disharmonie marquée avec les flores régionales, tant au point de vu taxonomique que fonctionnel. La flore et les habitats sont extrêmement menacés, en particulier les forêts denses humides sur substrat ultramafique. Aujourd’hui 43% des espèces évaluées selon la méthodologie de l’IUCN sont menacées d’extinction, les principales menaces étant les feux de brousses, l’activité minière et les herbivores introduits. Sept principaux types de végétations sont reconnus en Nouvelle-Calédonie dont les savanes et le maquis (principalement d’origine anthropique) qui sont les plus étendus, et la forêt dense humide qui est la plus diversifiée. Ces forêts se caractérisent, entre autre, par une densité élevée de tiges de petits diamètres. Parmi les facteurs principaux responsables de l’originalité de la flore néo-calédonienne, on reconnait notamment le substrat ultramafique (filtrant l’établissement des espèces et contraignant leur croissance), les changements climatiques du Quaternaires (générant des refuges pour des espèces sensibles à la sècheresse) et les cyclones (entre autre responsables des caractéristiques structurales des forêts).

Vers une nouvelle définition de la monocaulie : entre structure et fonction

L'approche architecturale apporte des critères intégrateurs et objectifs pour la définition des formes de croissance. Pour la monocaulie, la définition la plus aboutie est celle proposée par Hallé et all en 1978 : les monocaules sont définis comme des « arbres avec un seul tronc ou tige visible». À cette définition est associée trois modèles architecturaux : les modèles de Corner, Holttum, et Chamberlain. Notre étude s'intéressant à la signification adaptative des formes de croissance, nous avons ajouté une dimension fonctionnelle à la définition : les monocaules sont définies comme des « plantes autoportantes ligneuses dont les fonctions cardinales reposent sur une seule tige visible ». Les espèces conformes à cette définition sont donc constituées (i) d'un tronc (monoaxial ou pluriaxial), (ii) de structures latérales à croissance déterminée, fortement spécialisées dans la photosynthèse et présentant un point d'abscission, (iii) d'axes ou complexes d'axes hautement spécialisés dans la reproduction et dont la contribution à l'exploration végétative de l'espace et à la photosynthèse est négligeable, et éventuellement (iv) de réitéras opportunistes (c'est-à-dire la répétition de l'architecture élémentaire de la plante en réponse à un stimuli ou un stress environnemental). Cette définition inclut donc les modèles architecturaux de Corner, Holttum, Chamberlain, Cook et en partie celui de Tomlinson (si la répétition basale est opportuniste).

Constitution de la liste des espèces monocaules

À partir de la définition ci-dessus, une liste exhaustive des espèces monocaules de Nouvelle-Calédonie a été constituée. Nous nous sommes focalisés sur la flore Angiosperme non-monocotylédone car la monocaulie exprimée chez les monocotylédones (Palmiers, etc.)…) et fougères est structuralement et fonctionnellement différente. Pour cela, une extraction par mots-clés de la base de données de l'Herbier de Nouvelle-Calédonie (NOU) a été réalisée et complétée à dire d'expert et par une analyse bibliographique approfondie (flores, description d'espèces, etc.).

Ensuite, l'architecture de chaque espèce de cette liste (ainsi que d'autres espèces) a été vérifiée sur le terrain et à l'aide de photographies.

Chapitre 3 – La forme de croissance monocaule : une brève synthèse

Le terme monocaulie (du latin *monocaulis*) a été utilisé à de nombreuses reprises depuis au moins le 17ème siècle pour caractériser les plantes ou parties de plantes non-ramifiées. La vision actuelle de la monocaulie, caractérisant des plantes ligneuses non ramifiées et portant un toupet de grosses feuilles dans la partie distale de la tige, a été amenée par Corner en 1949. Le terme a ensuite été utilisé à différentes reprises avec des définitions plus ou moins larges jusqu'à la proposition d'une définition physionomique par Hallé et all en 1978, puis par la définition fonctionnelle proposée dans le cadre de ce doctorat.

L'architecture non-ramifiée est très ancienne chez les plantes terrestres, le modèle de Corner par exemple, faisant partie des plus anciens connus chez les plantes fossiles. Cette forme architecturale était particulièrement abondante dans les paléo-écosystèmes (notamment entre -350 Ma et -110 Ma). Elle a ensuite été progressivement remplacée par les plantes ramifiées de façon axillaire et ne représenterait aujourd'hui qu'environ 2% des espèces connues. Certains auteurs ont suggéré que l'ancêtre commun aux plantes à fleurs était monocaule et que les espèces monocaules actuelles sont des cas « relictuels » de cette forme ancestrale. D'autres suggèrent que ces espèces sont apparues dans plusieurs familles par évolution convergente. Les études récentes s'appuyant sur des phylogénies moléculaires ont finalement montré que la monocaulie est apparue de manière convergente dans plusieurs lignées. Deux voies évolutives, par processus hétérochroniques, ont été proposées pour l'évolution de la monocaulie. La première, déjà connue dans certaines lignées, suggère une évolution depuis des ancêtres herbacés dont la séquence développementale aurait été prolongée. La seconde, restant hypothétique, suggère une évolution depuis des arbres dont la séquence développementale aurait été tronquée.

Les traits d'histoire de vie associés à la monocaulie ont pour la plupart été inférés de façon empirique ou par le biais d'indices de ramification hétérogènes et difficiles à interpréter. Nous avons noté 16 principaux états de caractères potentiellement associés à la monocaulie selon la littérature. Les espèces monocaules sont restreintes aux régions tropicales et subtropicales d'où elles sont connues de trois principaux environnements: les milieux secs et ouverts (particulièrement sur les îles), les milieux alpins, et les forêts denses humides où il semble y avoir la plus grande diversité.

Chapitre 4 – *Novitates neocaledonicae VII* : Une nouvelle espèce monocaule de *Bocquillonia* (Euphorbiaceae) pour la Nouvelle-Calédonie

Le genre *Bocquillonia* est un genre d'Euphorbiaceae contenant quatorze espèces toutes endémiques de Nouvelle-Calédonie. Des études moléculaires suggèrent que *Bocquillonia* est phylogénétiquement inclut dans le genre pantropical *Alchornea*, mais cela reste à confirmer. Les espèces de *Bocquillonia* se caractérisent par la présence de glandes à la face abaxiale des feuilles, un système sexuel dioïque (rarement monoïque), des inflorescences glomeruleuses à étroitement racemiformes, des fleurs apétales, un calice bi- ou trilobé pour les fleurs mâles, un calice plus court que le gynécée pour les fleurs femelles et la présence de phloème interne (péri-médullaire) dans la tige. De nombreuses espèces sont conformes au modèle architectural de Corner et les formes de croissance varient depuis des arbrisseaux monocaules ou ramifiés à des arbres ramifiés. Cette diversité des formes de croissance est principalement due à des variations de la dimension des tiges et de la fréquence de la réitération opportuniste, ce qui en fait un modèle intéressant pour étudier l'évolution de la monocaulie.

Au court de ce travail de thèse une population de *Bocquillonia* monocaules pouvant atteindre 8 mètres et très peu réitérés – un caractère inédit dans le genre – a été observé. Des observations de terrain et de spécimens d'herbiers ont confirmé que cette population représentait un taxon distinct des autres espèces de *Bocquillonia* décrites.

Cette nouvelle espèce a été nommée *Bocquillonia corneri* en hommage à E.J.H Corner dont les hypothèses concernant les plantes monocaules ont inspirées des générations de botanistes. *Bocquillonia corneri* se distingue des autres espèces du genre par la combinaison de caractères suivante : (i) un arbre monocaule très peu réitéré, (ii) des inflorescences condensées, (iii) des fleurs femelles avec un calice fuchsia et (iv) des stigmates ovales appliqués contre l'ovaire. Les données suggèrent que *B. corneri* est très menacé par les feux de brousses, l'activité humaine et les herbivores introduits et l'espèce a été considérée en danger critique d'extinction (CR) selon les critères de la liste rouge de l'IUCN. Dans cet article une clé d'identification de toutes les espèces décrites de *Bocquillonia* est proposée.

Chapitre 5 – Un remarquable cas de convergence évolutive : évolution corrélée et contingences environnementales de la monocaulie dans la flore néo-calédonienne.

Dans ce chapitre nous décrivons un cas remarquable de convergence évolutive avec l'apparition multiple de la monocaulie en Nouvelle-Calédonie.

Par le bais d'une compilation de données issues de la littérature et de l'herbier de Nouvelle-Calédonie (NOU) ainsi qu'un travail de terrain intensif, nous avons dressé la liste des espèces monocaules de Nouvelle-Calédonie et codé six traits d'histoire de vie (le système sexuel, le type de fruit, l'attractivité des fleurs, le type de feuilles, la position de la sexualité et les rythmes de croissance) ainsi que deux traits environnementaux (la végétation et le substrat) de façon binaire pour les 2114 dicotylédones ligneuses et autoportantes de Nouvelle-Calédonie. L'évolution corrélée entre la monocaulie et ces traits a été testée à l'aide d'un super-arbre phylogénétique créé à partir des relations génériques publiées pour les clades calédoniens. Cet arbre a également été utilisé pour calculer le signal phylogénétique de la monocaulie, son nombre d'apparition minimal en Nouvelle-Calédonie ainsi que la relation entre la présence de monocaules dans un genre et sa diversité spécifique. L'endémisme (spécifique et générique) des espèces monocaules ainsi que leur risque d'extinction et principales menaces (selon les critères de l'IUCN) ont également été investigués.

Nous avons recensé 182 espèces dicotylédones monocaules appartenant à 41 genres, 30 familles et 15 ordres. Le modèle architecturale de Corner est de loin le plus représenté suivi par le modèle de Cook (mais présentant une faible diversité phylogénétique) puis par le modèle de Chamberlain. Avec plus de 31 apparitions indépendantes, l'évolution de la monocaulie en Nouvelle-Calédonie rejoint les plus grands cas de convergence décrits pour les systèmes insulaires comme la « secondary woodiness » (c'est-à-dire l'évolution du caractère ligneux dans des groupes herbacés) aux îles canaries. La monocaulie présente néanmoins un signal phylogénétique significativement différent d'une évolution aléatoire, indiquant une évolution préférentielle dans certains clades comme les Malpighiales, les Apiales ou les Sapindales. Ceci suggère l'existence de prérequis facilitant l'évolution de la monocaulie. Cette forme de croissance a préférentiellement évoluée en forêt dense humide et sur substrat ultramafique, ce que nous avons associé à un avantage compétitif dans les milieux denses, humides, ombragés et à faibles ressources lumineuses et minérales. L'évolution de la monocaulie a favorisé l'apparition de la cauliflorie et d'une croissance rythmique marquée chez les clades concernés, que nous relions respectivement à un nombre limité de nœuds foliés (contraignant l'apparition de la sexualité sur les parties défoliées) et à une nécessité accrue de protéger le méristème unique (contraignant la durée de la phase de croissance). Aucune préadaptation n'a pu être identifiée mais l'observation empirique d'un lien entre les modèles architecturaux monocaules et ramifiés ouvre une voie intéressante à investiguer. Les genres contenants des espèces monocaules sont significativement plus diversifiés que les autres. Ce résultat, en combinaison avec la quasi-absence de genres majoritairement monocaules, pourrait suggérer un accroissement de la diversification avec l'apparition de la monocaulie via un phénomène de partitionnement de niche. La flore monocaule semble plus gravement menacée que la flore ramifiée (proportion d'espèces « en danger » et « en danger critique d'extinction ») avec un impact particulièrement important des herbivores introduits. Par ailleurs la proportion significativement plus importante d'espèces monocaules dans la classe « données déficientes » montre que ces espèces restent particulièrement mal connues. Le taux d'endémisme très élevé de la flore monocaule (98.9 %) ainsi que l'apparente rareté de groupes externes monocaules suggère soit une évolution préférentielle de la monocaulie en Nouvelle-Calédonie, soit une disparition de cette forme dans les régions voisines. La remarquable convergence évolutive de la monocaulie en Nouvelle-Calédonie est ici reliée à quatre hypothèses majeures : (i) la très forte densité des forêts en lien avec la fréquence et l'intensité des cyclones dans la région favorisant le port monocaule, (ii) la persistance de refuges forestiers durant les fluctuations climatiques du Pleistocène dont les épisodes de sècheresse ont pu causer des extinctions massives dans le reste du Pacifique, (iii) l'importance sur l'archipel du substrat ultramafique dont les contraintes édaphiques peuvent contraindre le développement structural des plantes (« paupérisation architecturale ») et favoriser la réduction de la ramification, et (iv) l'absence de grands herbivores sur le long terme, empêchant la contre-sélection de la forme monocaule qui est particulièrement sensible au broutage.

Chapitre 6 – Evolution de l’architecture, diversification fonctionnelle et évolution divergente dans le genre *Atractocarpus* (Rubiaceae) en Nouvelle-Calédonie

L’évolution convergente et l’évolution divergente sont deux processus complémentaires parmi les plus importants liant l’écologie des plantes et leur diversification. La convergence est l’apparition de caractères similaires sous des pressions écologiques similaires mais non hérités d’un ancêtre commun. La divergence est la diversification des rôles écologiques entre des espèces proches, en compétition pour les ressources, aboutissant à l’exploitation différentielle d’un même environnement. Le genre *Atractocarpus* présente une diversité architecturale et un taux de diversification très rapide, ce qui en fait un modèle intéressant pour étudier l’implication de l’architecture végétative dans les processus de divergence et de convergence évolutive chez les plantes.

Atractocarpus est un genre Pacifique contenant une quarantaine d’espèces dont 32 sont endémiques à la Nouvelle-Calédonie et issues d’un seul évènement de colonisation. La grande majorité des espèces sont des arbustes monocaules à ramifiés inféodés au sous-bois des forêts denses humides. L’architecture de chacune des 27 espèces néo-calédoniennes d’*Atractocarpus* de sous-bois a été décrite. Pour chacune d’elles, un échantillonnage standardisé sur 5 individus a été réalisé sur lesquels un ensemble de 15 traits fonctionnels a été mesuré. Notamment, un indice de ramification fonctionnellement explicite et lié à l’architecture des plantes a été développé dans cette étude. Il consiste en la proportion de la fonction photosynthétique (approximée par la surface foliaire) et d’exploration (approximée par la longueur) assurée par les branches. Un indice de 0 signifie donc que ces fonctions sont assurées par le tronc (plante monocaule) et plus l’indice se rapproche de 1, plus les branches sont fonctionnellement importantes. Les indices de ramification photosynthétique et d’exploration ont été combinés à l’aide d’une Analyse en Composante

Principales (ACP) et cette nouvelle variable a permis de définir trois classes architecturales (monocaule, intermédiaire, ramifiée). L'évolution de ces classes architecturales dans le genre a été étudiée à l'aide d'une reconstitution d'état de caractère réalisée sur une phylogénie moléculaire récemment produite. Cette phylogénie a également permis de tester le lien entre les 14 traits fonctionnels et l'indice de ramification via des régressions phylogénétiques. L'effet de chacune des classes architecturales sur la diversification du genre a été comparé (MuSSE framework) et leurs différences en terme de stratégies écologiques ont été investiguées (ACP et Permanova).

La reconstitution d'état de caractère a montré que l'ancêtre commun aux *Atractocarpus* était probablement ramifié et que le caractère monocaule est apparu par convergence 2 à 3 fois dans le genre (aux alentours de -1,4 et -0,9–0,6 Ma respectivement). Les espèces ramifiées et monocaules ne sont jamais des espèces sœurs. Ce résultat, combiné à la variation graduelle de l'architecture chez les plantes actuelles, suggère une évolution graduelle de la forme ramifiée vers la forme monocaule en passant par la forme intermédiaire. Ceci est plus en cohérence avec la notion de continuum architectural qu'avec celle d'évolution par saltation, deux notions contradictoires proposées pour l'évolution de l'architecture des plantes. Les structures axillaires (axes de catégorie 2 : C2) des espèces monocaules ne participent presque pas à la photosynthèse et à l'exploration de l'espace et sont spécialisées uniquement dans la reproduction. Fonctionnellement autant que morphologiquement, il s'agit d'inflorescences qui sont donc homologues aux branches des espèces ramifiées. L'analyse architecturale montre que cette réduction des branches vers les inflorescences a eu lieu de deux façons différentes selon les clades : par la réduction du nombre de module ou par la réduction de la longueur des modules sur les C2. Ces processus impliquent donc deux processus hétérochroniques différents gouvernant l'évolution depuis le modèle architectural de Stone vers celui de Corner : la néoténie dans le premier cas et le « nanisme proportionnel » dans le second cas. Nos résultats montrent une corrélation négative entre l'indice de ramification et respectivement le volume du fruit, la surface des feuilles et le diamètre de la tige, ce qui confirme les lois de Corner. Outre cela, la corrélation entre l'indice de ramification et de nombreux traits fonctionnels suggère que les plantes monocaules ont plus une stratégie de conservation de la ressource adaptée au sous-bois denses et sombres que les plantes ramifiées. Cette diversification des stratégies écologiques en lien avec l'architecture pourrait illustrer un cas de radiation adaptative dans les forêts denses humides de Nouvelle-Calédonie. L'arrivée du genre *Atractocarpus* en Nouvelle-Calédonie coïncide avec la fin d'épisodes glaciaires, suivis par une période d'extension des forêts denses humides créant probablement de nombreuses niches vacantes. Cette vacance de niche, associée aux caractéristiques environnementales des forêts denses humides (forte variabilité de la disponibilité en lumière dans le sous-bois, densité du sous-bois) et à la faible capacité de dispersion des gros fruits du genre a pu promouvoir l'évolution divergente des *Atractocarpus* en Nouvelle-Calédonie.

Chapitre 7 – Retour à Corner : caractérisation fonctionnelle et relation feuille – tige chez les plantes monocaules

Le chapitre précèdent a montré que la monocaulie est une forme de croissance rare qui a beaucoup à apporter pour la compréhension des adaptations des plantes. Alors que chez la majorité des plantes les fonctions essentielles (photosynthèse, hydraulique, mécanique, stockage des réserves carbonées) sont réparties dans plusieurs catégories d'axes, les monocaules intègrent ces fonctions sur un seul tronc. Cette particularité est susceptible d'engendrer de fortes interdépendances entre les différentes fonctions résultant en une coordination particulièrement poussée de certains traits fonctionnels. Certaines dimensions fonctionnelles, représentant la corrélation systématique de plusieurs traits sont reconnus comme des déterminants majeurs de l'évolution et de la distribution des plantes. Ainsi, identifier des points extrêmes dans ces corrélations de traits est susceptible d'apporter des informations cruciales sur leur valeur adaptative. Les monocaules se situent justement à l'extrême de la relation entre le degré de ramification, la taille des feuilles et la taille de la tige définie comme une partie des lois de Corner. Particulièrement, les relations [surface de la feuille – taille de la tige] et [surface du feuillage – taille de la tige] sont parmi les corrélations de traits les mieux documentés. Malgré cela, les liens fonctionnels entre ces paires de traits restent flous, les hypothèses suggérant alternativement une importance des contraintes hydriques, mécaniques, ou photosynthétiques des feuilles sur la tige. Dans ce chapitre, nous avons pour but d'apporter une première caractérisation fonctionnelle de la monocaulie de forêt dense humide et d'apporter des éléments de compréhension quant aux liens fonctionnels gouvernant les relations [feuille – tige] et [feuillage – tige] chez les plantes.

Dix genres phylogénétiquement éloignés et contenant des espèces monocaules ont été sélectionnés. Pour chacun d'eux, une espèce monocaule et une espèce ramifiée poussant dans des conditions similaires (sous-bois de forêt dense humide, sur substrat ultramafique et entre 200 et 550 mètres d'altitude) ont été étudiées via un échantillonnage standardisé sur 5 individus. Un ensemble de traits (foliaires et caulinaires, anatomiques et morphologiques, microscopiques et macroscopiques) associés aux fonctions hydrauliques, biomécaniques et photosynthétiques a été mesuré. Les différences de traits entre espèces monocaules et ramifiées ont été testées via des anovas à effets mixtes. Les relations [surface d'une feuille – diamètre de la moelle], [surface d'une feuille – diamètre du rameau] et [surface foliaire du rameau – diamètre du rameau] ont été testées par des régressions linéaires. Les valeurs de certains traits représentant des dimensions importantes de l'adaptation hydraulique et photosynthétique des plantes ont été comparées à celles de la base de données globale TRY. Pour comprendre les implications fonctionnelles de la relation feuille – tige, les structures anatomiques de la tige ont été partitionnées selon leurs fonctions (hydrauliques, mécaniques et photosynthétiques) et leurs relations avec la surface foliaire ont été testées à différents niveaux.

Les espèces monocaules et ramifiées ont montré des valeurs significativement différentes pour plusieurs traits fonctionnels. Les plantes monocaules ont des tiges plus élancées et moins coniques car elles ont un diamètre basal plus faible (que nous relions à l'absence des contraintes mécaniques exercées par les branches) et un diamètre distal plus important (que nous relions aux contraintes mécaniques imposées par le toupet de feuilles massif). Ces contraintes mécaniques semblent plus compensées par la géométrie de la tige (diamètre, proportion de bois) que par des adaptations micro-anatomiques (fibres). Les monocaules ont une valeur de Huber (ratio de la surface de bois sur la surface foliaire qu'il alimente) plus faible qui est compensée par des vaisseaux de diamètre plus important permettant un accroissement de l'efficience hydrique. Les feuilles des plantes monocaules étudiées font partie des plus grandes feuilles au monde. Les traits foliaires ne permettent pas encore de conclure quant aux caractéristiques photosynthétiques des plantes monocaules bien qu'ils suggèrent plutôt une stratégie de conservation de la ressource (SLA et densité stomatique faibles). Les grandes feuilles (souvent simples) des plantes monocaules sont physiologiquement contraintes aux environnements humides et ombragés comme la forêt dense humide. Le partitionnement de la surface photosynthétique en peu de grandes feuilles, tout comme la réduction de la ramification, sont des stratégies peu couteuses et intéressantes lorsque les ressources lumineuses et minérales sont rares comme c'est le cas dans nos sites d'étude. Les plantes monocaules présentent une allocation plus faible dans les tissus de stockages (cortex, rayons du bois) mais la grande diversité des modalités et organes de stockage chez les plantes rend difficile de conclure à ce sujet. Nos résultats confirment l'existence d'une relation allométrique entre la surface foliaire et l'épaisseur de la tige à différents niveaux (phytomère, feuille individuelle, rameau). La relation feuillage – tige semble liée aux contraintes mécaniques et, dans une moindre mesure, hydrauliques exercées par les feuilles sur la tige. L'hypothèse suggérée dans la littérature d'un lien photosynthétique n'est pas supportée ici. La contribution importante du bois à la relation feuillage – tige suggère que la mise en place rapide de ce tissu plurifonctionnel est une adaptation majeure aux contraintes exercées par une surface foliaire importante. La relation feuille – tige découle directement de la relation feuillage – tige puisque la variation de la surface foliaire totale est plus liée à la taille des feuilles qu'à leur nombre. Nous suggérons par ailleurs que, pour une surface foliaire totale donnée, les contraintes mécaniques sont plus importantes lorsque les feuilles sont grandes que lorsqu'elles sont petites. Ainsi, les contraintes mécaniques exercées par les feuilles apparaissent être les causes principales du lien entre surface foliaire et taille de la tige en sous-bois de forêt dense humide ou les contraintes hydrauliques et photosynthétiques sont faibles. La relation suggérée dans la littérature impliquant une plus grande taille des entre-nœuds et donc une allocation structurelle moindre dans la tige chez les plantes à larges feuilles semble être de moindre importance. Ainsi, cette étude apporte une première description fonctionnelle détaillée de la monocaulie du sous-bois des forêts denses humides. L'étude des quelques espèces monocaules présentes en maquis (majoritairement à feuilles composées) apporterait d'autres éléments intéressants pour compléter cette étude. La stratégie monocaule identifiée ici contraste avec ce qui a été décrit pour d'autres régions où les monocaules étudiées ont souvent évolué à partir d'ancêtres herbacés et sont plutôt adaptées à des environnements secs ou alpins.

Chapitre 8 – Discussion générale

La monocaulie en Nouvelle-Calédonie : convergence évolutive et disharmonie fonctionnelle

Bien que le manque de données pour d'autres flores empêche toute comparaison rigoureuse, la richesse en espèces monocaules en Nouvelle-Calédonie peut être considérée comme faisant partie de la disharmonie fonctionnelle de l'archipel puisque cette forme est considérée comme rare dans la région et à l'échelle globale. Nous avons identifié 182 espèces non-monocotylédones appartenant à 41 genres, 30 familles et 15 ordres. Cela représente 5,5% de la flore de l'archipel, 9% de la flore ligneuses et 12,4% des espèces inféodées aux forêts denses humides. À titre de comparaison, la flore monocaule a été estimée à 2% de la flore mondiale (fougères et monocotylédones incluses) et la proportion de plantes divariquées en Nouvelle-Zélande, reconnue comme le syndrome le plus marquant de cette île, atteint 10% de la flore ligneuse.

L'abondance et la distribution des espèces monocaules est difficile à estimer à partir d'inventaires standardisés car ceux-ci concernent souvent les arbres de plus de 5 cm de diamètre à hauteur de poitrine. Les monocaules, comme la plupart des plantes de sous-bois, y sont donc très peu représentés. Des données provenant d'une étude peu étendue mais incluant toutes les tiges plus hautes que 1.3 mètres montrent effectivement que 95% des individus monocaules ont un diamètre à hauteur de poitrine inférieur à 5 cm. Sur les 0.576 hectares de l'étude, les plantes monocaules montrent une densité moyenne de 2135 tiges à l'hectare (maximum 3934 tiges à l'hectare) et représentent en moyenne 12.1% des tiges (maximum 16.1% des tiges).

La richesse en espèces monocaules peut être expliquée par 3 scénarios évolutifs non-exclusif (décrits en introduction) : (i) l'établissement en Nouvelle-Calédonie d'espèces monocaules semble être un phénomène rare puisque la monocaulie n'est ancestrale dans aucun des clades calédoniens pour lesquels des phylogénies sont disponibles (appuyé par l'absence de groupes frères monocaules), (ii) l'évolution *in situ* de la monocaulie semble avoir grandement participé à la diversité totale puisque nous avons identifié au moins 31 apparitions du caractère, (iii) la diversification des clades monocaules a également contribué à la diversité actuelle en espèces monocaules mais aucune grande radiation monocaule n'ait été mise en évidence jusqu'à présent.

Ainsi, l'évolution convergente de la monocaulie en Nouvelle-Calédonie est probablement le mécanisme principal responsable de la diversité en espèces monocaules sur l'archipel. L'apparition du caractère plus de 31 fois représente un cas de convergence au moins aussi marquant que celui de la « secondary woodiness » aux îles canaries. D'autant que cette indice sous-évalue probablement le nombre réel d'évolution de la monocaulie, car il se base sur une phylogénie des genres (et non des espèces). Ce phénomène de convergence suggère d'importantes pressions environnementales ayant favorisé l'apparition de la monocaulie en Nouvelle-Calédonie.

Les implications écologiques et évolutives de la monocaulie

Parmi les 16 caractères supposés être associés à la monocaulie selon la littérature, nous avons confirmé statistiquement la relation pour 8 d'entre eux, trouvé une relation non-significative pour 5 d'entre eux, une relation inverse pour 3 d'entre eux, et mis en évidence une association significative avec 8 nouveaux caractères. Ces caractères sont liés les uns aux autres et à la monocaulie par différentes coordinations fonctionnelles. Les lois de Corner ont été confirmées à plusieurs reprises, sauf en ce qui concerne la relation entre le degré de ramification et la complexité des inflorescences. La relation avec la taille des feuilles implique un compromis entre le nombre de feuille porté (faible chez les monocaules car peu de phytomères) et la taille des feuilles. Ces larges feuilles seraient responsables d'un épaississement distal de la tige, notamment via la proportion de bois, pour répondre aux contraintes mécaniques qui s'exercent sur la partie apicale de la tige. La réponse aux contraintes hydrauliques implique plutôt un élargissement des vaisseaux. La contrainte spatiale liée à la monocaulie (peu de phytomères) serait aussi responsable d'un compromis entre le nombre et la taille des fruits (plus gros chez les monocaules). Les espèces monocaules ont des tiges plus effilées et moins coniques que leurs congénères ramifiés. Ceci serait dû au diamètre distal plus important (augmentation acropète de la taille de la moelle et croissance secondaire plus active) en réponse aux contraintes mécaniques du large toupet de feuille, et au diamètre basal plus faible (croissance secondaire moins active) en réponse à la réduction de la charge statique (et dans une moindre mesure dynamique) résultant de l'absence de branche. Le module de Young (résistance à la flexion) mesuré au cours de ce travail n'est pas très différent de celui renseigné dans la littérature pour les espèces ramifiées. Ces données seront traitées dans une prochaine publication. Outre la taille des feuilles, les valeurs de traits foliaires investigués dans cette étude suggèrent une faible capacité photosynthétique chez les monocaules, bien qu'une étude plus approfondie soit nécessaire. Une publication scientifique en cours de rédaction s'est notamment intéressée à la diversité des traits foliaires dans l'une des familles calédoniennes contenant le plus d'espèces monocaules (les Araliaceae). Les résultats préliminaires montrent un lien entre les traits foliaires et le degré de ramification des individus. D'autres caractères comme des entre-nœuds courts ou la forte croissance secondaire des parties apicales, en combinaison avec les résultats préliminaires d'un suivi phénologique, suggère une croissance très lente des espèces monocaules. L'ensemble de ces caractères suggère une stratégie de conservation de la ressource plus marquée pour les plantes monocaules que pour leurs congénères ramifiés.

Ces valeurs de traits particulières des plantes monocaules sont sujettes à de fortes contraintes environnementales. Notamment, leurs très grandes feuilles sont particulièrement sensibles aux températures extrêmes et aux fortes variations environnementales, en raison de leur plus lente thermorégulation et grande surface d'évapotranspiration, ce qui les contraints aux environnements humides, ombragés et non-venteux. Cela est cohérent avec l'occurrence préférentielle des espèces monocaules dans les forêts denses humides en Nouvelle-Calédonie.

Néanmoins, certaines espèces monocaules sont présentes en milieux ouverts comme dans le maquis. Celles-ci ont, dans la majorité des cas, des feuilles composées, des rameaux phyllomorphiques ou sont de petite taille, chaque cas représentant un moyen de limiter la surface foliaire individuelle. Finalement, des études montrent que répartir une surface foliaire donnée en peu de grandes feuilles plutôt qu'en beaucoup de petites feuilles est économiquement plus intéressant. La stratégie monocaule est donc susceptible d'être favorisée dans les environnements pauvres en ressources lumineuses et minérales, comme dans le sous-bois et sur substrat ultramafique.

Les caractéristiques fonctionnelles et contraintes environnementales associées à la monocaulie nous permettent de poser quatre hypothèses pouvant expliquer la convergence vers cette forme en Nouvelle-Calédonie. (i) Les cyclones sont particulièrement fréquents et intenses dans la région, ce qui est supposé être le facteur principal de la remarquable densité des tiges dans les forêts de Nouvelle-Calédonie. Cette forte densité, ainsi que les débris tombant de la canopée lors des cyclones, est susceptible d'avoir favorisé l'exploration unidirectionnelle de l'espace et donc les espèces monocaules. (ii) La persistance des forêts denses humides sous forme de refuges en Nouvelle-Calédonie lors des épisodes glaciaires aurait permis le maintien des espèces monocaules sur le territoire. Et l'expansion post-glaciaire de ces forêts aurait fourni de nombreuses opportunités écologiques pour ces espèces qui auraient alors subi une diversification importante, comme dans le genre *Atractocarpus*. (iii) Les contraintes édaphiques du substrat ultramafique auraient favorisé une stratégie plutôt orientée vers l'économie des ressources représentée par les plantes monocaules qui ont une surface foliaire équivalente mais moins coûteuse que les espèces ramifiées. (iv) L'absence de grands herbivores sur le long-terme n'a pas contre-sélectionné les espèces monocaules dont les grandes feuilles et le méristème unique les rendent particulièrement sensible au broutage.

La monocaulie est supposé avoir contribué à la diversification des lignées en Nouvelle-Calédonie, non pas à la manière d'une innovation clé (impliquant une importante radiation après apparition du caractère) mais plutôt via le phénomène de partitionnement de niche (exploitation différentielle des ressources entre espèces proches). La monocaulie aurait permis la colonisation de sous-bois particulièrement denses et sombres contribuant à la diversification générale des lignées. Le genre *Atractocarpus* en est un bon exemple et pourrait représenter un des rares cas de radiation adaptative observés en Nouvelle-Calédonie.

L'approche architecturale, un outil clé pour comprendre l'évolution des plantes

Notre approche fonctionnelle de la monocaulie, basée sur une hiérarchisation quantifiée des fonctions à travers un indice de ramification, et renforcée par la définition de types structuraux permettant l'utilisation de critères objectifs, s'est révélée être particulièrement appropriée dans le contexte de cette étude. Cette approche mérite d'être testée sur d'autres formes de croissance et dans des études plus globales sur l'évolution des formes de croissance.

Dans cette étude, nous avons mis en évidence deux processus non suspectés conduisant à l'évolution de la monocaulie : la réduction des branches en inflorescences par (i) la réduction de la longueur des modules (« nanisme proportionnel ») ou (ii) la réduction du nombre de module (« néoténie »). Nous suggérons que ces phénomènes d'hétérochronie développementale (c'est à dire un changement dans le timing d'un ou plusieurs évènements de la séquence ontogénétique) sont prépondérants dans l'évolution de la monocaulie et plus généralement dans l'évolution des formes de croissance. Pour appuyer cette hypothèse, nous illustrons la diversité architecturale observée dans quatre genres contenant des espèces monocaules.

La convergence évolutive est souvent vue comme une démonstration des contraintes environnementales et phylogénétiques s'appliquant à l'évolution des traits. Cela implique deux notions sous-jacente : la présence de prérequis facilitant l'apparition d'un caractère, et la présence de contraintes empêchant certaines transitions. Nous supposons que certaines lignées néo-calédoniennes ont effectivement présenté des prérequis facilitant l'évolution vers la monocaulie, comme l'expression de certains modèles architecturaux particuliers (Rauh, Leeuwenberg). Ceci a probablement été le cas pour les Gardenieae auquel appartient le genre *Atractocarpus*. Cependant, aucune contrainte empêchant l'apparition de la monocaulie n'a été mise en évidence. Nous argumentons que l'évolution vers cette forme très simple est relativement « facile », notamment via des processus hétérochroniques puisque la plupart des espèces passent par une phase monocaule au cours de leur ontogénie. Cette facilité évolutive et les nombreuses contingences environnementales en Nouvelle-Calédonie sont probablement responsables de son apparition dans plusieurs lignées éloignées et de la diversité des scenarios évolutifs représentés (évolution depuis des herbes, des arbres, des arbustes et des lianes).

Nous avons montré une évolution graduelle de la monocaulie dans le genre *Atractocarpus*, contrairement à l'évolution par saltation qui a été proposée pour les traits architecturaux. Ainsi, le passage d'une forme de croissance à une autre n'implique pas forcement des changements fondamentaux dans l'architecture des plantes, une variation continue mais directionnelle pouvant conduire rapidement à l'évolution de la monocaulie. Si les formes de transitions entre les deux modèles sont moins stables que les extrêmes (ici ramifié et monocaule) est une question très intéressante qui mérite d'être approfondie.

La réitération est définie comme un processus morphogénétique par lequel un organisme duplique son architecture élémentaire, c'est-à-dire son unité architecturale. Plusieurs modalités ont été définies, notamment la réitération séquentielle (génétiquement programmée) qui s'oppose à la réitération opportuniste (dépendante des conditions environnementales). Cependant, notre étude montre que la distinction entre ces deux modalités de réitération n'est pas toujours facile sur le terrain et qu'elles semblent parfois être les deux extrêmes d'un même gradient. Ceci représente la difficulté majeure résidant encore dans notre définition de la monocaulie puisque certaines plantes définies comme monocaules peuvent devenir de grands arbres de canopée. Nous pensons qu'une caractérisation plus fine de la différence entre réitération séquentielle et opportuniste est nécessaire pour mieux comprendre la morphogénèse et phylogénèse des formes de croissance.

Conservation de la Flore

La Nouvelle-Calédonie est connue pour l'extrême menace qui pèse sur sa flore. Dans cette étude, nous avons montré que la flore monocaule est encore plus menacée d'extinction que la flore ramifiée avec un effet particulièrement dramatique des herbivores introduits. Ceci concerne particulièrement le cerf avec le broutage des feuilles et méristèmes et les rats avec la consommation des fruits et méristèmes. Par ailleurs, les prédictions climatiques suggèrent une augmentation de la fréquence et de la durée des épisodes de sécheresse, qui affecteront en premier lieux les espèces sensibles comme les monocaules. Ainsi, certaines espèces monocaules font probablement partie des espèces les plus menacées par l'augmentation des pressions sur la flore néo-calédonienne. Ceci est particulièrement inquiétant étant donné leur contribution importante aux écosystèmes néo-calédoniens en termes de diversité, d'abondance et de fonctions.

En dehors de la Nouvelle-Calédonie : des monocaulies plutôt qu'une monocaulie ?

Notre étude a montré une certaine cohérence fonctionnelle entre les espèces monocaules étudiées et plus généralement avec les grandes caractéristiques suggérées dans la littérature. Cependant, certaines différences majeures montrent que la monocaulie illustrée dans ce travail de thèse est différente de certaines autres formes de monocaulie, notamment lorsque les espèces ont évolué depuis des ancêtres herbacés et poussent dans des milieux secs ou au sommet des montagnes tropicales. Plus particulièrement au niveau macro-anatomique, ces espèces présentent une moelle et un cortex très large mais un bois en proportion plus fin et parenchymateux. Pour les espèces de milieux secs, ces caractéristiques anatomiques sont des adaptations au stockage de l'eau. Ces espèces sont en général de plus petites tailles et ont des vaisseaux relativement étroits, probablement pour limiter les risques d'embolismes. Pour les espèces des milieux tropicaux alpins, les caractéristiques anatomiques permettent aussi le stockage et la remobilisation rapide de l'eau lorsque celle-ci n'est pas disponible dans le sol en raison du gel. Contrairement aux espèces néo-calédoniennes, les feuilles sont le plus souvent étroites, pubescentes et marcescentes, ce qui représenterait des adaptations majeures au froid et à l'insolation. Ainsi notre étude a permis la caractérisation de la monocaulie de sous-bois, qui est probablement la plus commune, mais des espèces fonctionnellement très différentes correspondent aussi à notre définition de la monocaulie. Cela demande de nouvelle étude combinant traits fonctionnels, architecture et phylogénie pour comprendre l'importance relative des différentes pressions environnementales et des prérequis morphologiques conduisant à l'évolution de la monocaulie.

Conclusion et perspectives

Dans ce travail de thèse, nous avons utilisé une approche transversale combinant architecture végétale, taxonomie, phylogénie et écologie fonctionnelle pour caractériser la monocaulie et illustrer son histoire évolutive en Nouvelle-Calédonie. Notre approche originale de la forme de croissance a permis la mise au point d’une définition de la monocaulie adaptée dans le cadre écologique et évolutif qui était le nôtre. Cette définition doit cependant être appliquée dans d’autres contextes pour pouvoir être affinée. Notamment, le processus de réitération et son implication dans la morphogénèse des plantes a besoin d’être mieux appréhendé. Le genre *Acropogon* semble être particulièrement adapté pour investiguer cela.

À partir de cette définition, nous avons montré que la monocaulie représentait 5,5% de la flore vasculaire néo-calédonienne et qu’elle était apparue plus de 31 fois, illustrant ainsi l’un des cas les plus marquants de convergence évolutive en milieu insulaire. Nous avons identifié quatre hypothèses majeures expliquant l’importance de ce phénomène en Nouvelle-Calédonie : la fréquence et l’intensité des cyclones, la persistance de la monocaulie dans des refuges forestiers au cours des dernières glaciations et sa diversification lors des expansions postglaciaires, l’importance des substrats ultramafiques sur le territoire, et l’absence de grands herbivores autochtones. Des données sur les espèces monocaules dans les flores affines permettraient de tester certaines de ces hypothèses. L’hypothèse concernant les épisodes glaciaires pourrait être testée plus facilement en regardant les dates d’apparition et périodes de diversification des clades monocaules à travers plusieurs phylogénies datées.

Notre étude suggère que, en Nouvelle-Calédonie, la monocaulie a principalement évolué à partir d’ancêtres ligneux via des processus hétérochroniques et que son apparition a pu contribuer à la diversification des lignées à travers le partitionnement des niches. Ces hypothèses doivent encore être testées en prenant en compte des données environnementales. Le genre *Bocquillonia* semble particulièrement prometteur pour cela.

La monocaulie en Nouvelle-Calédonie est caractérisée par un ensemble de caractères fonctionnellement reliés les uns aux autres. Ces caractères suggèrent une stratégie de conservation des ressources adaptée mais contrainte aux sous-bois des forêts denses humides où la monocaulie a préférentiellement évoluée, plus particulièrement sur substrat ultramafique. Néanmoins, nous avons encore beaucoup à apprendre sur les caractéristiques fonctionnelles des espèces monocaules et cela demande plus d'études comparatives dans différents groupes phylogénétiques et différents environnements. Nous avons effectivement montré que les espèces monocaules étaient plus que de simples curiosités botaniques et que leur étude pouvait apporter des éléments forts intéressants pour comprendre l'écologie et l'évolution des plantes.

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Résumé: L'évolution convergente des formes de croissance est un phénomène fondamental reliant l'écologie et l'évolution des plantes. Remarquablement illustré dans plusieurs systèmes insulaires, ce phénomène n'a jamais été clairement identifié en Nouvelle-Calédonie, pourtant connue pour la richesse et l'originalité de sa flore. Par une approche combinant architecture des plantes, traits fonctionnels, taxonomie, phylogénie et données environnementales, cette thèse analyse l'histoire évolutive de la monocaulie, une forme de croissance mal connue, en Nouvelle-Calédonie. Les monocaules sont des plantes autoportantes ligneuses dont les fonctions majeures sont assurées par une seule tige apparente. En Nouvelle-Calédonie, elles sont représentées par 182 espèces dicotylédones appartenant à 41 genres et 30 familles et sont souvent menacées d'extinction. L'évolution répétée de la monocaulie en Nouvelle-Calédonie, issue d'au moins 31 événements d'apparition, est l'un des cas les plus remarquables de convergence en milieu insulaire. Dans le genre *Atractocarpus*, la monocaulie est apparue récemment deux à trois fois via diverses réductions des branches en inflorescences, montrant l'importance des processus hétérochroniques dans l'évolution des formes de croissance. La monocaulie est fortement corrélée à plusieurs traits démontrant des contraintes majeures dans la coordination fonctionnelle. L'évolution de la monocaulie est fortement associée aux forêts denses humides et au substrat ultramafique, et pourrait avoir contribué à la diversification des lignées par des phénomènes de partitionnement de niche. La remarquable convergence de la monocaulie en Nouvelle-Calédonie peut s'expliquer par quatre hypothèses majeures liées (i) à la structure particulière des forêts denses humides (en lien avec les cyclones) favorisant l'exploration unidirectionnelle de l'espace, (ii) aux contraintes édaphiques liées aux substrats ultramafiques induisant une paupérisation architecturale, (iii) à l'absence historique de grands brouteurs, auxquels les monocaules sont particulièrement sensibles, et (iv) à la persistance des forêts denses humides lors des épisodes glaciaires (servant de refuges pour ces espèces sensibles) et leur expansion post-glaciaire (fournissant de nombreuses opportunités écologiques).

Mots-clés : Architecture des plantes, Convergence évolutive, Forme de croissance, Îles, Phylogénie, Traits fonctionnels

Abstract: Convergent evolution in growth habit is a fundamental phenomenon linking plant ecology and evolution. Remarkably illustrated in island biotas, this phenomenon has not clearly been identified in the distinctive and megadiverse New Caledonian biodiversity hotspot. Through an approach combining plant architecture, functional traits, taxonomy, phylogeny and environmental data, this thesis analyses the evolutionary history of the poorly known monocaulous growth habit in New Caledonia. Monocauls are self-supporting woody plants whose cardinal functions rely on a single visible stem. In New Caledonia, they are represented by 182 dicotyledonous species belonging to 41 genera in 30 families and are often endangered. The repeated evolution of monocauly in New Caledonia, resulting from at least 31 independent events, is one of the most remarkable cases of convergence in insular environments. In the genus *Atractocarpus* (Rubiaceae), monocauly evolved recently two or three times through branch reductions into inflorescences, emphasizing the importance of heterochronic processes in the evolution of growth habit. Monocauly is strongly correlated with several traits illustrating major constraints in functional coordination. The evolution of monocauly is strongly associated with rainforests and ultramafic substrate, and could have contributed to the diversification of lineages through niche partitioning. The remarkable convergence toward monocauly in New Caledonia can be explained by four major hypotheses: (i) structural features of rainforests (related to cyclone frequency and intensity) favoring unidirectional exploration of space, (ii) the edaphic constraints associated with ultramafic substrates inducing architectural pauperization, (iii) the historical absence of large native browsers to which monocauls are particularly sensitive, and (iv) the persistence of rainforest during glacial episodes – and expansion afterward – that served as refugia and further provided ecological opportunities.

Keywords: Convergent evolution, Functional traits, Growth habit, Islands, Phylogeny, Plant architecture