# THE EVOLUTIONARY LEGACY OF AL GENTRY: UNITING PATTERNS AND PROCESSES OF NEOTROPICAL RAINFOREST EVOLUTION[1,2]

*Serafin J. R. Streiff,*[3] *Roy H. J. Erkens,*[4]
*and Thomas L. P. Couvreur*[5]

Abstract

Alwyn Gentry had unique insights into the diversity of Neotropical rainforests. He observed plant diversity with incredible detail and used the data he and colleagues collected to answer questions on the distribution, ecology, and evolutionary origins of tropical rainforest diversity. Leaning on patterns of species distributions accumulated from intense fieldwork, Gentry discussed numerous ideas and proposed important hypotheses on the evolution of Neotropical rainforests. However, he never advanced these evolutionary ideas in a unified and consistent framework across all scales he treated. For instance, comparing intercontinental differences in rainforest taxa, he suggested Neotropical forests to be "uniquely and phenomenally enriched" compared to other rainforests. This he attributed, among other factors, to increased speciation especially in Andean-centered taxa, linked both directly and indirectly to the uplift of the northern Andes. Even at the smallest scales, he put forward specific hypotheses on the processes of speciation in the Neotropics, ranging from specialization to edaphic conditions in Amazonia to founder-effect–mediated speciation in the Andes. The ensemble of hypotheses and ideas proposed by Gentry on tropical and Neotropical plant evolution, his evolutionary legacy, remains relevant even today. Despite this, many of his contributions may not have received the attention they rightly deserve. Overall, those hypotheses put forward by Gentry that have been tested are well supported, in particular the ones concerning regional and intercontinental scale processes. However, many of his smaller-scale hypotheses have not been tested to our knowledge, or remain inconclusive, highlighting significant knowledge gaps in our understanding of tropical rainforest diversity and evolution. Furthermore, his work and thinking, 30 years on, emphasize significant biases in our current understanding, that being concentrated on large woody plants and specific taxa. Contrary to this, Gentry's perspective is refreshingly encompassing, not being limited to specific taxa or growth forms. To consolidate and underline his important contributions to tropical plant evolution, we summarize and assemble Al Gentry's evolutionary ideas and hypotheses here. Leveraging his comprehensive view of tropical rainforest diversity, his ideas provide succinct starting points for future research across disciplines on the ecology and evolution of tropical rainforests.

*Key words:* Amazonia, Andes, biodiversity, biogeography, macroecology, macroevolution, speciation, tropical rainforest.

> "[T]hose of us interested in evolutionary processes have an added incentive for preserving our planet's dwindling remnants of tropical forest: We need them if we hope ever to truly understand the processes of speciation and evolution that have given rise to the diversity of life on earth" (Gentry, 1989: 127).

Alwyn Gentry (1945–1993) is remembered as a specialist in a number of disciplines. For many he was an ecologist, explorer, and plant collector, for some a taxonomist, and for others a conservationist, and for many a teacher and a mentor. Perhaps you see him even in a different way. Here, we summarize Gentry's ideas and hypotheses about the evolution of Neotropical flora, underlining yet another quality in his list of contributions to Neotropical biodiversity research: that of an influential evolutionary biologist.

Gentry, in collaboration with many researchers and students, gathered floristic datasets at a scale no one had done before him (Phillips & Miller, 2002). Indeed, he undertook ca. 220 0.1-ha transects, referred to as "Gentry transects," across the Neotropics in tandem with the collection of tens of thousands of vouchered specimens (Miller et al., 1996), which produced a quick measure of local plant diversity, taxonomic composi-

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[1] This article is part of a special collection commemorating the life and work of Alwyn Gentry (1945–1993), a highly respected botanist whose contributions left a lasting impact on the field. August 3, 2023, marked 30 years since his passing. Thomas L.P. Couvreur, Carmen Ulloa Ulloa, and J. Sebastián Tello served as guest editors.

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[3] DIADE, Université Montpellier, CIRAD, IRD, Montpellier, France. sjrstreiff@gmail.com; https://orcid.org/0000-0002-8462-7956

[4] System Earth Science, Faculty of Science and Engineering, Maastricht University, Venlo, The Netherlands. https://orcid.org/0000-0002-1093-0370

[5] DIADE, Université Montpellier, CIRAD, IRD, Montpellier, France. https://orcid.org/0000-0002-8509-6587

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tion, and forest structure (Phillips & Miller, 2002). He gained a unique view of species diversity at the local scale while always retaining "a continental view of the flora" (Rueda in Miller et al., 1996). Gentry's ecological work and legacy are explored by Phillips (2025) in a companion paper to this one. The data collected by Gentry and colleagues, alongside his experience, paved the way for him to address long-standing questions in tropical ecology but also provide a unique insight into what drives the evolution of Neotropical floras.

Gentry didn't work in a vacuum: evolutionary biology, and particularly research on the modes of speciation, was resurgent in the 1980s, based on the original "modern synthesis" of evolution of the 1930s to 1950s that had integrated ideas of speciation, heredity, natural selection, and biogeography (Coyne & Orr, 2004). Renewed discussions surrounded the geography of speciation (e.g., Mayr, 1963; Endler, 1982a) and, albeit slowly, the role of ecology in speciation (e.g., Templeton, 1981; Morell, 1999; Coyne & Orr, 2004). An improved understanding of geological processes at regional and global scales led to clearer ideas about plant biogeography, directly linked to plate tectonics (Raven & Axelrod, 1974). This was coupled with advances in ecological (summarized in e.g., Ricklefs & Schluter, 1993) as well as biogeographical theory (e.g., MacArthur & Wilson, 1967). Gentry was also actively involved in these discussions and proposed specific hypotheses on the evolution of the striking diversity of Neotropical rainforests.

The Neotropical region encompasses a wide array of different biomes, spanning lowland rainforests, seasonally dry forests and mid-elevation montane forests, savannas, deserts, and high-elevation grasslands (reviewed in e.g., Hughes et al., 2012). To facilitate comparisons, Gentry, in the first of his seminal works on evolutionary processes in Neotropical plants, tabulated distribution data of plant taxa based on, at the time, recent revisions in Neotropical taxonomic literature (Gentry, 1982a). He noted larger-scale patterns emerging from the dataset, of growth form (i.e., canopy trees or lianas vs. epiphytes, shrubs, or palmettos) as well as regional endemism, suggesting that most Neotropical taxa could be classified into two main distributional patterns: the "Amazonian-centered" group and the somewhat complementary "Andean-centered" group (although these groups are not completely mutually exclusive). Amazonian-centered species are mainly confined to Amazonia and surrounding lowland rainforests and are dominated by canopy trees and lianas. Based on Gentry's data, these made up 38% of Neotropical plant species (Gentry, 1982a). In addition, he noted that Amazonian-centered taxa are not well represented in Central American rainforests in terms of species numbers, despite some being ecologically dominant in Central America. Andean-centered species, in contrast, are distributed in and around the Andes and are characterized by epiphytic, palmetto, and shrub habits and made up 33% of the taxa in his list. In addition, several Andean-centered groups also have important centers of diversity in Central America and the Chocó region (western Colombia and Ecuador). Together with the Amazonian group, these patterns accounted for the distribution of about 71% of recently monographed taxa according to Gentry's tabulation (Gentry, 1982a).

Other phytogeographical patterns are centered on dry areas of the Neotropics. Gentry highlighted the Brazilian Cerrado and Caatinga as well as the Colombian and Venezuelan Llanos, the Caribbean islands as well as the Guiana Highlands. All these areas harbor endemic taxa, and as Gentry put it they are "significant and interesting components of the Neotropical flora" (Gentry, 1982a: 583). However, in Gentry's tabulations, compared to the rainforest groups, these areas held only a relatively small number of species (together making up the rest of Gentry's tabulated taxa; Gentry, 1982a).

Due to the recurring use of these Amazonian and Andean distribution patterns since their publication, they have now been termed the "Gentry-patterns" (Antonelli & Sanmartín, 2011). These phytogeographical patterns served as the basis for Gentry to explore evolutionary hypotheses explaining Neotropical diversification (Table 1). However, Gentry's ideas on diversification and speciation, in particular in the Neotropics, have flown mostly under the radar. We judge these ideas to be important contributions to the discussion on the evolution and assembly of Neotropical and global rainforest evolution in general. We present a comprehensive overview and synthesis of Gentry's ideas grouped by levels, adding (modern) context where applicable. Across spatial and temporal scales, this creates a framework for testing these ideas in a more formal, hypothesis-driven way.

Since the time of Gentry's writings, many concepts about tropical plant diversification have been refined. This is embodied by research focusing on and leveraging the fields of phylogenetics and molecular dating to provide estimates of the timing of diversification (speciation minus extinction; Morlon, 2014) and macroevolutionary as well as biogeographical models to test specific hypotheses, unavailable to Gentry at the time. We do not attempt to review Neotropical biodiversity evolution in general, and the reader is directed to more recent reviews for this (Antonelli et al., 2018a; Dick & Pennington, 2019; Guayasamin et al., 2024). Finally, we highlight some gaps and opportunities in both data and specific ideas of tropical plant evolution that can serve to investigate in more detail the origins and diversification of Neotropical diversity as proposed by Gentry.

Table 1. Key ideas of tropical speciation and evolution discussed by Gentry, grouped by context discussed in text.

| | Idea | 30 years on | Reference |
|---|---|---|---|
| Ia | Neotropical diversity elevated over Afrotropics | confirmed | e.g., Parmentier et al., 2007; Silva de Miranda et al., 2022 |
| Ib | Elevated Neotropical diversity explained by higher speciation in Neotropics; extinction remains comparable between continents | some evidence | Bardon et al., 2012; Baker & Couvreur, 2013; Armstrong et al., 2014 |
| Ic | Generally drier environments in Afrotropics leading to species with wider ranges, less endemism | refuted | e.g., Silva de Miranda et al., 2022 |
| Id | Fewer coevolutionary opportunities in Afrotropics than Neotropics | unclear, untested | |
| IIa | Andes: dispersal barrier separating Amazonia and Central America/Chocó | confirmed, not universal | Erkens et al., 2007; Pirie et al., 2018; Serrano et al., 2021 |
| IIb | Panama land bridge: dispersal barrier before, dispersal pathway after closing of Central American Seaway | unclear, dependent on dispersal capacity | e.g., Cody et al., 2010; Bacon et al., 2015; Serrano et al., 2021; Loza et al., 2025 |
| IIc | Chocó: diversity largely derived from ancestrally Andean and Central American floras | some evidence | Pérez-Escobar et al., 2019; Michelangeli et al., 2022 |
| IId | Chocó: in situ diversification leading to species swarms | untested | |
| IIe | Mata Atlântica: center of origin of lineages dispersing into surrounding regions | unclear | see Antonelli et al., 2018b |
| IIf | Guianas: ancient surviving lineages with low diversification | some evidence | Givnish et al., 2011; Roncal et al., 2013; Liu & Smith, 2021 |
| IIg | Dry forests: recent diversification linked to increasing aridification | conflicting evidence | Särkinen et al., 2011; Fernandes et al., 2022 |
| IIIa | Amazonia: edaphic specialization leading to adaptation and speciation | some evidence | Fine et al., 2013, 2014 |
| IIIb | Andes: founder-effect–mediated speciation | untested | |
| IIIc | Andes: plant-pollinator coevolution leading to specialization and speciation | partially confirmed | e.g., Lagomarsino et al., 2016, but see Tripp & McDade, 2013 |
| IIId | Amazonia/Andes: pre-adaptation to specific Andean habit leading to explosive speciation | some evidence | Givnish et al., 2014; Linan et al., 2021 |

I: intercontinental patterns; II: Neotropical biogeographical patterns; III: local speciation processes.

## Excess Diversity Versus Failure to Speciate: Intercontinental Hypotheses

Most of Gentry's career was focused on the Neotropics, but he did deploy the 0.1-ha transect plots across Africa, Madagascar, and Southeast Asia as well (Phillips & Miller, 2002), leading to a truly unique transcontinental insight in terms of plant-community composition. These extra-Neotropical experiences must have had a lasting impact on him, as in many of his papers he refers to the diversity patterns he observes in the paleotropics as a point of comparison when discussing more regional Neotropical patterns (e.g., Gentry, 1986).

In the 1980s, the Neotropical flora presented an enigma that largely stands to this day: Neotropical rainforests are more species rich than other tropical rainforests (Raven, 1976; Raven et al., 2020). This "excess" diversity, as Gentry referred to it, is based on his estimates mainly found in the herbs, epiphytes, or shrubs distributed in and around the Andean foothills, making up around half the Neotropical flora (Table 1: Ia; Gentry, 1982a: 589; Gentry & Dodson, 1987b). Africa, in contrast, was suggested to be "depauperate" in terms of plant diversity when compared to the Neotropics, being famously labeled the "odd man out" (Moore, 1973; Richards, 1973). Explanations for these intercontinental differences rely on a number of processes (see Parmentier et al., 2007; Couvreur, 2015; Pokorny et al., 2015; Terborgh et al., 2016), but the most common one advanced at the time (Richards, 1973; Raven & Axelrod, 1974) suggested increased extinction rates of tropical rainforest plants linked to increased aridification during the Neogene in Africa (see Couvreur, 2015, for a review; see also Morley, 2000; Terborgh et al., 2016; Couvreur et al., 2021).

Interestingly, Gentry's views diverged from the status quo of the time. Having visited tropical Africa several times (Phillips & Miller, 2002), Gentry was "pleasantly surprised" (Gentry, 1993: 502) by the overall similarity at the community level of the floras of African and American tropics, being "more floristically similar than often supposed" (Gentry, 1993: 510). Based on a comparative analysis between the Neotropics and Africa, using his and other plot data, he favored the view that Africa was not as depauperate as suggested, concluding that at smaller community levels diversity patterns were quite similar (Gentry, 1993). This impression was later confirmed by extensive data for trees showing similar local taxonomic organization, where locally diverse families tend to be species rich on both continents (Silva de Miranda et al., 2022). The differences in overall (continental) species richness remains marked (Parmentier et al., 2007; Sullivan et al., 2017; Silva de Miranda et al., 2022). Notable is that, even to this day, estimating the composition of tropical floras beyond trees is uncommon, with other growth forms rarely surveyed in tropical forest plots. For example, many accounts for estimating the epiphyte flora are still largely based on Gentry's work (Cascante-Marín & Nivia-Ruíz, 2013), despite epiphytes being known to make up an important part of the floras of such highly diverse regions (Taylor et al., 2022) and likely contributing strongly to the intercontinental difference in species diversity.

With this personal experience in mind, Gentry proposed what he referred to as an "antithesis," writing "rather than the flora of tropical Africa [. . .] being impoverished with respect to the Neotropics, the latter may be considered as uniquely and phenomenally enriched" (Gentry, 1982a: 588). He extended this hypothesis in his 1993 comparative analysis, again suggesting a difference in speciation rather than extinction as the main underlining reason, referring to a "failure to speciate" of the African flora (Table 1: Ib; Gentry, 1993: 543). In evolutionary terms, this hypothesis suggests that differences in diversity between both continents were the result of *higher speciation* rates in South America, rather than *higher extinction* rates in Africa as was generally suggested. Essentially, Gentry saw the main difference between the two continents in strongly increased speciation rates centered around the low- to mid-elevation rainforests of the Andean foothills, the areas generally the most species diverse (Gentry, 1982a; Pérez-Escobar et al., 2022).

At macroevolutionary scales, comparative studies of diversification rates between African and Neotropical plant clades have been limited. Nevertheless, diversification analyses based on dated molecular phylogenetic trees of intercontinental groups tend to support Gentry's prediction of higher speciation in the Neotropics rather than increased extinction in Africa (Hughes et al., 2012). Indeed, a genus-level diversification analysis of palms, one of the most iconic "odd man out" tropical plant groups (Moore, 1973; Gentry, 1993), favored an increase in diversification rates in clades outside of Africa rather than a decrease in diversification rates for the African lineages (Baker & Couvreur, 2013). A dated phylogenetic tree of tropical Chrysobalanaceae also favored an increase in speciation rates as the main factor explaining the present-day imbalance in species diversity between the Neotropics and the Paleotropics (Bardon et al., 2012). Finally, in the pantropical Sapotaceae genus *Manilkara* Adans., elevated speciation rates for the Neotropical clades were also detected (Armstrong et al., 2014). Although these results are overall consistent with Gentry's hypothesis, they must be taken with caution, as they are highly dependent on our ability to estimate extinction rates from reconstructed phylogenetic trees of modern clades (Rabosky, 2010; Louca & Pennell, 2020; but see also Helmstetter et al., 2022; Morlon et al., 2022; Kopperud et al., 2023). Interestingly, when diversification rates were estimated within 66 Neotropical plant clades representing 6225 species (Meseguer et al., 2022), a scenario of gradual increase in species richness (i.e., constant speciation and extinction rates) was largely favored (60%–71% of trees). The exponential model, with faster increases in species richness toward the present, was supported for ca. 30% of trees. Thus, bursts or increased rates of diversification might explain species diversity in some clades (e.g., *Cinchona* L. or *Fuchsia* L., Meseguer et al., 2022; *Inga* Mill., Richardson et al., 2001; *Guatteria* Ruiz & Pav., Erkens et al., 2007) but is not necessarily the most prevalent model across all Neotropical plant lineages.

In addition to this "higher speciation" hypothesis, Gentry proposed two non-exclusive hypotheses leading to these discrepancies (Gentry, 1982a, 1993). First, he suggested that overall drier ecological conditions for the African vegetation when compared to the Neotropics might have led to lower speciation rates in Africa. The premise was that species of drier vegetation types in Africa (tropical dry forests, savannas) are more widespread (thus less endemism and diversity) than species of wetter rainforests (Table 1: Ic; Gentry, 1993). This, however, might not hold true: despite covering a much larger area, African dry forests harbor only around half the number of species compared to Neotropical dry forests (Silva de Miranda et al., 2022). Thus, vegetation type per se cannot really explain discrepancies in continental species diversity. Second, Gentry explicitly contrasted the available opportunities for biotic interactions in the Neotropics and Africa (Table 1: Id; Gentry, 1982a, 1993), for example in terms of pollinators (hummingbirds vs. perching birds; small bats vs. larger bats) or dispersal (i.e., elephant vs. agouti). He also linked these differences in co-evolution to the uplift of the Andes, an aspect explored below. Unfortunately, much less is known about the comparative power to explain speciation differences when it comes to pollination differences, as most studies have looked at the co-evolutionary impact from single regional perspectives (see below for examples), rather than in comparative frameworks.

## From Barriers to Local Adaptation: Diversification and Speciation in the Neotropics

Despite his pantropical perspectives, Gentry's work primarily focused on the Neotropical rainforests, where he established most of his transects and collected the majority of his specimens (Phillips & Miller, 2002; Phillips, 2025). Based on plot data, as well as his strong grasp of Neotropical taxonomy in general (Miller et al., 1996), Gentry observed similarities and differences in the representation of taxa between different localities of Neotropical rainforests. This led to the insights he developed over the years, exploring the roles of both climatic and geological barriers as causes for disjunctions and endemism (Gentry, 1979, 1982b; Gentry & Dodson, 1987b), which formed an integral part of Gentry's discussions on his phytogeographical patterns (Gentry, 1982a). However, they also laid the basis for the biogeographical and evolutionary considerations he presented for many of his phytogeographical groups.

Gentry's phytogeographical patterns leaned on concrete examples of different growth forms and taxa being confined to different Neotropical subregions (Gentry, 1982a), the so-called Andean- and Amazonian-centered groups. He suggested that taxa within a group potentially shared similar biogeographic and evolutionary histories at regional and local scales. He connected these biogeographic and evolutionary histories to the geological processes of Central and South America, focusing specifically on the role of the uplift of the Andes and closing of the Isthmus of Panama in facilitating and limiting migration at different times.

To explain the evolution of the diversity within both these groups, Gentry explored processes of speciation likely to be dominating in Neotropical rainforests. Gentry's most focused attempt came in 1989 in his aptly titled book chapter "Speciation in Tropical Forests" (Gentry, 1989) in which he revisited and strongly revised positions he held earlier (Gentry, 1981, 1982b; but in particular Gentry, 1982a). His earlier views centered on tropical speciation driven by Pleistocene climatic refugia: in the so-called refuge hypothesis, a mosaic of forest-savanna patches, changing continuously through varying precipitation regimes from Pleistocene climatic changes, led to (repeated) isolation and re-coalescing of populations and subsequent allopatric speciation (Mayr, 1963; Haffer, 1969; Prance, 1973). While it was a popular theory in the 1980s (Mayr & O'Hara, 1986; Rocha & Kaefer, 2019), the underlying assumptions of it were increasingly questioned (Benson, 1982; Endler, 1982a, 1982b; Colinvaux, 1987) and were later found to derive in part from sampling artifacts (Hooghiemstra & van der Hammen, 1998; Bush & Oliveira, 2006; Rocha & Kaefer, 2019). In his 1989 publication, Gentry rejected the refuge theory and presented and refined his theories, ideas, and opinions on tropical evolution. In particular, he provided a rebuttal to some contemporary scientists who suggested that tropical rainforests were of little evolutionary interest, as the species there are "mostly trees that all look about alike" (Stebbins cited in Gentry, 1989: 117).

### ANDEAN UPLIFT AS A BARRIER TO LOWLAND TROPICAL SPECIES

The Andes, by far the largest tropical mountain chain in the world, occupied a prominent place in Gentry's explanation of elevated Neotropical diversity. He is probably one of the first to convincingly suggest the fundamental role of the Andean orogeny in generating Neotropical diversity (Antonelli & Sanmartín, 2011). The Andean uplift influenced the Neotropical floras in numerous perspectives. Uplift and erosion led to topological differentiation and the creation of new environments in which species could establish (e.g., Hughes & Eastwood, 2006; reviewed in Rahbek et al., 2019). Acting as a barrier to air masses, the Andes had an important impact on large-scale environmental conditions across the entire region (Sepulchre et al., 2010), in particular creating a strong gradient in precipitation from west (high) to east (lower) across the Amazon basin (Killeen et al., 2007; Hoorn et al., 2023). Moreover, the sinking of the continental crust due to loading by the Andes, together with a rise in sea level, led to the marine incursions of the Pebas system in central Amazonia during the Miocene (Hoorn et al., 2010). Ultimately, this led to the Amazon River as it is today, flowing from the Andes to the Atlantic Ocean (Albert et al., 2021; Hoorn et al., 2023). Toward the Late Miocene and Early Pliocene, the uplift in the northern Andes completely blocked the potential dispersal paths of many lowland species of the Amazonian-centered groups between Amazonia and Central America. It was with this barrier that Gentry explained the apparent difference in taxa between ecologically similar Amazonian and Central American taxa (Table 1: IIa; Gentry, 1982a). Thus, the history of Andean uplift led to important changes in habitats, not only in the mountain range itself but also throughout Amazonia from the Miocene until present (Hoorn et al., 2010, 2023).

Numerous studies at macroevolutionary levels have now shown correlations between the barrier to plant dispersal presented by the uplifted Andes and time of disjunction, as well as diversification within clades. For instance, studies in the Neotropical Annonaceae genera *Guatteria* (Erkens et al., 2007), *Cremastosperma* R. E. Fr., and *Mosannona* Chatrou (Pirie et al., 2018) found parallel diversification on either side of the Andes, the timing of which coincides with the final uplift of the northern Andes. Other examples are found in Rubiaceae (Antonelli et al., 2009). This is, however, not a universal pattern. Some lowland tropical clades show evidence of continued dispersal across the Andes during the presence of a physical barrier (e.g., in the Sapotaceae subfamily Chrysophylloideae, Serrano et al., 2021). Furthermore, within lowland species distributed on either side of the northern Andes, population genetic structure seems also to be shaped by cross-Andean dispersal (Bemmels et al., 2024). This suggests that not all groups of plants are equally affected by the Andes as a barrier, with dispersal documented either across the Andes or around the north of the Andes through drier savannas and dry forests (Honorio Coronado et al., 2014; Bemmels et al., 2018).

### CLOSING OF THE PANAMA ISTHMUS: EXCHANGE OF ISOLATED FLORAS?

Besides the barrier formed by the uplifting Andes, the other major geological event affecting Neotropical biogeography cited by Gentry was the closing of the Central American Seaway. The emergence of the Panama land bridge (PLB) connecting Central and South America ended the "splendid isolation" of South America (Table 1: IIb; Simpson, 1980; Gentry, 1982a; Loza et al., in review). In the classical sense, as documented by Gentry's contemporaries, the general consensus was on a relatively strong isolation of the South American biota from Central America since the Mid Tertiary until ca. three million years ago (Ma) (e.g., Simpson, 1980; Stehli & Webb, 1985; Burnham & Graham, 1999). However, to this day, the timing of the exact formation of the PLB remains uncertain and hotly debated and is out of the scope of this review (Montes et al., 2015; Erkens & Hoorn, 2016; O'Dea et al., 2016; Jaramillo et al., 2017; Molnar, 2017). It is clear, however, that the isolation of plant taxa before the formation of the PLB was not as strong as believed in Gentry's time.

The barrier posed by the Central American Seaway before the emergence of the PLB provided a scenario to explain the differences in forest composition that Gentry found between Central American and South American rainforests (Gentry, 1979, 1982b). His elaborate review of paleobotanical literature on Central American rainforests presented him with explanations of the assembly of these forests: while elements of the flora of tropical South America could be found in Central America, these were rarer and not as ecologically dominant as they are today (Gentry, 1982a: 561). In contrast, fossil floras of northern South America of a similar age were composed of elements comparable to present lowland rainforests of the region. In concordance with the phytogeographical patterns he put forward in the same article, Gentry found that few species of Amazonian taxa were present in Central American forests (Gentry, 1982a). In Gentry's words, "it is tempting to think of such patterns as reflecting a two pulse migration," wherein older dispersals at the end of the Cretaceous would have differentiated significantly from originally South American ancestors (Gentry, 1982a: 580). Conversely, recent dispersal after the emergence of the PLB presented an opportunity for dispersal but not enough time for significant differentiation. Consequently, while South American taxa were present at least since the Paleocene, the younger dispersal pulse likely occurred only after the formation of the PLB, with many species from this migration considered ecologically dominant in Central America today.

Indeed, evidence for plants suggests that dispersal across the Central American Seaway separating the continents has taken place at intermittent intervals dating from the start of the Miocene (Cody et al., 2010; Bacon et al., 2015; Erkens, 2015; Hoorn & Flantua, 2015; Montes et al., 2015; Pirie et al., 2018). Moreover, older dispersal events have also been documented for numerous groups. For example, Cano et al. (2022) found evidence that Central American palms originated from South American ancestors during the Eocene, but also later dispersed multiple times during the Late Miocene. These younger migrations were followed by radiations leading to much of the currently observed understory palm diversity of Central America. Similarly, timed events were documented, e.g., for *Guatteria*, where dispersal from Central to South America was followed by a radiation in South America, followed by multiple dispersals back into Central America in the Pleistocene (Erkens et al., 2007).

The earlier pulse suggested by Gentry might also just represent the remnants of older Eocene boreotropical rainforests, which covered large parts of the Northern Hemisphere before the global cooling of the Eocene-Oligocene transition (~33.9 Ma; e.g., Wolfe, 1975; Lavin & Luckow, 1993; Morley, 2000; Davis et al., 2004; Givnish & Renner, 2004; Muellner et al., 2006; Couvreur et al., 2011; Baker & Couvreur, 2013). However, such a scenario does not change the premise of the assembly of these forests presented by Gentry (Gentry, 1982a), based on the barrier of the Central American Seaway up to its narrowing and subsequent closure during the Miocene.

Alternatively, long-distance dispersal is increasingly found as one of the major migration pathways for many plant lineages and has been a major part of the assembly of the Neotropical flora (Givnish & Renner, 2004; Dick & Pennington, 2019), thus reducing the importance of the exact timing of full closure of the land bridge for plants (Cody et al., 2010; Erkens, 2015; Antonelli et al., 2018b). Other tests of the closure can be undertaken using present-day diversity patterns, in the vein of much of Gentry's work (Gentry, 1982a, 1993), and the reader is referred to Loza et al. (in review) for a recent example.

While the two major geological events presented above were mainly discussed within the context of his Amazonian- and Andean-centered groups, Gentry also discussed evolutionary trends in other Neotropical regions. True to his style, whenever describing distribution patterns, he ended by trying to provide some kind of evolutionary explanation to these.

### CHOCÓ: RECENT AND DYNAMIC SPECIATION

Gentry undertook significant floristic research on the flora of the Chocó, which extends from southern Panama along the western coasts of Colombia and Ecuador and is dominated by some of the wettest forests in the world (i.e., Gentry & Dodson, 1987a; Dodson & Gentry, 1991). The region is a global epicenter of plant diversity and a biodiversity hotspot, hosting an estimated 3% of all plant species, with high levels of species endemism (Gentry, 1982b; Mittermeier et al., 2011) and threat (Couvreur et al., 2024). In Gentry's sampling, Chocóan forests showed some of the highest plant diversity, comparable to and sometimes surpassing diversity in plots from western Amazonia (Gentry, 1986; Phillips & Miller, 2002). Compared to Gentry's Andean and Amazonian phytogeographical regions (Gentry, 1986), however, the Chocó has very few endemic genera (i.e., *Ecuadendron* D. A. Neill [Fabaceae]), and no endemic plant family is known to date (Pérez-Escobar et al., 2019). Although geologically complex, the Chocó is comparatively young, taking its present landscape form toward the start of the Pleistocene (Gentry, 1982b; Pérez-Escobar et al., 2019).

Gentry found that the Chocó displayed strong floristic similarities to the nearby northern Andes and Central America, rather than to the Amazon (Gentry, 1982b). These similarities were explained through the barrier presented by the northern Andes, essentially cutting off the lowland Central American and Chocóan flora from the Amazonian floristic stock (e.g., as seen for ferns and lycophytes, Morris & Moran, 2025). Gentry illustrated this with the Rio Palenque flora of western Ecuador (Dodson & Gentry, 1978) that shared less than 4% of its species with the Amazon in contrast to the 70% shared with Central America, which he characterized as "hardly surprising" given the presence of the Andes (Gentry, 1982b: 123). In agreement with Haffer (1967), Gentry suggested that the Chocó flora was derived from *recent* immigration via the northern Andes during favorable climates of the Pleistocene (Table 1: IIc). Based on his data, he rejected the hypotheses that the Chocó flora originated either by vicariance of a once present pre-Pleistocene continuous rainforest that was separated by the Andean orogeny or frequent long-distance dispersal from the Amazon (Haffer, 1967; Gentry, 1982b). In addition, in situ evolution was initially suggested by Gentry to fit into the refugia hypothesis (see above) explaining Neotropical rainforest diversification (Haffer, 1967, 1969; Prance, 1982). Indeed, based on the study of plant distributions, Gentry identified three main regions of endemism in the north, central, and south of the Chocó, which he interpreted as three distinct refugia (Gentry, 1982b). However, he revised his position several years later, underlining that these endemism patterns were the result of sampling bias (Gentry, 1989; White et al., 2024).

The biogeographic history and diversification of the Chocó flora have been little studied to date. A recent comparative review of evidence from a few plant phylogenetic trees with appropriate sampling in the region supported a Northern Andean and Central American origin of some clades (Pérez-Escobar et al., 2019). In temporal terms, most species seem to have originated before the Pleistocene (Winterton et al., 2014; Pérez-Escobar et al., 2019; Escobar et al., 2022; Michelangeli et al., 2022), except for orchids (Pérez-Escobar et al., 2019; Escobar et al., 2022). This also suggests only a minor role for Pleistocene climate fluctuations in species' origins. Rather, a role for refugia in the Chocó region was suggested at the *intraspecific* level, with populations within species taking refuge in some of the areas suggested by Gentry (1982) and Prance (1982) during adverse climatic times (Escobar et al., 2021).

Finally, Gentry was also intrigued by what he referred to as "species swarms" in the Chocó, referring to highly diverse genera (i.e., *Piper* L., *Miconia* Ruiz & Pav.) accounting for a high proportion of the observed diversity at the local level (Table 1: IId; Gentry, 1982b). He noted that species within these swarms tended to occur sympatrically, and he thus excluded allopatric speciation as the main reason for their existence. He suggested implicitly that these species swarms originated in situ, i.e., are monophyletic. However, several studies have revealed that some of these genera dispersed to the Chocó several times independently, for example, *Miconia* (Michelangeli et al., 2022). Nevertheless, to date, no studies have explicitly addressed the origin or evolutionary dynamics of these Chocó species swarms, even though the term is now used in the literature (e.g., Sedio et al., 2012).

As an interesting conclusion on a broader scale, Gentry suggested that the Chocó flora represented an "unequivocal" example of tropical rainforest diversity being the result of "dynamic and continuing evolutionary processes" rather than long-term accumulation of species through time (Gentry, 1982b: 134; i.e., bearing resemblance to an evolutionary cradle as opposed to a museum, Stebbins, 1974; Winterton et al., 2014; Eiserhardt et al., 2017).

### MATA ATLÂNTICA AND THE GUIANA SHIELD: SUBSETS OF AMAZONIAN TAXA?

Gentry briefly discussed the evolutionary origins of plant diversity of the Guiana Shield and the Mata Atlântica rainforests. Both these regions were not considered as important centers of endemism in his dataset (Gentry, 1982a), although the Mata Atlântica is now recognized as such today (Lima et al., 2020).

The apparent "concentration of often primitive species" in the Brazilian coastal Mata Atlântica forests (as exemplified by taxa of Dilleniaceae, Bambusae, and Bignoniaceae; Gentry, 1982a: 584) led Gentry, based on previous ideas, to postulate that this region may be important as a source for other phytogeographic areas (Table 1: IIe). This suggests there is a pattern of species origination in this region, followed by dispersal to other regions.

Contrary to Gentry's hypothesis, a meta-analysis of biogeographical patterns in the Neotropics suggested that the Mata Atlântica forests acted rather as a sink of diversity with frequent dispersal from the Amazon region (Antonelli et al., 2018b). However, this meta-analysis relied on an absolute number of reconstructed dispersal events to and from both biogeographical regions. This definition of a "source" differs from that used by Gentry. In the context of his idea, the Mata Atlântica might have presented a *center of origin* for Amazonian taxa, i.e., dispersal from Mata Atlântica to Amazonia predating a radiation, irrespective of potential dispersals back from Amazonia to the Mata Atlântica. This definition of a "macroevolutionary source" does not reference to the *absolute number* of dispersals per se, but emphasizes the *timing and phylogenetic context* of dispersal events (e.g., see Goldberg et al., 2005, for discussion of these terms).

Compared to the Mata Atlântica and Amazonia, the Guiana Shield has a lower tree diversity (ter Steege et al., 2000). The presence of closely related taxa disjunct between the Guiana Shield and outside the Neotropics (e.g., Sarraceniaceae, Tetrameristaceae), combined with comparatively few endemic taxa on the Guiana Shield, led Gentry to suggest that diversification was not high in the Guianan area. Instead, these taxa represented ancient surviving lineages (Table 1: IIf). In practice, Gentry considered at least the lowland Guianan flora as a subset of the Amazonian lowland flora (Gentry, 1982a). Recent single-lineage biogeographic studies have underlined the importance of the Guiana Shield as a center of origin for several groups including some palms such as *Astrocaryum* G. Mey. (Roncal et al., 2013), the diverse Bromeliaceae family (Givnish et al., 2011; Zizka et al., 2019), as well as the carnivorous *Heliamphora* Benth. genus of Sarraceniaceae (Liu & Smith, 2021).

### ARID BIOMES IN THE NEOTROPICS

Gentry also expressed views and hypotheses about the evolutionary origins of the drier biomes in the Neotropics, although these were little expanded on. Despite a broad coverage, his plot data were less representative in Neotropical dry forests. Much of the lowland rainforest of the Neotropics are bounded by drier areas. These include the Llanos region of Venezuela and Colombia, the Cerrado–Chaco–Caatinga of the Brazilian shield, as well as northern Central America and Mexico (DRYFLOR, 2016). With species generally quite disjunct between the different dry areas (Gentry, 1982b), even beyond the Neotropics, Gentry saw dry-centered taxa as representing "at the most superficial level [. . .] a depauperate subset of the moist/wet forest flora" (Gentry, 1995: 167). Furthermore, he suggested that these resulted from more recent diversification, largely due to increasing aridification (Table 1: IIg; Gentry, 1982a: 583). He also noted that the significant smaller-scale floristic differences between the separate dry forest regions might be more attributable to biogeographical than ecological drivers (Gentry, 1995). This is partly supported by more recent studies, which find establishment of lineages in the Brazilian Caatinga followed by in situ diversification in the last four million years, albeit intermixed with the presence of significantly older lineages (Fernandes et al., 2022). Similarly, recent diversification has been documented in savannas of the Cerrado (Simon et al., 2009), contrasted by older diversification in dry forests in general (Pennington et al., 2009; Särkinen et al., 2011), suggesting overall a combination of both older and younger diversification in arid Neotropical regions.

As with all subsidiary patterns listed so far, due to their relative lower number of species (compared to Neotropical rainforests), Gentry did not focus more on local-scale speciation patterns within these biomes.

### TEMPERATE-DERIVED MONTANE SPECIES OF THE ANDES

The one example of low-number species groups that Gentry focused on is temperate taxa reaching their southernmost distributional limits in the montane regions of Central America and the northern Andes. For these taxa, Gentry remained puzzled: despite the "evolutionary opportunity" presented by the uplift of the Andes and the subsequent novel emergence of montane biomes, these taxa "show little tendency to speciate" (Gentry, 1982b: 127). As a result, while frequently dominant ecologically in the Neotropical montane forests, these taxa are rarely species rich. However, examples of these taxa, such as species of *Viburnum* L., have been documented to be the origin of rather recent radiations (Donoghue et al., 2022) and might be in the phase of incipient speciation (Maya-Lastra et al., 2024). Furthermore, taxa that might belong to this group present important Andean radiations, such as *Lupinus* L. (Hughes & Eastwood, 2006), despite Gentry never referring to them.

## Explaining the Two Major Distribution Patterns of Neotropical Plant Diversity

In this last section, we synthesize Gentry's hypotheses explaining the origin of diversity within the two dominant Gentry-patterns explained above: Amazonian- and Andean-centered taxa. The processes hypothesized here describe speciation, acting on a local scale, where macro-geological processes do not play out as prominently anymore.

### PARAPATRIC SPECIATION AND EDAPHIC SPECIALIZATION IN AMAZONIAN TAXA

In the lowland rainforests of Amazonia and surroundings, Gentry suggested parapatric speciation associated with specialization to local edaphic conditions as the prevalent mode of speciation of Amazonian floristic diversity (Table 1: IIIa; Gentry, 1989). Explicitly, species' specialization to locally different edaphic environments would lead to the high β-diversity turnover observed between the different habitat types (Gentry, 1989). However, this view represented an evolution of his own thinking: Previously, local adaptation and specialization played a smaller role in his ideas on tropical speciation (Gentry, 1982a), despite his work illustrating the importance of these factors (Gentry, 1981). Diversity in the Amazon was posited to originate mainly by allopatric speciation facilitated by Pleistocene climatic cycles (as described by the refuge hypothesis; Haffer, 1969). However, increasing evidence contradicting some of the major predictions of the refugia theory across Amazonia (see above) led the community to question and ultimately reject the refugia hypothesis as a motor for species origins (Bush & Oliveira, 2006; Rocha & Kaefer, 2019). Gentry also voiced his own critiques on the refuge hypothesis, countering some of his earlier ideas (Gentry, 1982a, 1982b). His revised ideas on speciation, emphasizing local adaptation and specialization (Gentry, 1989), seem to have been quietly validated in the decades since he reformulated them. Ecological and evolutionary studies across the Amazon are identifying local edaphic conditions as strong predictors for the diversity of these rainforests (Fortunel et al., 2014; ter Steege et al., 2023). While this process is acknowledged to most likely contribute to the diversification across Amazonia (Antonelli et al., 2018a), very few studies explicitly test this hypothesis. While studies have investigated patterns of genetic divergence between closely related species specialized to differing edaphic conditions, they have been inconclusive on the impacts on speciation. In Burseraceae, Fine and colleagues (Fine et al., 2013, 2014) found a high degree of specialization to specific edaphic conditions both within and between closely related species. Their results indicate that edaphic specialization may have an important influence on speciation processes in Amazonia. Along with edaphic conditions, local interactions with herbivorous insects might also play an important role (Fine et al., 2004, 2014). Edaphic adaptation has been suggested as an important factor explaining morphogroup diversity in large species complexes such as the understory palm *Geonoma macrostachys* Mart. (Bacon et al., 2021). A similar role of edaphic adaptation has been hypothesized to explain the lack of morphological divergence in the radiation of Amazonian *Guatteria* species (Erkens et al., 2007).

However, while this pattern of specialization and local adaptation may well be the dominant process of speciation in Amazonian-centered groups, most likely it is only one of many processes contributing to the overall assembly of species diversity, as also acknowledged by Gentry (Gentry, 1989). Thus, the emphasis on edaphic specialization across Amazonia needs to be considered in the context alongside other, complementary processes such as biotic interactions also driving specialization (Ehrlich & Raven, 1964; Fine et al., 2014).

### EXPLOSIVE SPECIATION IN ANDEAN TAXA

For the generally herbaceous epiphytes, understory shrubs, and palmettos that characterize Andean-centered groups, Gentry posited that speciation was "exceedingly dynamic, even explosive," and included adaptive radiation (Gentry, 1982a: 588–589).

He presented the environmental conditions of the Andean region, which ultimately would drive founder-effect–mediated speciation (Gentry, 1989). Microgeographical differentiation of microclimate, resulting from orientation of a slope, local rain shadows, or regular disturbances from landslides strongly structure species distributions (Gentry, 1989: 126). In the Andean rainforests, frequently disturbed and heterogeneous microhabitats, along with small, dispersed populations associated with strong ecological interactions, would lead to small-ranged and easily isolated species. It is in this scenario that Gentry proposed founder-effect–mediated speciation: small and localized populations would present optimal conditions for genetic drift and selection to create diverging founder populations (Table 1: IIIb; Gentry, 1989: 126). Despite the focus on founder effects as the underlying process, Gentry's discussion also elaborated on the role of co-evolution of plant-pollinator relations (Table 1: IIIc; Gentry, 1989).

Generally, founder-effect–mediated speciation has been found to be exceedingly rare compared to other modes of speciation (Coyne & Orr, 2004; Templeton, 2008). In a global review of orchid population genetic studies, Phillips et al. (2012) found that genetic differentiation is generally small between populations of orchid species. However, only a fraction of the data used for this study was from epiphytic species, whose small, dispersed populations might be strongly influenced by genetic drift. Despite the strong focus of the meta-analysis on genetic drift, the authors emphasized, among other contributions, the important role of plant-pollinator interactions in the diversification history of orchids (Phillips et al., 2012). Even beyond the Andes, in lowland Amazonian rainforests, long-distance dispersal leading to founder effects has been hypothesized (Dexter et al., 2017).

Dynamics of speciation, concurrent with the Andean orogeny and co-evolutionary processes, have been investigated recently with molecular phylogenetic methods for many of the examples Gentry named. These included groups such as Orchidaceae (e.g., Pérez-Escobar et al., 2017, 2024), *Heliconia* L. (Iles et al., 2017), Campanulaceae (Lagomarsino et al., 2016), but also *Lupinus* (Hughes & Eastwood, 2006), an emblematic genus of Fabaceae not mentioned by Gentry. However, co-evolution was not found to be the main driver in some cases. A study based on molecular phylogenetic data of *Ruellia* L. (Acanthaceae) found that diversification was not in fact driven by the co-evolution of hummingbirds and *Ruellia*. Hummingbirds had diversified as much as 20 million years before the plants. Nevertheless, the pre-existing diversity of hummingbirds facilitated the diversification of the plant group within the Andean region upon establishment there (Tripp & McDade, 2013). Another study on the Campanulids of the Andean cloud forests found that while traits facilitating both pollination and dispersal are correlated with increased diversification, other factors such as the Andean orogeny and climatic change have also influenced speciation and extinction (Lagomarsino et al., 2016). In particular, the heterogeneity of habitats in the Andes allowed repeated parallel diversification of pollination syndromes and fruit types, which strongly underlines Gentry's original insight of (micro)-geographic specialization (Givnish et al., 2014; Lagomarsino et al., 2016). While all these studies investigated processes at a scale too large for any inference of the underlying genetic process of speciation, the macroevolutionary patterns do not rule out support for a hypothesis that founder effects might be implicated in the speciation process.

Results based on molecular phylogenetics also highlight inconsistencies in Gentry's interpretations, in particular on the temporal scale of speciation. In one specific case of orchids he estimated speciation to have taken just 15 years, while for the genus *Heliconia* he assumed 100 to 1000 years for speciation to take place (Gentry & Dodson, 1987b; Gentry, 1989). This might have taken one or more orders of magnitude longer, certainly in *Heliconia* (Iles et al., 2017). These estimates of species ages were most likely rather dependent on the known species ranges and endemism. Through more exploration and floristic studies since Gentry's work, the distributional ranges of similar strongly endemic species of these cloud forests seem to be not quite as restricted as Gentry had suggested (e.g., Pitman et al., 2022; White et al., 2024). As from the perspective of Gentry's speciation processes, endemism and species age should conceptually be tightly linked; the relaxation of the endemism criteria would bring about changes in the estimates of species age. Nevertheless, compared to lowland taxa, Andean taxa tend to be range restricted (e.g., Larsen et al., 2011). However, only a fraction of the Andean flora is sampled in phylogenetic studies to date. As such, for many taxa we lack insights as to the processes and timescales shaping the striking diversity found in the Andean tropical forests.

Gentry considered the highest diversity of the Andean region to be in the lower elevations of the Andes. While he did explicitly separate the Andean and Amazonian phytogeographical regions, he did not define an explicit boundary between them. Biogeographical meta-analyses have highlighted the floristic closeness in terms of dispersals between the regions in both directions, across many lineages (Pérez-Escobar et al., 2022). As such the border between the two regions is blurry.

### CONNECTING AMAZONIAN AND ANDEAN REGIONS

Gentry only briefly touched on evolutionary links between both regions, discussing this more implicit idea in less depth than the evolutionary ideas above. For example, in the concluding remarks on his phytogeographical patterns (Gentry, 1982a), but also when discussing epiphytes (Gentry & Dodson, 1987b), he conceptually linked the evolution of Amazonian and Andean regions: The novel environmental opportunities of the uplifting of the Andes created the opportunity for lowland plants with "evolutionary potential" to exploit different strategies such as epiphytic, shrub, or palmetto habit (Gentry, 1982a: 589). This would have contributed to the explosive speciation seen in the Andean region. This evolutionary potential, which might be equated to the more widely used term "pre-adaptation" or "evolvability" (Jablonski, 2022), allowed these specific groups to proliferate (Table 1: IIId). Of course, hypothetically such evolutionary potential extends beyond just growth form, also playing a role for instance in edaphic specialization or plant-pollinator interactions. Such historical sequences have been inferred for epiphytic bromeliads, where multiple (pre-)adaptations to the epiphytic habitat allowed the group to radiate within Gentry's Andean region (Givnish et al., 2014). Here, trait and habitat data were assembled to infer the transitions into epiphytic habitat, as well as traits that might have facilitated epiphytic lifestyles such as the characteristic tank habit or CAM photosynthesis. Integrating this data with molecular phylogenetic trees and geographical data showed that key innovations facilitated diversification of bromeliad species, especially in allowing them to effectively take advantage of the epiphytic habitat (Givnish et al., 2014). Similar preadaptations to Andean distributions have also been suggested at the community level, e.g., for the genera *Aegiphila* Jacq., *Erythroxylum* P. Browne, *Erythrina* L., *Guatteria*, *Hieronyma* Allemão, *Meliosma* Blume, *Piper*, *Prunus* L., *Styrax* L., and *Symplocos* Jacq. (Linan et al., 2021). This line of reasoning, while merely implicit in Gentry's paper, might play an important part in the assembly of the Andean flora and in evolution in general (Jablonski, 2022).

## GENTRY'S EVOLUTIONARY LEGACY

Gentry's ideas present a basis for testing hypotheses describing the evolution and assembly of Neotropical rainforests in particular and tropical rainforests generally. As underlined here, Gentry did not just stop at describing diversity of the tropics but actively sought to try and explain "why" we see these diversity patterns. In most of his accounts on distribution patterns—be it for specific regions like the Chocó, or across continents—he also advanced hypotheses about the evolutionary processes behind them. Some of these have become highly relevant today, like the impact of Andean uplift on Neotropical plant diversification, while others have had less support or are yet to be properly tested using modern-day tools. Importantly, Gentry was interested in all plant diversity, from trees to epiphytes and lianas (i.e., epiphytes: Gentry & Dodson, 1987b; lianas: Gentry, 1991). This gave him insights into rainforest evolution across scales, a field where processes are still today generally inferred from data representing only trees.

Al Gentry's views and hypotheses (Table 1) present a great inspiration and an ideal starting point for constructing robust and testable hypotheses on the evolution and assembly of (Neo-)tropical rainforest flora. Crucially, these hypotheses extend beyond just woody plants and highlight the importance of also including diverse plant growth forms like epiphytes and herbs in future research. With new data becoming available at ever faster rates, testing of these hypotheses is becoming more achievable. Indeed, we are well into the genomic era, and massive molecular data are becoming available at rates unimaginable a few years ago (Buerki & Baker, 2016). Leveraging phylogenomics with improved estimates of molecular dating and macroevolutionary diversification models (i.e., Helmstetter et al., 2022; Morlon et al., 2022; Lambert et al., 2023) will enable more accurate testing of Gentry's ideas across scales (e.g., Meseguer et al., 2022; Zuntini et al., 2024). Along with increased exploration and recognition of the importance of taxonomic work on tropical taxa (Hortal et al., 2015; Barlow et al., 2018; Ondo et al., 2023), accelerating efforts are making complementary data available across disciplines. In particular, herbaria are rapidly increasing their digitization capabilities for tropical regions (Corlett, 2023; Davis, 2023; Delves et al., 2024; Streiff et al., 2024) as well as providing DNA material for rare species (Brewer et al., 2019; Davis & Knapp, 2025). Integrating species' associated traits (e.g., Onstein et al., 2019; Lopes et al., 2024), biotic data (e.g., Dellinger et al., 2024), or abiotic data (e.g., Lagomarsino et al., 2016; Richardson et al., 2018) will further allow for more detailed inference of macroevolutionary patterns. Methods are actively developed, fine-tuned, and adapted to address complex questions pertaining to the evolution and assembly of communities (Landis et al., 2022; Wright et al., 2022). Integrating these complementary arguments in a multidisciplinary setting, in the spirit of many of Gentry's ideas, promises to help elucidate the processes of evolution and assembly of the Neotropical rainforests (e.g., Richardson et al., 2018).

It is to be noted that surprisingly few studies cite Gentry's later publication (Gentry, 1989) focusing heavily on tropical speciation (160 citations, Google Scholar, February 2025). It is here where his ideas come into focus. One may only speculate what might have grown out of his body of research had his life not been cut short. Gentry's perspective as a highly skilled botanist with incredible in-depth knowledge of species on small community scales across large geographical areas put him in a unique position to investigate the commonalities and differences that could be found across the Neotropics. His cross-disciplinary thinking and ideas provide a great example of how to approach the study of complex biological systems, such as the evolution of Neotropical rainforests. Having been referred to as "one of the greatest botanists of the 20th Century" (Hughes et al., 2012: 13), now more than 30 years after his untimely death, his ideas continue to challenge biologists to better understand the patterns and processes of the Neotropical tropical flora and the tropics in general.

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