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Phillips, O.L. orcid.org/0000-0002-8993-6168 (2025) How Al Gentry Changed Tropical Ecology. Annals of the Missouri Botanical Garden, 110. pp. 111-127. ISSN 0026-6493

https://doi.org/10.3417/2025931

HOW AL GENTRY CHANGED TROPICAL ECOLOGY[1,2]

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Abstract

Alwyn Gentry's ecological legacy is rich and vibrant. It comes from his drive to revolutionize plant identification and to apply these innovations to understand tropical forests both in detail and as a whole. It stems too from his passion for plants and forests, and the attention he gave those who shared his love for the natural world. Here I explore the impacts of Gentry's approach and findings on tropical ecological science today. The big challenges that always face those wanting to understand tropical forests are their high diversity and the fact that most of the time plants here are sterile, while identification depends on reproductive structures. Because flowers are least accessible for the canopy trees and lianas that dominate tropical forests, this affects our ability to measure biodiversity, understand it, and monitor its persistence over time. Gentry has helped to make all these possible. Thanks to his innovations in plant identification and his vision in applying them to whole forests, tropical floristic inventory and ecological monitoring have become almost commonplace and, crucially, replicated across time and space. We now know which forests are most diverse, and why, and how their composition changes over space, climate, and soil. Gentry's insights and methods help us better understand where conservation needs to focus, how forest people use their environment, and how global changes impact the biodiversity and carbon of Earth's most complex ecosystems. Finally, his influence includes lasting impacts not simply on what we have learned, but also on how we do our science, and even on who does it.

Resumen

El legado ecológico de Alwyn Gentry es rico y vibrante. Proviene de su impulso por revolucionar la identificación de plantas y aplicar estas innovaciones para comprender los bosques tropicales tanto en detalle como en su conjunto. También surge de su pasión por las plantas y los bosques, y de la atención que brindaba a quienes compartían su amor por el mundo natural. Aquí exploro los impactos del enfoque y los hallazgos de Gentry en la ciencia ecológica tropical actual. Los desafíos a los que siempre se han enfrentado quienes quieren comprender los bosques tropicales son su diversidad y el hecho de que la mayoría de las veces las plantas aquí son estériles, mientras que la identificación depende de las estructuras reproductivas. Puesto que las flores de los árboles del dosel y las lianas que dominan los bosques tropicales son menos accesibles, esto limita nuestra habilidad para medir la biodiversidad, comprenderla, y monitorear su persistencia en el tiempo. Gentry ayudó a que todo esto sea posible. Gracias a sus innovaciones en la identificación de plantas y su visión para aplicarlas a bosques enteros, el inventario florístico tropical y el monitoreo ecológico se han vuelto casi comunes y, fundamentalmente, replicados en tiempo y espacio. De este modo sabemos qué bosques son más diversos, por qué, y cómo cambia su composición en el espacio, el clima y el suelo. Sus conocimientos y métodos nos ayudan a comprender mejor dónde debe centrarse la conservación, cómo los habitantes de los bosques utilizan su entorno y cómo los cambios globales impactan la biodiversidad y el carbono de los ecosistemas más complejos de la Tierra. Finalmente, la influencia de Gentry incluye impactos duraderos no solo en lo que hemos aprendido, sino también en cómo hacemos nuestra ciencia e incluso en quién la hace.

Key words: Amazon, Andes, biodiversity, climate, climate change, composition, conservation, forests, global change, lianas, soils, South America, trees.

Our lives are influenced profoundly by but a few. For many who knew him well, Alwyn Gentry was one of these. In this personal reflection on Gentry's work and his impact, I consider what he did to change the science of tropical ecology through his innovations, his discoveries, and the unique ways in which he worked and encouraged those around him. Gentry's passions for plants and forests, people and ideas drove him to accomplish an extraordinary amount in his 48 years. Although he died in 1993, his scientific legacy endures today in multiple ways.

Recruited to the Missouri Botanical Garden as a Ph.D. student by Walter Lewis in 1969, Gentry within a few years became the leading figure in the Garden's remarkable and ambitious program in tropical botany, led by Peter Raven. Trained and encouraged by some of the greats of North American botany, Gentry was keenly aware that many of the biggest botanical mysteries of all—and therefore the most exciting challenges—lay far to the south. The challenges involved in collecting and describing tropical species and understanding their complex evolutionary and ecological relationships were

[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.

[2] I thank Carmen Ulloa Ulloa, Thomas Couvreur, and J. Sebastián Tello for the opportunity to contribute this assessment of Gentry's ecological legacy. Georgia Pickavance prepared the map. Toby Pennington, Aaron Floden, and two anonymous reviewers kindly contributed ideas or suggestions that helped improve the writing.

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Version of record first published online on 13 March 2025.
doi: 10.3417/2025931

many. They constrained not only taxonomy and taxonomists, but also almost anyone interested in tropical plants. Gentry's career was powered by his desire to tackle these questions and challenges. His tireless energy, virtuoso skills, and general disregard for convention meant that in a relatively short career Gentry had a revolutionary impact on tropical plant community ecology.

From the start, Gentry combined extraordinary botanical skills and detailed focus with a broader vision that encompassed the wider forest and his deep drive to understand it. When he first arrived in the tropics in 1967 as a student on an Organization of Tropical Studies (OTS) course in Panama, tropical ecology hardly existed as a field. Full inventories of tropical tree communities were almost unheard of, so diverse were the forests and so challenging were their tree species to collect and identify. Gentry collected his first tropical transect as a master's student at the age of 22, and further inventories as part of his Ph.D. work. Initially these allowed him to discover, and quantify, how the many genera of Bignoniaceae collectively dominate tropical American liana communities, but soon his method set in motion a wider revolution in how botanists and other scientists came to perceive tropical forests as a whole. Before we consider the multiple ecological findings and impacts of Gentry's ecological work, we must first review the scene when he started, and then consider how remarkable his approach and methodological innovations were.

For most of its post-Enlightenment history, taxonomic botany, and hence most formal plant identification, has relied on reproductive structures, in particular flowers, which are the essence of Linnaeus's sexual system for classification. The core reasons for this are that flowers are at once often highly conserved and yet almost infinitely variable, meaning that they can beautifully reveal the extraordinary evolutionary relationships among plants. But this reliance on reproduction for identification becomes a huge problem for those attempting ecological inventory, let alone assessing how communities function or change over time, since most of the time most plants neither flower nor fruit. The problem is most acute in tropical forests. Here there are more families, genera, and species of trees, lianas, and epiphytes than anywhere else, almost all flowering far above one's head. For centuries these practical challenges have restricted our ability to inventory forest biodiversity, much less understand it or monitor its changes. So, just where the scientific need is greatest, in tropical forests, inventory is hardest. As a result, few ecologists had attempted it before Gentry, and none had dared try it in a standardized, large-scale way across nations, biomes, and continents. By the late 20th century, these challenges and knowledge gaps became especially urgent and perilous because of the persistent drumbeat of deforestation and the pervasive threat of loss. When nature is vanishing, the ability to assess it accurately and at scale is not just an academic exercise, but a vital pursuit if scientists are to assist biodiversity conservation.

The genius of Gentry was to recognize all this, understand how to resolve it, and then attack the challenges with extraordinary energy.

Gentry's Method

Trained primarily as a taxonomist, Gentry was able to take on challenges that no ecologist had attempted. Two separate but tightly linked methodological innovations were key, and together they made the impossible possible.

First, confronted by the diversity of tropical forests and their overwhelming greenness, rather than simply searching for the few flowers, Gentry quickly realized that the only way to distinguish the species and attempt complete inventories was to rely not on flowers, but rather on the many "sterile" characters that plants also possess. Over time, with the help of colleagues at Missouri and numerous specialists around the world, Gentry used his burgeoning experience and immense powers of observation and organization to build keys to families and genera from scratch, based almost entirely on nonreproductive characters. He did this not simply for the Bignoniaceae but eventually *for all woody tropical South American families*—and some herbaceous ones too. Characters as diverse as leaf arrangement, form, venation, and margin; tendril type; liana stem cross sections; bark form and odor; and latex color and consistency were all used. These tools were constantly developed, revised, and improved but were not published for many years, until the year he died. More than 30 years on, "Gentry's Bible" (Gentry, 1993a) remains the essential field companion for any botanist or ecologist setting out to work with tropical American plants. More than any other single innovation, it has enabled an explosion of forest inventory and provided an accessible way in for taxonomists and non-taxonomists alike to access the complexity of tropical forests. We must recall that before the internet and artificial intelligence, it was only possible to conceive of and implement this revolution by one person first acquiring an unprecedented encyclopedic grasp of the great depth and breadth of botanical diversity.

Second, in concert with his revolutionary approach to identifying individual plants, Gentry applied it to whole forests using a systematic community inventory protocol. Initially devising it to help document the role of Bignoniaceae in Central American forests, he soon set himself the tasks of learning which forests were most diverse, why, and how their floristic composition varied from place to place. At the time, scientific knowledge was remarkably poor. Beyond the fact that tropical forests were very diverse and there was a latitudinal gradient in diversity—empirical understanding that dated back at least to the time of Darwin—we understood little about how tropical forest diversity varied. Major gradients in the compositional makeup of tropical forests—such as the marked large northeast-to-southwest gradient in Amazon familial dominance (Terborgh & Andresen, 1998; ter Steege et al., 2006)—were also unknown, much less understood. Hardly anyone had attempted macroecological analyses of tropical forest diversity and community ecology. Those who had done so worked with sketchy datasets and nonstandardized protocols.

As we have seen, initially Gentry's canvas was a few doctoral sites in Panama, but it quickly grew across the Americas to include dry forests, the Caribbean, the Brazilian Atlantic Forest, the Colombian and Ecuadorian Chocó, and especially the Andes and the Amazon (Fig. 1). All the while, his even bigger ambition was to address questions of how, where, and why forests vary globally; that is, to encompass world forests. Tackling these questions requires standardized ecological sampling from many sites across the world. The ecological tool ("protocol") Gentry adopted was an adaptation of Whittaker's 0.1-hectare system (Whittaker, 1972, 1977), which he realized had potential for applying at scale. Such samples never capture every species in a forest, but they do achieve a first-order estimate of local community diversity ("alpha diversity"), and crucially they do it much faster than larger inventories of 1 ha or more. Gentry developed his modified 0.1-ha sampling design to be able to inventory diversity and composition as quickly as possible in species-rich tropical forests. His adaptations captured all stems ≥ 2.5 cm in diameter, whether tree, liana, or large shrub, whereas most other tropical forest ecologists focused only on the trees. Gentry's design also differed in stringing together multiple 2 × 50 m transects, with 10 of these totaling 0.1 ha. This required no laying out of the plot other than running a string on a compass bearing. Of course, unlike the 1-ha protocol that he also helped develop and that is now a permanent sample plot standard (e.g., Malhi et al., 2002), Gentry's 0.1-ha transects are not suited for long-term monitoring. But the central simplicity of the 0.1-ha transects confers great convenience and exceptional efficiency in allowing botanists to inventory diverse communities rapidly (Phillips et al., 2003a).

Gentry and his colleagues applied this protocol throughout South, Central, and North America, as well as in parts of Africa, Madagascar, India, Southeast Asia, Australasia, and Eurasia, in northern and southern temperate forests, and even in tropical island forests in the Caribbean Sea and the Indian and Pacific Oceans. By the time of his death at the age of 48, Gentry had completed 226 of these samples, comprising an inventory of thousands of tree and liana species. In a separate book, Jim Miller and I described the protocol he developed in more detail (Phillips & Miller, 2002). We also acknowledged Gentry's many colleagues who contributed to this effort in the field and in the herbarium, and assessed the key findings and implications arising from Gentry's global 0.1-ha forest sampling effort. The global species-by-species, site-by-site dataset itself has been organized and is widely available. Together with later work based on the same or similar protocols by many others (e.g., Duivenvoorden & Lips, 1995; Duque et al., 2002; Phillips et al., 2003b; Draper et al., 2021), Gentry's community inventories have contributed to even more new science after his passing than they did before. His transects and his larger permanent plots have been assimilated into active continental and global plot networks and database initiatives (e.g., ForestPlots.net et al., 2021; Sabatini et al., 2022). And as noted by many, almost wherever he laid out a transect or plot, Gentry and his colleagues would encounter species new to science. In some cases, they were well known by communities living nearby, such as *Caraipa jaramilloi* Vásquez and *C. utilis* Vásquez, described from Loreto in northern Peru. Here *C. utilis* has long been sought after as the preferred species for constructing homes (Vásquez, 1991). Across Loreto alone, long-term plots with collections have led to the discovery of more than two dozen new tree species, equivalent to half the tree diversity of the United Kingdom (Baker et al., 2017). In a companion paper to the current one, Streiff et al. (2025) assess Gentry's impact on evolutionary biology, which also stems in part from his insistence on attempting complete inventories of forest vegetation. Some remarkable discoveries based on collections in Gentry's transects and plots have changed our understanding of evolution and plant geography. For example, these revealed that the center of diversity of *Caryodaphnopsis* Airy Shaw, a genus that includes dominant canopy trees, was actually in South America—rather than it being an exclusively Asian genus as thought before (Gentry, 1989).

Gentry's Results

The impact of Alwyn Gentry on tropical ecology runs deep and wide. Much of this comes directly from the heavily cited publications he produced and the lasting influence of his ideas, methods, and datasets. And more still from the colleagues, students, and others whom he influenced in his lifetime.

Gentry's energy and the diversity of ideas, countries,

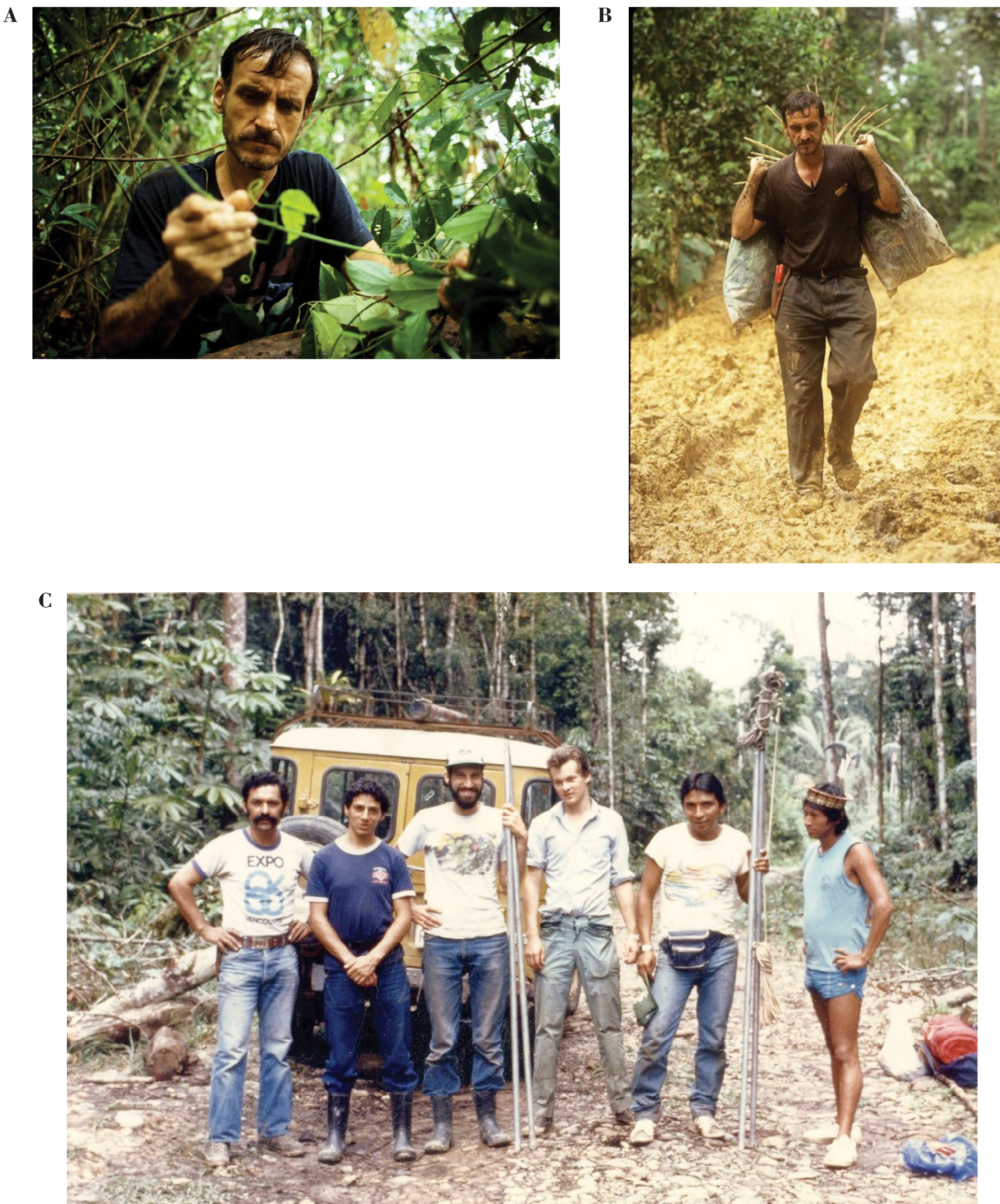

Figure 1. Al Gentry's work in South America. —A. Gentry at work in wet forest in Ecuador, examining a vine from his beloved Bignoniaceae. —B. Gentry returning to camp at day's end with multiple collections from a 0.1-ha transect. —C. Team of collaborators for a Gentry transect near Palcazú in Amazonian Peru; from left to right: Camilo Díaz Santibañez, Fernando Cornejo Valverde, Daniel Gorchov, Oliver Phillips, William Pariona Arias, and the Yanesha leader of the Shiringamazú community. Photos A and B by Randall Hyman, 1991. Photo C by Alwyn Gentry, 1988.

and people he engaged make it challenging to do justice to his complete legacy. In evaluating what his work led to and inspired, I attempt to cover the range of his ecological influence. This almost certainly omits some contributions, so broad has been his influence. Gentry not only surveyed the world's forests but did it with the help of hundreds of colleagues and wrote more than 200 scientific articles about it, the large majority as lead author. I have compiled first a referenced summary of all the key aspects of his ecological influence that I know of (Table 1), including his own work and his long-lasting and deep impact on others' work and ideas.

Table 1. How Al Gentry changed tropical ecology: 50 years of scientific impact from Gentry's innovation, publication, and education. This table is organized by the ecological themes of his work and influence. It exemplifies where Gentry's work made a difference and brings together the long-term legacy impacts of his approaches, science, and training. See text for more details and contextual assessment. In many cases these interventions were critical and irreplaceable, while in others his work helped to shape what was to come. In all cases Gentry's innovations and insights have pervasive and long-lasting impact.

Science theme	Key examples (authored by Gentry or influenced by him)	Gentry's critical contribution
Botanical discovery, exploration, and publication	Gentry made 89,271 collections, described 382 new species, and had 85 more named after him. He authored at least 200 publications.	Species discovery and description across multiple families; worldwide collection of trees, lianas, shrubs, epiphytes, and herbs; many highly impactful papers, the majority as sole author.
Plant identification in nature	*A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru)* (Gentry, 1993a)	Gentry's tour de force. This book embodies his lifetime's work of passionate inquiry and provides the universal codebreaker to the practical challenge that faces everyone working in the world's most diverse forests.
Standardized community sampling across geographic and environmental gradients	Gentry developed his standard 0.1-ha technique by heavily modifying Whittaker's (1972, 1977), to adapt to the tropical forest need for rapid sampling of woody plant composition and diversity. He made 226 0.1-ha inventories; more than 1000 further 0.1-ha inventories in South America alone have followed (e.g., Duivenvoorden, 1995; Duque et al., 2002; Phillips et al., 2003a; Tello et al., 2015; Draper et al., 2021).	Gentry's second great innovation rapidly generated the most extensive standardized dataset of tropical and nontropical woody plant community inventories. Contributed to several networks that came after.
Community composition of global forests	Hundreds of forests characterized floristically worldwide	Never attempted before Gentry's combination of unique botanical knowledge, his radical identification system, his rapid 0.1-ha field protocol, and its application worldwide
Composition and diversity patterns at biome-scale	Dry forest community composition and diversity surveyed (Gentry, 1995a)	Never attempted or demonstrated before at this scale
Mapping composition, species richness, diversity	Tropical American forest community composition and diversity, and elevational and latitudinal variation (Gentry, 1995b)	Never attempted or demonstrated before at this scale
	Discovery that western Amazonia is the global epicenter of large tree diversity, using 1-ha plots (Gentry, 1988b)	Gentry discovered this. Enabled by being almost unique in establishing, collecting, and identifying multiple 1-ha plots in South America before 1985. These were later foundational for several networks.
Diversity: drivers of species richness, diversity, and dominance	South American lowland and Andean forests *identified as the global epicenter of woody plant diversity*, and *explained* by interplay of wet equatorial climates, climatic and topographic diversity, and biogeographic history (Gentry, 1982a, 1982b, 1988a, 1992; Cazzolla Gatti et al., 2022; Sabatini et al., 2022; others)	Community diversity patterns discovered with his system and standardized 0.1-ha plots especially. Drivers of large-scale tropical community diversity were largely unknowable before.
	Rainfall seasonality and total rainfall—rather than soils—control tropical community diversity (Gentry, 1988a; Clinebell et al., 1995; Esquivel-Muelbert et al., 2017; others)	Discovered with his system and plots, and unknowable before them
Spatial landscape ecology: how soils drive forest composition	Soil conditions control tree community composition and diversity in Amazonian landscapes (Gentry, 1988a; Duque et al., 2002; Phillips et al., 2003b; ter Steege et al., 2006; Fortunel et al., 2014; others)	Gentry's 0.1-ha and 1-ha plots and his soil sampling laid the groundwork for later research.

Table 1. Continued.

Science theme	Key examples (authored by Gentry or influenced by him)	Gentry's critical contribution
Beyond trees: lianas	Liana composition, diversity, and dominance across tropical forests (Gentry, 1991; van der Heijden & Phillips, 2008)	These were quantified with his system and plots, and unknowable before them.
Beyond trees: hemiepiphytes	Hemiepiphyte composition, diversity, and dominance in tropical American forests, shown to respond positively to elevation and rainfall, inversely with lianas (Gentry, 1988a, 1991).	These were quantified with his system and plots, and unknowable before them.
Beyond trees: epiphytes	Huge contribution of epiphytes and hemiepiphytes to diversity of wet American forests (Gentry, 1986; Gentry & Dodson, 1987a), and assessment of overall epiphyte diversity and biogeographic patterns (Gentry & Dodson, 1987b)	Gentry's 0.1-ha program, associated intense collecting, and specialist colleagues enabled surveys of hard-to-access epiphytic floras, helping to derive macroecological rules of epiphyte diversity, and increase recognition of the importance of non-tree plants for diversity and conservation.
Spatial macroecology: continental mapping of forest biodiversity and carbon	Species composition drives large-scale gradients in biomass and wood density across Amazonia (Baker et al., 2004; ter Steege et al., 2006; Patiño et al., 2009; Phillips et al., 2019).	Gentry's inventories contributed to revealing the different composition, wood density, and biomass of western Amazon forests, with his plots becoming foundational sites for continuing research.
Spatial macroecology: forest ecosystem function	Pan-Amazon variation in biomass, productivity, and dynamics, and the key role of soil physical and chemical factors (Baraloto et al., 2011; Quesada et al., 2012; Johnson et al., 2016)	Gentry's 0.1-ha and especially 1-ha plots and his original soil sampling helped enable later work.
Global change and tropical ecology: changing ecosystem structure, stem dynamics, and biodiversity	Increasing tree turnover (forest dynamics), increasing biomass (carbon sink), increasing liana dominance, and changing species composition (Phillips & Gentry, 1994; Phillips et al., 1998, 2002; Esquivel-Muelbert et al., 2019; Fadrique et al., 2019)	Gentry's long-term plots contributed to much of RAINFOR's initial permanent plot monitoring as well as multiple findings after his death.
Global change and tropical ecology: changing carbon processes and their sensitivity to climate change	Increasing productivity, woody growth and biomass mortality in Amazonia, and their transient and equilibrium sensitivities to drought and temperature, and how ecosystem changes are modified by biodiversity and impact species composition (Pan et al., 2011; Brienen et al., 2015; Esquivel-Muelbert et al., 2019; Hubau et al., 2020; Sullivan et al., 2020; Bennett et al., 2023; Tavares et al., 2023)	Gentry's long-term plots contributed to monitoring forest responses to climate and other drivers of change.
Global change and tropical ecology: estimating forest carbon sequestration	Establishing IPCC Tier I defaults for nation-states to estimate their carbon uptake in tropical forests (Requena Suarez et al., 2019)	Gentry's long-term plots contribute to quantifying changes in tropical forest carbon stock.
Models of nature: initiating, calibrating, and validating dynamic vegetation models	Stand structure used to parameterize demography models, and plot dynamics used to validate model estimates of CO_2-induced biomass gains (e.g., Huntingford et al., 2013)	Gentry's long-term plots contributed to RAINFOR structural and dynamic analyses of Amazon forests.

Table 1. Continued.

Science theme	Key examples (authored by Gentry or influenced by him)	Gentry's critical contribution
Mapping carbon: interface with remote sensing	Size and species of trees in diverse tropical forests linked with laser scanning and other remote-sensing techniques to improve maps of tropical forest carbon (e.g., Labrière et al., 2023).	Some of Gentry's long-term plots and inventories help validate remotely sensed structural and dynamic analyses and mapping of forests, including contributing to national forest carbon inventories and GEO-TREES sites in Peru.
Ethnobotany: methodological innovation	New quantitative approaches to systematizing ethnobotanical knowledge (Phillips & Gentry, 1993a, 1993b)	Gentry's inventories provided the living herbaria in forests needed for botanically validated, socially contextualized, and replicable ethnobotanical assessments.
Ethnobotany: quantifying subsistence, commercial, and cultural biodiversity values in hyperdiverse ecosystems	Revealing the potential of Amazon forest fruit commercialization, and the impact of harvest methods (Vásquez & Gentry, 1989). Showing which ecosystem types are most valuable for traditional forest people and why (Phillips et al., 1994).	Gentry's methods and training enabled botanically validated surveys of hyperdiverse Amazon food markets and botanically validated assessment of traditional and commercial ecosystem values. His plots later contributed to mapping traditional peoples' use of Amazon species.
Impacting how science is done: where to focus	Building coalitions for a field station model for tropical ecology with multidisciplinary synergy (Gentry, 1993b)	Gentry coordinated a foundational meeting and edited a text for leading ecological stations in the Neotropics.
Impacting how science is done: how to connect	Establishing the first global forest biodiversity plot network (Gentry, 1982b, 1988a, 1992; Phillips & Miller, 2002), thus laying the groundwork for contemporary ecological networks and meta-networks (e.g., Malhi et al., 2002; DRYFLOR, 2016; Malizia et al., 2020; ForestPlots.net et al., 2021)	Gentry's contribution was critical. He developed the first set of standardized global forest community samples, and his work was directly incorporated into subsequent plot networks.
Impacting what science can achieve: conservation applications	Lead member of Conservation International's RAP team to assess biodiversity and mobilize support for conservation in Earth's richest ecosystems (e.g., Foster et al., 1994). Providing biodiversity baseline assessments to support Myers's revolutionary "hotspots" concept and analysis of global conservation priorities (cf. Myers et al., 2000).	Conservation International's RAP team depended on him in the field. The critical global hotspot analysis pioneered by Myers was directly informed by Gentry's encyclopedic authority on tropical forest diversity, especially for the Andes.
Impacting who does science	Gentry's Ph.D. and master's students, including the two high-level courses he gave in St. Louis (Tropical Forests and Phylogeography) and guest contributions in Latin America	For about 20 students studying in St. Louis, Gentry was the lead supervisor and/or the key influence on their careers.
	Training and enthusing of many botanists, especially in South America and including Brad Boyle, Rick Clinebell, Alvaro Cogollo, Hermes Cuadros, Camilo Diaz, Gracielza dos Santos, Washington Galiano, Miryam Monsalve, Percy Nuñez, Rosa Ortiz, Ariane Peixoto, Ivón Ramírez, Carlos Reynel, Ricardo Rueda, David Smith, and Rodolfo Vásquez	Gentry helped to develop a generation of botanists in Latin America, as well as interacting with and supporting peers in the region and at the Missouri Botanical Garden.

IPPC, Intergovernmental Panel on Climate Change; RAP, Rapid Assessment Program.

Below, in the text that follows to accompany the table, I draw out two especially critical areas of Gentry's legacy. These are (1) Gentry's revolutionary impact on understanding forest diversity, practically relevant for conservation and including large parts of what we call "macroecology" today; and (2) the influence his approach to science, forests, and people has on how we do tropical science today, who does it, and what we have learned.

GENTRY DISCOVERED WHERE FORESTS ARE MOST DIVERSE, AND WHY, AND HOW THEIR PLANT SPECIES COMPOSITION CHANGES WITH CONTINENT, REGION, CLIMATE, AND SOIL

Gentry was the first to address all these questions at large, tropical scales, using standardized sampling of ecosystems across geographic and environmental gradients. The combination of his unparalleled botanical knowledge, systematic and rapid pan-angiosperm plant identification techniques, fixed-area ecological sampling, and the almost unrelenting pace and intensity at which he worked made this possible. His work was conducted mostly in the tropical Americas. Having essentially mastered the most diverse flora on the planet, he continued to apply the same techniques in forests elsewhere, aiming to span the forests of the world. At the time of his death, many further campaigns were planned, but the planetary span of forests was already almost fully attained (Fig. 2).

Gentry transcended the limits of geography and taxonomic family specialism more than any botanist before or since. This put him in the unique position of being able to describe authoritatively how geography controls world forest ecology, and precisely how forests are made up of particular branches of the floral tree of life. Among his many findings, several stand out. These include the following:

Seeing the trees but also seeing that the forest is more than trees

Gentry's technique permitted assessing not just arboreal composition and diversity, but that of all woody plants. In particular, lianas (free-climbing woody plants) are traditionally neglected by ecologists in spite of their great contribution to diversity and leaf production (Gentry, 1983; Hegarty, 1991) and are largely ignored by related professions such as forestry and arboriculture. This is largely because of the challenges of identifying and measuring them (e.g., van der Heijden et al., 2010). As the specialist in Bignoniaceae—which, as Gentry discovered, turns out to be the number one or number two liana family in almost all lowland forests in Central and South America (Gentry, 1991, 1992)—he had a way into this complex world. But it was his persistence in developing and mastering a full, sterile character–based family and generic key that unlocked other liana inventories too. By developing all the necessary tools to "see" beyond trees, Gentry could also incorporate lianas into standard plot inventory techniques. These permitted evaluation for the first time of liana diversity in tropical forest communities. They also became the foundation of later work, described below, to assess liana ecological change over time. Gentry's non-tree interests transcended lianas too. He and Calaway Dodson sampled 0.1-ha areas for *all* vascular plants in three west Ecuadorian forests and used this to show that by ignoring epiphytes in particular, we greatly underestimate total floristic diversity—especially in wet forests (Gentry & Dodson, 1987a). Their wet forest sample (367 species in one tenth of a hectare, of which 127 were epiphytes) was the most species-rich whole sample ever recorded at the time and has periodically inspired attempts at similar inventories elsewhere. Not least, farther up the same Pacific Chocó coast, at El Amargal in Colombia, Gloria Galeano (1958–2016) and her colleagues later recorded an even greater total—442 species in 0.1 ha, dominated by treelets, herbs, epiphytes, and hemiepiphytes (Galeano et al., 1998). These and other inventories were later incorporated into a global analysis confirming western South America as the richest place on Earth for plants (Sabatini et al., 2022). A separate initiative by Gentry and Dodson (1987b) to analyze floras and collections enriched by their own work allowed them to draw wider conclusions: at the family level, African and American epiphytic floras share similar diversity, yet the number of tropical American epiphyte species (at least 29,000) is many times more, probably more than in all other regions on Earth combined. A key reason for this is the hyperdiversity of American orchids, especially in the Andes and nearby lowland wet forests in the western Amazon and Chocó (e.g., Gentry, 1986).

Measuring the composition and diversity of American dry tropical forests

Most earlier biological studies of dry forest communities treated them very broadly or in terms of differences from moist or wet forests (e.g., Holdridge et al., 1971; Rzedowski, 1978; Gentry, 1982b, 1988a), or provided findings or inferences based on single or few sites (e.g., Hubbell, 1979; Lott et al., 1987; Janzen, 1988). Gentry himself started by describing the contrast among wet, moist, and dry west Ecuadorian forests (e.g., Gentry & Dobson, 1987a). By the 1990s, Gentry's large-scale sampling was sufficient to analyze dry forests in

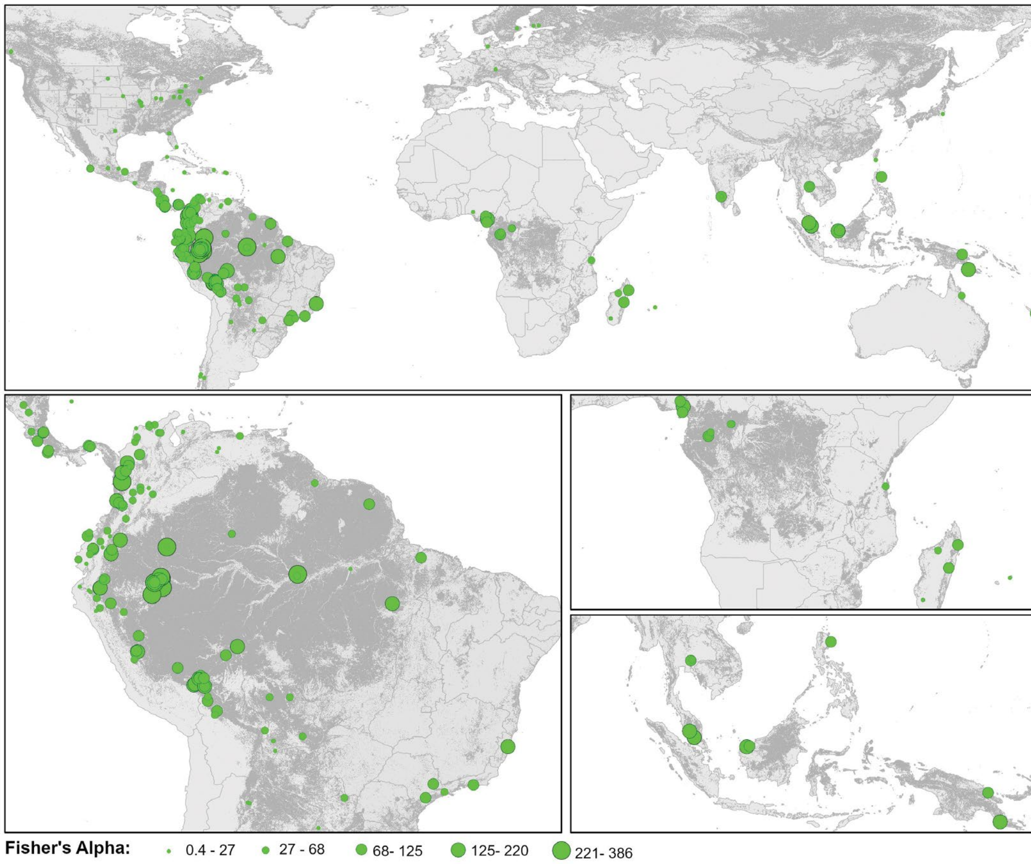

Figure 2. Global locations of Al Gentry's forest tree and liana inventory plots. The map displays all 226 of the 0.1-ha transects he surveyed and collected for all plant stems $\geq$2.5 cm diameter. Plot symbol size is scaled by the species diversity (Fisher's alpha) of each. Tropical regions are expanded to better illustrate the fuller coverage there. The background forest layer is taken from the GLC2000 dataset (Global Land Cover 2000 database, 2003). We used the tree cover global classes 1, 2, 4, 5, and 6 for unflooded forests (broadleaved, evergreen; broadleaved, deciduous; needle-leaved, evergreen; needle-leaved, deciduous; mixed leaf type). Several clusters in western Amazonia and the Chocó overlie 16 additional 1-ha forest plots that he also collected, most of which have become permanent. Figure prepared by Georgia Pickavance.

Note how Gentry's work had global biome and biogeographic coverage but was concentrated in tropical South and North America. All of the top 10 most diverse 0.1-ha sites he encountered are in Amazonia and the Chocó, with Fisher's alpha reaching as high as 386 in one north Peruvian Amazonian plot. Twenty-five years later a similarly comprehensive study using 1-ha tree plots, but requiring more than 100 contributors (Sullivan et al., 2017), confirmed that northwest South America holds the most diverse forests in the world (Sullivan et al., 2017).

their own right. He showed for the first time that Fabaceae are the dominant tree family and Bignoniaceae the dominant liana family in American tropical dry forests, with others such as Myrtaceae, Sapindaceae, and Euphorbiaceae also being particularly speciose (Gentry, 1995a). While these match family dominance patterns in moist forests to some extent, dry forests were found to have much greater proportions of wind-dispersed and deciduous species. By probing the distinctive floristic composition of dry forests and exploring large-scale patterns among dry forest woody plant communities for the first time (Gentry, 1995a), Gentry also suggested that the tropical forests of Mexico and Bolivia may be more diverse than dry forests closer to the equator, therefore contradicting the supposedly universal pattern of a latitudinal diversity gradient where species diversity increases toward the equator. This work demonstrating compositional and diversity differences was the landmark study toward biome-wide ecofloristic understanding. In revealing key patterns, proposing key ideas, and stimulating increased sampling by others using his method, Gentry also contributed to the evidence base for dry forest vicariance during glacial periods (e.g., Pennington et al., 2000), and to later networked Neotropical analysis of the biome that, for example, confirmed a "reverse latitudinal gradient" in dry forests (DRYFLOR, 2016). As described below, Gentry's dry forest work also allowed him and others to place these systems in still broader context, assessing for the first time the impact of climate and soil factors on forest diversity across the full tropical moisture gradient (Clinebell et al., 1995).

Measuring the composition, species richness, and familial makeup of Andean forests

Gentry showed us which plants dominate in which montane tropical forests, and how these compositional dominance patterns follow predictable elevational patterns. Characteristically, his data were able to show not only that the dominant families are predictable even before communities have been sampled, but also precisely which families and which genera dominate at which elevation, showing that to a large extent the physical environment predictably determines the coarse-scale floristics of tropical forests. In the Andes, for example, Lauraceae are the most speciose family, directly replacing legumes in importance as one traverses upslope above about 1500 m and maintaining this dominance to around 2900 m. These transitions, he suggested, reflect a wider shift from lowland flora to dominance by families with Laurasian (Northern Hemisphere) origin, with a progressively smaller suite of families and genera contributing with increasing elevation (Gentry, 1995b). (See also Loza et al. [2025] for an appraisal of the Great American Biotic Interchange [GABI] and its impacts, including current understanding of family biogeography). Above 3000 m, familial dominance switches again, with Asteraceae leading the tree community here, followed by Melastomataceae, Ericaceae, and Myrsinaceae (now Primulaceae). This essential predictability of forest familial composition extends to plant habit too. Gentry discovered that the diversity of lianas and of hemiepiphytes (beginning life in the canopy and sending roots downward, and rooted climbers that become epiphytic and may send down new roots) is essentially complementary. Lowland forests tend to have high liana diversity and dominance, and they become progressively replaced by hemiepiphytes up mountain slopes (Gentry, 1988a). Gentry also showed that lianas and hemiepiphytes are similarly out of phase when moving from dry forests (lianas) to the wettest forests (hemiepiphytes) (Gentry, 1988a, 1991). The under-appreciated hemiepiphyte plant guild thus partially compensates for (or perhaps helps cause) the loss of lianas in cooler and wetter tropical forests.

Gentry's standardized data also provide the means to test ideas about the dependence of wider plant diversity on latitudinal, thermal, and moisture controls, across the full altitudinal gradient of tropical forests. There are several theoretical reasons to expect that plant and animal diversity might peak at intermediate elevations—for example because moisture stress is often less than in the lowlands, while frost, cold, and UV radiation are less hazardous than near the tree line. Much work before and since has documented such a peak, but the best evidence for plants tends to involve moisture-loving epiphytes (e.g., Cardelús et al., 2006) and/or where adjacent lowland forest is relatively dry. Already by the 1980s Gentry's sampling along the wet Andean elevational gradient permitted detection of maximal woody plant diversity in the lowlands and a linear decrease from about 1500 m to near the highest forests above 3000 m. This led him to reject the idea of a "mid-elevation bulge" in diversity for trees and lianas (Gentry, 1988a, 1995b). Notably, all 17 of his exceptionally diverse 0.1-ha samples with more than 200 woody species come from Amazon or Chocó forests below 1000 m (Phillips & Miller, 2002). Yet, even with the sharp decline in diversity with altitude, the highest Andean forests are still as diverse as the most diverse temperate forests in his global dataset. Andean forests are also more diverse than Central American montane forests, which in turn are more diverse than Mexico's mountain forests (Gentry, 1995b).

Discovering which ecological factors control tropical American forest diversity and composition

While Gentry showed how rainfall and warm temperature provided some of the necessary conditions for maximizing tropical diversity, as noted by Streiff et al. (2025), he was also deeply interested in how a wide range of evolutionary, biogeographic, and ecological factors may explain patterns in forest composition and diversity. Among the potential ecological factors, soils were the big unknown. Again, standardized sampling, including soil samples, clearly showed that even adjacent forests support different woody plant communities, and these differences relate to the precise soil type. This is the case in the wet Amazon lowlands of north Peru and in seasonally dry sites in south Peru (e.g., Gentry, 1988a). This primacy of local soil for local Amazon floristics was later tested, demonstrated, and explored more systematically by others, including Tuomisto et al. (1995, 2003) for understory plants, and Condit et al. (2002), Duque et al. (2002), Phillips et al. (2003b), and others since for trees. We now know that large-scale differences in soil chemistry and physical properties, not climate, are also the main drivers of forest compositional and functional differences across the Amazon (e.g., ter Steege et al., 2006; Quesada et al., 2012; Fortunel et al., 2014). It turns out not only that the great, green carpet of the Amazon is underlain by complex variation in soils, drainage, and geomorphology, but that this heterogeneity strongly controls the forest above.

Of course, how climate and soil influence diversity may be very different from how they influence composition. Again, Gentry helped reveal how. His graduate student Rick Clinebell used the Gentry American tropical dataset in the first, elegant large-scale environmental analysis of tropical forest plant community diversity (Clinebell et al., 1995). This was made possible not only by Gentry's inventories but also because, unusually for a botanist, he collected soil too, using a rapid sampling protocol appended to his 0.1-ha community surveys. Thus, Gentry ensured that his widespread ecological sampling of species composition and diversity was directly linked to equivalent sampling of soil nutrients. Clinebell's analysis showed that rainfall seasonality and total rainfall exert the strongest ecological controls on tropical community species richness, while the impact of soil is negligible. This was true for the whole Amazon-Andean-Chocó-Caribbean-Chaco–Central American dataset, and for most subsets with sufficient sampling. Soil variables were correlated with precipitation—drier forests had more nutrient-rich soils—but after rainfall was accounted for, available soil nutrient concentrations contributed little to explaining variation in species numbers. Therefore, and unlike the species composition of tropical forests, forest *diversity* is remarkably independent of soil quality. This provides critical large-scale evidence in support of local observations both before and after Gentry's work—plants in many mature tropical forests are highly evolved to obtain nutrients via tight nutrient cycles, allowing remarkable diversity and ecosystem function to persist in even the poorest of soils (e.g., Went & Stark, 1968; Herrera et al., 1978; Aragão et al., 2009). Gentry's findings have several key implications for strategic conservation planning. Forests on poor soils can support exceptional biodiversity, and conservation here will have lower opportunity costs because such soils have less agricultural value than richer soils. Yet protecting only poor-soil forests is not enough, as richer soils support equally diverse but very different communities. Similarly, as forests with abundant rainfall lack the filter of seasonal drought (cf. Esquivel-Muelbert et al., 2017), they harbor the greatest concentrations of plant species, so wet forests must be a focus of conservation, but, critically, not to the exclusion of drier sites. Dry forests have distinct floras, often high levels of endemism (cf. Pennington et al., 2000; DRYFLOR, 2016; Dick & Pennington, 2019), and typically more fertile soils; they have now been mostly destroyed due to their agricultural suitability.

At still bigger scales, Gentry discovered where the most diverse forests on Earth grow

These are, for trees, the forests of western Amazonia and the adjacent lower Andes and Chocó, especially the wet, equatorial northwest Amazon in parts of Peru, Ecuador, and Colombia (Gentry, 1988a, 1988b). For all woody plants the picture is subtly different, because while alpha diversity tends to decline with elevation, especially above 1500 m, the great climatic and topographic variation induced by the Andes ensures that species turnover ("beta diversity") between communities is higher here. Species are reproductively more isolated than mere horizontal distance would suggest, leading to more adaptive and/or stochastic genetic differentiation. Via evolutionary and ecological processes, therefore, these narrow ranges drive great levels of landscape-level species packing (classically "gamma diversity"). This can pertain especially to some highly speciose small plants such as orchids, which Gentry hypothesized had undergone "explosive speciation" as a result of sharp environmental contrasts, strong reproductive isolation, and genetic drift (Gentry, 1982a, 1989; Gentry & Dodson, 1987b). Gentry was fully aware that if he could somehow conduct complete epiphyte inventories across tropical forests, as he had for woody plants, then the exceptionalism of wet Andean forests and their adjacent lowland forests would be even more remarkable.

Before Gentry's work, some elements of this were known or suspected, but he made the critical contributions of revealing the true variation in forest diversity and composition globally, demonstrating where tropical forests differ from one another, and exploring why. Since then, the key patterns have been amply confirmed and the geographic extent of the highest-diversity forests refined, but not substantially changed. Recent large-scale analyses of the world's forests using ecological samples of trees (Cazolla Gatti et al., 2022) and vascular plants (Sabatini et al., 2022) confirm the wetter Amazon regions and the Andes as Earth's greatest concentration of plant diversity. Recent work by the > 2000-plot Amazon Tree Diversity Network (ATDN) supports this as a center of community diversity (alpha diversity) but also shows extreme high alpha diversity farther east in the well-surveyed equatorial forests north of Manaus (ter Steege et al., 2023). Ter Steege et al. (2020) estimated a total of more than 15,000 tree species in Amazonia, and Cazolla Gatti et al. (2022) more than 31,000 tree species in South America. These plot-based estimates are controversial, as they imply that many thousands remain to be described by botanists. Regardless of the precise numbers, all accept that these are the richest forests, and no one doubts that in tropical South America still lie the greatest number of undescribed plant species on Earth (cf. Antonelli et al., 2023; Ondo et al., 2024).

IMPACTS ON OUR SCIENCE AND LIVES TODAY

Gentry believed in the power of inductive, bottom-up science

Gentry expected that by decoding the detail of nature, the bigger picture will be revealed. With this, theoretical ideas can be tested against empirical reality, and new conceptual insights may emerge. Gentry's work is proof that this approach can drive major scientific advances when the empirical work is ambitious and executed with great skill. Beyond this, his work also shows the potential for fertile and unpredictable interaction when this approach is then combined with theoretical, conceptual, and methodological advances, echoing through the decades.

Examples abound. Many of the statistical and biological aspects of patterns of tropical beta diversity and species richness revealed by Gentry have been much debated since. An influential analysis (Kraft et al., 2011) suggested that the trend of declining species richness–based beta diversity with latitude that is apparent in Gentry's data disappears once species pool size is controlled for. Others since have validated the findings of Kraft et al. (2011), while others have refuted them. Chao et al. (2023) devised a solution to remove the dependence of beta diversity on alpha and gamma diversities, and so reflect "pure" among-subplot differentiation, suggesting that latitudinal beta diversity trends do in fact exist both for richness-based and abundance-sensitive beta diversity. In another example of highly influential and debated ideas, Enquist and Niklas (2001) proposed that key macroecological features of communities emerge from a few allometric principles operating at tree level. Gentry's dataset was key for exploring predictions of invariant relationships among tree size–frequency distributions, biomass, species richness, and number of trees per unit area. Again, the conclusions have been contested, leading to further conceptual and theoretical developments. Such debates are part of Gentry's enduring legacy. His work motivated or enabled them, with the quality and ambition of Gentry's fieldwork stimulating conceptual and methodological development decades later. His impact on our understanding of how and why forest diversity and composition vary remains theoretically relevant for ecology and practically relevant for conservation, encompassing large parts of what we today call "macroecology" (cf. Table 1).

Gentry knew that he could not do it all alone

By developing and applying a global ecological protocol and taking on the challenge of identifying all plants in extremely diverse forests, Gentry inspired generations of botanists throughout Latin America in his lifetime and afterward. Gentry's legacy also owes much to his emphasis on local and national collaborations and training. His great masterpiece, the panoptic *Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru)* (Gentry, 1993a), had a long and hugely collaborative gestation. Gentry developed numerous family-level drafts to be shared, commented on, and improved by specialist colleagues, as well as expertly illustrated by his close Peruvian colleague Rodolfo Vásquez. As many who knew Gentry attest (e.g., in Miller et al., 1996), in his fieldwork Gentry always made sure he worked with local and national experts and students, and openly engaged with, trained, and gave back to those wanting to learn. Many of the leading Central and South American forest botanists and ecologists in the time since Gentry took part in his courses and field trips. They contributed critically, sharing their knowledge of the plants and the practicalities of remote tropical fieldwork, becoming research partners. Gentry thus helped to connect and grow science within South, Central, and North America and beyond. Most of all, he brought tropical plant identification within the reach of new generations and a much wider demographic than was possible before, when ecologists had available, at best, only highly technical descriptions of a narrow set of largely unknowable reproductive characters.

In short, Gentry truly democratized tropical American plant botany. More than anyone before or since, he took it to the forests, people, and countries where it actually belonged.

Gentry's approach inspired other revolutions

Alwyn Gentry's ambition, methods, book and papers, many of the plots he installed, and the people he inspired all helped lay the groundwork for the network revolution in tropical ecology that followed in the 2000s. This impact began in 1999 with RAINFOR ("Red Amazónica de Inventarios Forestales"), the first international tropical forest network to encompass highly distributed long-term plots (Malhi et al., 2002). RAINFOR's large-scale and many-site collaborative approach was inspired by Gentry's approach and achievements in establishing the first globally standardized floristic inventories. He embodied the approach of working collaboratively with many people in many places, the ambition to combine efficient ecological sampling with high-quality identifications, and the aim to replicate these inventories to create a picture of the world's forests (e.g., Gentry, 1988b; Clinebell et al., 1995; Phillips & Raven, 1997; Phillips & Miller, 2002). He also established many of the permanent plots (Gentry, 1988a, 1988b) that feature in the first continental and global analyses of tropical forest carbon and dynamics (Phillips & Gentry, 1994; Phillips et al., 1994, 1998) and that have contributed to many other impacts ever since (cf. ForestPlots.net et al., 2021; Phillips, 2023).

The emergence of standard plot protocols (e.g., Condit, 1998; Phillips et al., 2002) widely adopted by networks such as RAINFOR and ForestGEO (e.g., Davies et al., 2021), and the connectivity enabled by the internet have catalyzed a 21st-century wave of plot-based networks to assess and monitor forest dynamics and species. These include Gentry-style, distributed floristic and ecological plots for American dry forests (DRYFLOR, 2016), Amazonia (ter Steege et al., 2006), Borneo (Qie et al., 2017), African rainforests (Lewis et al., 2009), and Andean and African mountain forests (Malizia et al., 2020; Cuni-Sanchez et al., 2021). Forest monitoring with replicated long-term, small plots in South America and beyond has revealed much change in forest carbon and forest species. These networks, including Gentry's own 1-ha plots, have detected widespread biodiversity change caused by global change factors including increasing lianas (Phillips et al., 2002), drying (Esquivel-Muelbert et al., 2019), and heating (Fadrique et al., 2019). One-hectare plots including Gentry's have also been intensively applied by the ATDN to map the diversity, composition, function, and indigenous influences of the greatest forest on Earth (ter Steege et al., 2003, 2006, 2013; Levis et al., 2017; Peripato et al., 2023).

Recently, a further wave of global-scale meta-networks, data-sharing initiatives, and high-profile publications has emerged. These include ForestPlots.net (Lopez-Gonzalez et al., 2011; ForestPlots.net et al., 2021), sPlot (Bruelheide et al., 2019), the Global Forest Biodiversity Initiative (GFBI) (Liang et al., 2022), and GEO-TREES (Labrière et al., 2023), all incorporating plots, sites, and methods of Gentry's original work and working with people he trained. Using multiple analytical and technical approaches, these ensure that Gentry's contributions continue to influence areas as diverse as mapping planetary species and functional diversity, exploring the impacts of pre-Columbian people on forests, tracking contemporary global change, and validating remote sensing of biomass carbon from space.

Gentry contributed radical new approaches to global conservation and helped save forests

Directly related to his work showing where the richest forests on Earth are, and why, Gentry's findings and passionate arguments made a key contribution to what became the hugely impactful "hotspot" concept developed by Norman Myers (Myers, 1988; Myers et al., 2000). Gentry provided critical biological evidence that parts of the Andes were the hottest hotspots on Earth. This is where the greatest concentrations of species and especially narrow-range and endemic species are, and where they face grave threats. By identifying the world's hotspots, Myers and colleagues were able to show where conservation investments can have the greatest impact. The strong base of this work in real data, a global synthetic approach, and conceptual clarity led to a huge influence on conservation investments and policies of foundations, NGOs, and governments (Pimm & Raven, 2020).

Similarly, Gentry was one of a select group of biologists deeply engaged in providing evidence to support the conservation of remaining Andean-Amazon forests. This led him and colleagues to carry out Conservation International's Rapid Assessment Protocol (RAP) surveys of poorly known and endangered forests in Venezuela, Colombia, Peru, Ecuador, and Bolivia, several of which provided a key evidence base and political impetus for directing conservation investments and developing new legally protected areas (e.g., Foster et al., 1994). The tragic loss of Al Gentry, Ted Parker, and Eduardo Aspiazu at the tail end of one such expedition in Ecuador holds special poignancy for those who heard Gentry talk passionately about the unique species apparently lost with the destruction of the mist forests of Centinela, Ecuador, one of his transect sites (cf. Dodson & Gentry, 1991).

More than three decades after Gentry, it remains difficult to be optimistic about what is left of Andean forests especially, hugely reduced as they are and surely the site of Earth's greatest contemporary extinction rates. But hope persists. For example, many species previously known only from Centinela's lost forests have been found in small surviving fragments nearby, offering a chance for their survival (Pitman et al., 2000, 2022). More generally, it is substantially thanks to Gentry and the colleagues who shared his labors and love for these forests that what is known is known, what has been achieved has been achieved, and that what prospects for conservation and restoration exist, exist.

Al Gentry was both a kind and gentle man, and an intensely driven, original scientist. His discoveries have revealed some of the great mysteries of nature, enabling us to see farther and wider than was possible before.

His book changed how we carry out tropical botany and tropical ecology. And his scientific approach—wildly ambitious, radically unconventional, and openly inclusive—continues to inspire many working today at the front line of tropical ecology, botany, and conservation.

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