A Half Century of Tropical Forest Research *A Roadmap for the Future*

BY GARY HARTSHORN, DIANA LIEBERMAN, AND MILTON LIEBERMAN

In 1969, no one knew how vital tropical forests would become to the future of the planet. A study that began that year in Costa Rica has much to tell us about what may lie ahead.

In 1969, a year better remembered for Woodstock, Neil Armstrong's moon walk, and the breakup of the Beatles, a unique scientific venture was initiated, without fanfare, in a lowland rainforest in Costa Rica. The goal was simple: to tag, identify, and map a large sample of tropical trees and follow them over time, throughout their lives if possible. At that time, much was still unknown about tropical trees—even their lifespans were a matter of conjecture—and an understanding of the vital role of tropical forests for the well-being of the planet was still in its infancy.

The permanent plots study (which we called "PLOTS") began as the research project of University of Washington College of Forest Resources graduate student Gary Hartshorn, who tagged, identified, mapped, and measured the first 6,000 or so trees. This work, carried out at the La Selva Biological Station, which is run by the Organization for Tropical Studies (OTS), formed the baseline for what may now be considered "Time Zero."

THE LEAD-UP TO TIME ZERO

With funding from the National Science Foundation, OTS launched a comparative ecosystems research project in August 1968 with a month-long tropical dendrology field course taught by dendrologist Leslie Holdridge, a faculty member at Costa Rica's Instituto Tecnológico. Hartshorn was an invited participant in this short course, which ran in the Sarapiquí region at Finca La Selva, the property OTS had purchased from Leslie Holdridge four months earlier. Also participating in the short course was Hans Riekerk, a postdoctoral research fellow in forest soils at the University of Washington. After the course, Riekert stayed on at La Selva, where he set up a 200-by-200-m grid over the entire 587-ha (~1,500-acre) La Selva property.

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An *Alsophila* fern tree on the 750 m plot, photographed in June 2020.

Riekerk categorized the major landforms at La Selva and established three permanent forest inventory plots: Plot 1, 4.4 ha (11 acres) was on old alluvium in a formerly flooded river terrace; Plot 2, 4.0 ha (10 acres) was on low-lying swamp forest with a better-drained low hill; and Plot 3, 4.0 ha (10 acres), was on soil weathered from underlying bedrock with steeper slopes and dissected terrain.

Each plot was subdivided into 20-by-20-m subplots. All trees and lianas 10 cm (4 inches) or more in diameter at breast height were labeled with numbered aluminum tags, measured in diameter at breast height or above buttresses or stilt roots, mapped to the nearest meter, and identified by species or morpho-species (a provisional name). These initial efforts revealed the hyperdiversity for which tropical rainforests are justly famous: 269 tree species were recorded across these three plots. Contrast that with the checklist of native trees for the entire continental U.S. of just 881 species.[1]

The first inventory of the three Washington plots, as they were initially known, began in 1969 under Riekerk's supervision. When Riekerk left Costa Rica to join the forestry faculty at the University of Florida, Richard Grotefendt, a recent forestry graduate from Southern Illinois University, was brought on board to lead the ongoing forest inventory.

Hartshorn returned to Costa Rica at the end of December 1969 to devote half his time to identifying the tagged trees on the three plots and the other half to his doctoral research on the demography of the tall canopy tree *Pentaclethra macroloba* (Mimosaceae). Hartshorn's major professor, William Hatheway, newly hired by the University of Washington, came to La Selva in early February 1970 to assist with the field identifications of the tagged trees. The initial inventory of the three permanent plots was completed in 1971.

FOLLOW-UP CENSUSES: 1982–1995

Beginning in 1981, Hartshorn was joined by co-investigators Diana Lieberman of the University of Ghana and Milton Lieberman of the University of California, Irvine, in collaboration with Rodolfo Peralta Lobo, a forest engineering graduate of the Instituto Tecnológico. In 1982 and at irregular intervals thereafter, the tagged trees were remeasured, deaths were recorded, and new recruits were tagged, identified, measured, and surveyed; from this work, information emerged regarding how fast trees grew, how and why they died, how long they lived, and where and under what conditions each species and its offspring best survived.

Each successive inventory amplified the value of the data set, establishing the long-term growth history of thousands of trees and expanding our understanding of tropical forest dynamics. Now foresters could begin to answer many questions: What factors determine the small-scale distribution of these tree species?[2] What are the rates of mortality and recruitment[3] and of stand turnover?[4] How are species distributed with respect to canopy closure?[5] How fast do tropical trees grow, and how long do they live?[6]

Among the findings: mortality was approximately balanced by

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recruitment over a sixteen-year period, based on stem density, basal area, and biomass. Of 320 tree species in La Selva, 155 (48 percent) are classified as shade intolerant and depend on some form of canopy opening for regeneration. The proportion varies by stature: shade intolerance is seen in 63 percent of canopy species, 43 percent of subcanopy species, and only 38 percent of understory species. Very few of the shade-intolerant species require large gaps. And as adults, the great majority of tree species behave as generalists.

(Data sets and project details from the La Selva permanent plot inventories (1969–1995) are archived through Environmental Data Initiative at https://edirepository.org, ensuring free, open access for scientific colleagues and the public.[7])

UP THE MOUNTAIN

New questions emerged, and in 1985 the PLOTS project was expanded to include a large-scale elevational gradient, reaching from La Selva in the lowlands to the summit of the dormant Barva Volcano at 2,906 m, a distance of 35 km (~22 miles). The gradient passes through four life zones and two transitional zones of the Holdridge Life Zone system.[8]

Much of the study area is trackless wilderness, and of it is undisturbed old-growth forest within the Braulio Carrillo National Park. Notably, the study site represents the largest elevational transect in Central America having uninterrupted old-growth cover.[9] In fact, the establishment of the 48,000-ha (184-square-mile) Braulio Carrillo National Park, which ensures its continued protection, was in part inspired by the efforts of the PLOTS team and its local allies.

The first six Barva plots, each 1 ha, were set up in 1985 with participation by young volunteer "Venturers" from the British Operation Raleigh program,[10] led by John Proctor of the University of Stirling and Hartshorn; these plots were located at elevations of 100, 500, 1,000, 1,500, 2,000, and 2,600 m.[11] Between 1986 and 1988, five additional 1-ha plots were set up at elevations intermediate to the first six, at 300, 750, 1,250, 1,750, and 2,300 m.[12] A review of initial results showed little overlap in species composition among the first six plots, which were located at intervals of around 500 m elevation. Additional plots were therefore established at elevations intermediate to the existing plots, improving coverage and representation of the forest communities on the gradient. The plots were recensused in 1989 and 1995.

With this establishment of 11 Barva plots, the total number of permanent

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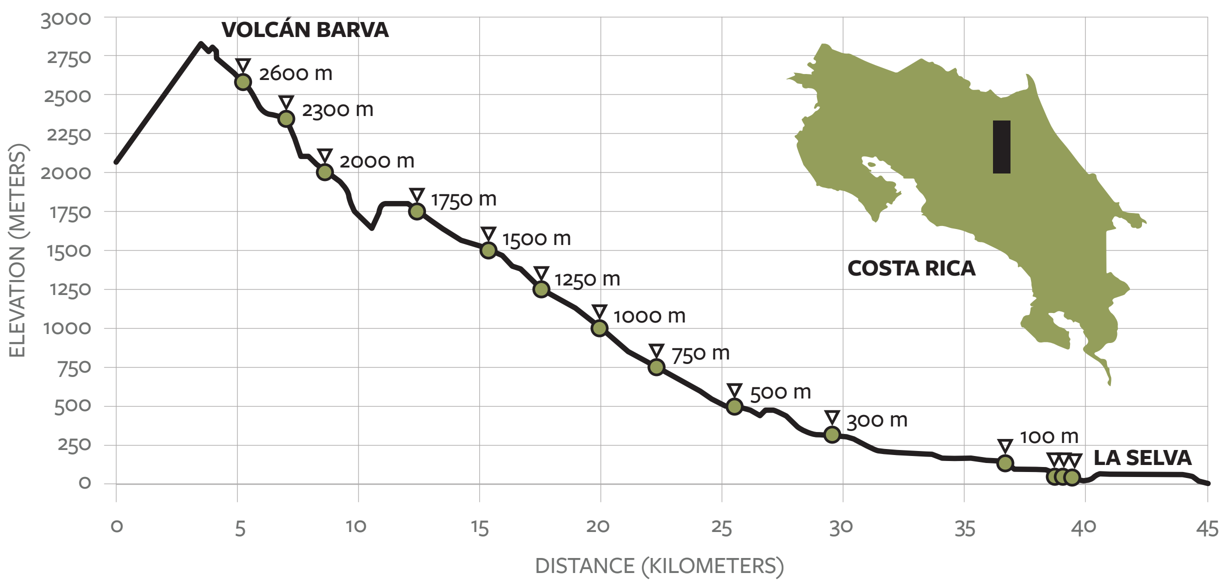
FIGURE 1. Topographic profile of study area between La Selva Biological Station and summit of Volcán Barva.



The location of each permanent forest inventory plot (from 30 m at La Selva to 2,600 m near the summit) is indicated by an arrow.

Conducting inventory in the Costa Rican rainforest is full of challenges. Much of the study area is in trackless wilderness, and many of the tree species were unknown to science before the study began. Recensusing during the Covid pandemic in 2020 was another challenge. Victor Robles assisted with that effort.

inventory plots grew to 14, the total plot area expanded from 12.4 to 23.4 hectares, the number of tagged trees more than doubled, and the number of tree species rose to nearly 700, many of which were new to science.[13] Diversity and canopy height were greatest in the foothills, at 300 m, and lowest at the summit, at 2,600 m. The inventories led to insights about the determinants of forest physical structure, diversity, life-form distribution, species composition, population structure, tree growth behavior, and forest dynamics.[14]

Environmental data were also collected to document the patterns of temperature, relative humidity, and other factors over the transect. On the Barva slope, the drop in mean temperature with elevation (moist lapse rate) is around 6.3°C per 1,000 m (3.5°F per 1,000 feet).[15] In other words, if it's a comfortable 20°C (68°F) in the lowlands at La Selva, it could be a chilly 3.8°C (38°F) at the summit of Barva. There is a close linear correspondence between elevation and mean temperature, such that one can be substituted for the other.

Information from the PLOTS project found application in the tropical forestry and conservation programs of private landowners, government agencies in the United States and Costa Rica, and NGOs such as FUNDECOR.

From both a theoretical and an applied perspective, one question was of particular interest: are tropical trees on this mountain broadly or narrowly adapted with respect to elevation? Because temperature decreases in a predictable manner with increasing elevation, the distribution of tree species reflects tolerance to varying temperatures—a pattern noted by Alexander von Humboldt in 1807.[16] The answer to the question is remarkable: most of the tree species in our study were not broadly adapted but occurred over a very limited vertical range of elevations and temperatures. Of the 524 tree species we mapped, 48 percent occurred within an elevational range of 200 m (~650 feet) or less.[17]

THE CURRENT INVENTORY . . . 50 YEARS ON

In 2018, colleagues at OTS urged us to carry out another inventory representing the fiftieth year of the project—keeping the PLOTS legacy alive and in effect rescuing a program that had been dormant for the last twenty years. The team agreed, and preparations began for mounting a wilderness field project. The answer to a new question was now within reach: as climate change affects tropical forest communities, which species will be winners and which will be losers?

Challenges soon arose, not least of which was the Covid-19 pandemic. Funding was scarce, international travel was suspended, and logistics were a nightmare. Since the last survey, access trails had become overgrown or lost, plots were difficult to relocate, and field shelters were either in disrepair or had disintegrated entirely: it *is* the tropics, after all. Purchase and resupply of basic field gear—diameter tapes, compasses, GPS units, flagging, PVC, rebar, tree tags, aluminum tree nails—were hampered by supply chain issues. Meetings between senior scientists and field technicians, whose (rubber) boots would be on the ground, had to be conducted by video conference. Climate change itself, with record

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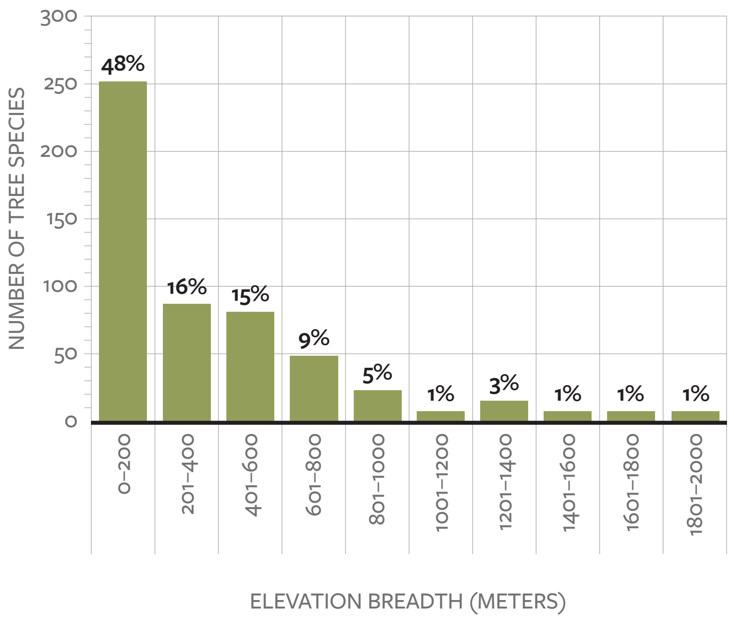
FIGURE 2. Elevational breadth (amplitude) of 524 tree species in permanent plots on Volcán Barva gradient.



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Most species occur within a very narrow range of elevations. In our samples, 251 species (48% of the total) were found over a vertical range of 200 m or less. Altogether, 86 species (16% of the total) showed somewhat more breadth in their distribution, with up to 400 m in elevational range. No species was found across the entire gradient; the species with the greatest amplitude occurred at 45–2,000 m, an elevational difference of 1,955 m.

Orlando Vargas, Gary Hartshorn, Craig Brubakker, Enrique Salicetti, and Gilberth Hurtado take a break near the 300 m plot in March 2019. Gary has been conducting research on this land for more than fifty years.

floods and weather anomalies, impeded the fieldwork.

By April 2024, the collection of field data was complete, the painstaking, laborious work of tree identification and taxonomic revision was under way, and the follow-up stages of data entry, analysis, and preparation of the data set for archiving had begun. More than fifty years of fieldwork has produced a wealth of data, and the resulting publications have brought major findings before the community of scientists and decision makers.

Yet what of the original goal—to follow the trajectory of tropical trees over their lifetimes? Analysis of the PLOTS data has shown that some tropical tree species have a maximum lifespan of only 45 years, but others may reach 450 years of age.[18] Some short-lived, fast-growing species will have completed their lives during the time period encompassed by this study to date, but some forest giants that were tagged in 1969 might have first raised their crowns to the sun as long ago as the early 1500s. Viewed from this perspective, fifty years in the timescale of forests is but a beginning.

CLIMATE CHANGE: AN EXISTENTIAL THREAT TO TROPICAL TREE DIVERSITY

Climatic upheavals, sometimes with cataclysmic consequences, have occurred throughout Earth's history. This current episode is clearly the first in which our human species can play a role in mitigating and managing the consequences of rapid warming.

Our work has established that many tropical tree species live within narrow ranges of elevation and thus occur within narrow temperature ranges.[19] Trees have long generation times, compared with other organisms, and they cannot move, which leaves them particularly vulnerable to rapidly changing climates: they can neither adapt quickly nor migrate to more favorable habitats.

Furthermore, unlike temperate zones, tropical climates show little seasonality with respect to temperature. Tropical species are thus normally exposed to, and likely to be adapted to, a much narrower range of temperatures than those living in the temperate regions. At La Selva, for example, the coldest month (January) might average 25°C (67°F), and the warmest month (October) might average 28°C (71°F). Thus, tropical trees are at even greater risk from global warming than temperate trees, which are annually exposed to, and thus adapted to, wide-ranging seasonal variations in temperature.[20]

So our work on the La Selva–Volcán Barva gradient now takes on new significance. Because temperature changes with elevation, the response of the tree species mapped with respect to elevation can be used as a surrogate or proxy of their response and potential vulnerability to climate change. The equivalence between temperature and elevation is applicable in both space (in terms of current species distributions on the Barva gradient) and time (in terms of the effects of climate change). A simple, preliminary prediction regarding one consequence of global warming is that the optimum elevation—representing the temperature "sweet spot"—for a given tree species on the Barva slope would be shifted or displaced upslope by 158 m for every 1°C increase in mean temperature.[21]

THE ELEVATIONAL GRADIENT AS A PROXY OF CLIMATE CHANGE

Analysis of tree species' responses to climate warming at high elevation must consider factors other than species-specific sensitivity to temperature, such as changes in stand density and consequent competition for resources. Though many nonclimatic factors can influence tree seed germination, growth, and survival, tree species with the narrowest elevational ranges are likely to be most at risk in the face of warming.[22]

Some tree species will be more vulnerable, and some more resilient, to warming. Our calculations indicate that with an increase of 1°C, equivalent to 158 m of elevation, 35 percent of tree species would find themselves entirely outside their preferred temperature window. With increases of 2° or 3°C, 58 percent or 70 percent of tree species, respectively, would be left outside their present range.

But how much warming is likely to happen? Current estimates are that Earth has warmed about 1°C (1.8°F) since the Industrial Revolution, by an average of 0.8°C (0.14°F) per decade since 1880; the rate of warming since 1981 is more than twice as fast: 0.18°C (0.32°F) per decade.[23] Climate scientists now project actual temperature increases of 2° to 6°C over the coming decades; the wide range of these forecasts is partly due to uncertainty about the extent and effectiveness of human mitigation. In the absence of sustained, coordinated, and ambitious efforts, the loss of tropical tree diversity—including species as yet unknown to science[24]—is likely to be nothing short of catastrophic. By some estimates, approximately 9,200 species of trees remain undiscovered, of 73,300 total species. The vast majority of these as-yet-undiscovered trees are likely to be in the tropics. Some of these missing species might well lie along the Barva transect.

CALL TO ACTION: TRIAGE, ASSISTED MIGRATION, AND RESCUE

Our PLOTS team proposes a program of "assisted migration" of targeted, at-risk tree species, relocating seeds and seedlings of species to sites higher on the gradient with cooler, more favorable temperatures. To efficiently maximize the number and diversity of species rescued, soil would also be moved and planted, with its intact seed banks and associated mycorrhizae.

Development of triage strategies to identify and target the most suitable species for rescue requires data on preferred elevation, elevational range, habitat preference, population density, rates of recruitment, growth behavior, and longevity—information that has been collated as part of the PLOTS project over the decades.

The focus of the project through its first fifty years has been the collection, analysis, publication, and archiving of data on tropical forest trees. It is now time for action: to capitalize on this wealth of information in real-world applications, and to plan and implement, as expeditiously as possible, the rescue of the most vulnerable tropical tree species and the biodiversity these forests represent. It's time for our understanding of these tropical forests to be repurposed for creating a roadmap to their rescue.

Our PLOTS program will, without a doubt, outlive us, a fraction of the full team of investigators. The future of the project should be calibrated in terms of the lifespan of tropical trees, not the lifespan of scientists or the timespan of a single forest inventory.

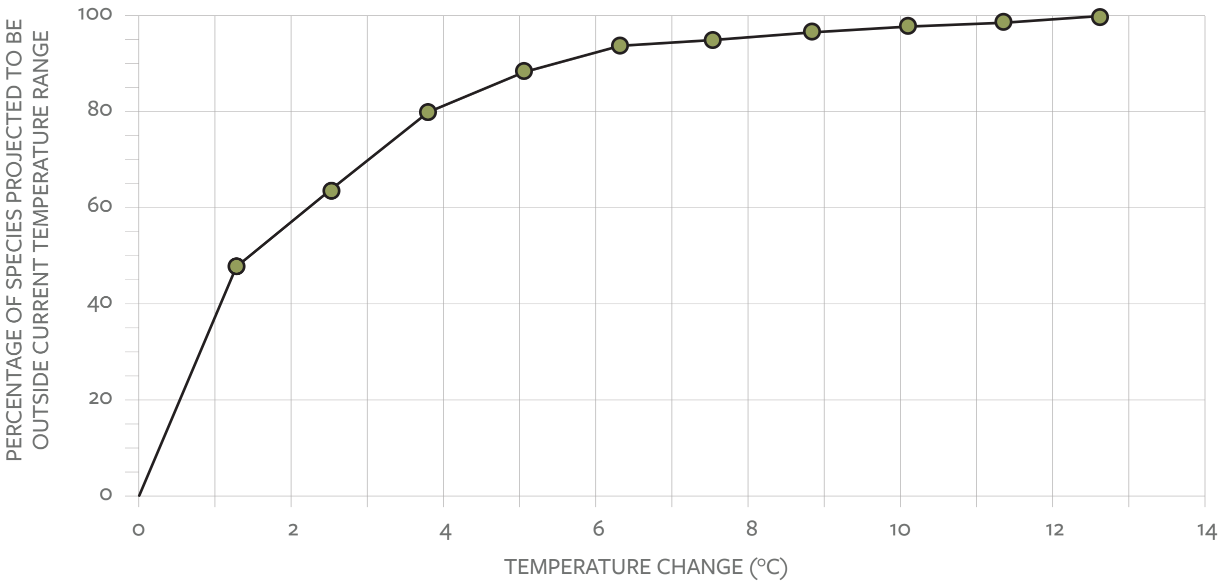
In 1969, no one knew how vital tropical forests would become to the future of the planet, nor could anyone anticipate the urgent ecological challenges that the PLOTS project is now helping to remedy. As inventory work and assisted migration efforts continue, the results of this project should be magnified. One legacy of the PLOTS project will be the application of new knowledge for the benefit of our species and the rescue and repair of our planet in ways that cannot be known as of this time.

Gary Hartshorn is past president of the World Forestry Center, Portland, Oregon, and former executive director of the Organization for Tropical Studies. During his long and distinguished career in tropical forestry research, he has held leadership positions with the World Wildlife Fund and the Institute of Current World Affairs, published more than 250 scientific papers and technical reports, and worked on the ground in the forests of 35 countries. Diana Lieberman and Milton Lieberman have worked together as tropical biologists and educators for the past 55 years. Their publications range from tropical forest ecology to subtidal marine biology, seed dispersal by baboons and elephants, and the vegetation of sacred groves. They have held faculty positions at the University of Ghana, University of North Dakota and University of Georgia; their current academic affiliation is with California State University, Monterey Bay. In recognition of their conservation work, they were named "Guardaparques de Honor" by the Costa Rican government. The Liebermans' small coffee farm in the mountains of Costa Rica remains the epicenter for data management, analysis, and preparation of manuscripts for the PLOTS project.

ACKNOWLEDGMENTS

We are immensely grateful to the colleagues, technicians, and field assistants who have contributed so much to this project over the years. Access to the study sites and logistical support have been generously provided by the Organization for Tropical Studies and the Costa Rican National Park Service. The PLOTS project has received grant support from the National Science Foundation (BSR-8117507, BSR-8414968, EHR-9108770), NASA (NAGW-1033), the National Geographic Society, the Andrew W. Mellon Foundation, and the University of North Dakota; we are especially grateful for the continuing interest of the Organization for Tropical Studies, through which a fundraising campaign has been launched to rescue and maintain these vital and beautiful tropical forests.

FIGURE 3. **Estimated percentage of tree species outside their normal temperature range, by level of global warming.**



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This estimate is based on the frequency distribution of elevational breadth of tree species (Figure 2), together with the temperature equivalent of that range for the Barva gradient. With an increase of 1°C, equivalent to a shift of 158 m of elevation, 35% of the tree species would find themselves entirely outside their temperature tolerance. With an increase of 2°C, 58% of tree species would be left outside their present temperature range. Current climate models predict a likely increase of 2° to 6°C in the coming decades.

NOTES

1. Christina Carrero et al., "Data Sharing for Conservation: A Standardized Checklist of US Native Tree Species and Threat Assessments to Prioritize and Coordinate Action," *Plants, People, Planet* 5 (2023): 600–16. The checklist of trees native to the contiguous United States can be accessed at https://mortonarb.org/science/projects/data-sharing-for-conservation-us-trees.
2. Milton Lieberman et al., "Small-Scale Altitudinal Variation in Lowland Wet Tropical Forest Vegetation," *Journal of Ecology* 73 (1985): 505–16. Tree species composition (269 species in 12.4 ha) varies continuously with elevation at a small scale, over a range of just 39 m. Stands on seasonally flooded sites differ in diversity and composition from those on higher ground. Milton Lieberman and Diana Lieberman, "Patterns of Density and Dispersion of Forest Trees," in *La Selva: Ecology and Natural History of a Neotropical Rainforest*, ed. Lucinda A. McDade et al. (Chicago: University of Chicago Press, 1994), 106–19. Analysis of spatial patterns of 104 populations belonging to sixty-five tree species found that 83 percent of the populations surveyed (representing fifty-nine species) were randomly dispersed, 5 percent (representing two species) showed a hyperdispersed pattern, and 13 percent (representing thirteen species) were clumped. Milton Lieberman and Diana Lieberman, "Nearest-Neighbor Tree Species Combinations in Tropical Forest: The Role of Chance and Some Consequences of High Diversity," *Oikos* 116 (2007): 377–86. The frequency of nearest-neighbor species pairs was analyzed for 5,060 trees in the La Selva plots; the overwhelming majority of pairs were found to occur at frequencies predicted from their individual abundances, as expected from a random-mixing probability model.
3. Gary Hartshorn, "A Matrix Model of Tree Population Dynamics," in *Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research*, ed. F. Golley and E. Medina (New York: Springer-Verlag, 1975), 41–51. Population modeling of *Pentaclethra macroloba* (Mimosaceae), a dominant canopy species in the La Selva plots, was done using estimates of mortality, recruitment, and growth. Diana Lieberman et al., "Mortality Patterns and Stand Turnover Rates in Wet Tropical Forest in Costa Rica," *Journal of Ecology* 73 (1985): 915–24. Mortality was 2.03 percent per year; stand half-life, based on stem mortality, was thirty-four years. Mortality risk was independent of size for individuals ≥ 10 cm dbh. Of the dead individuals, 31 percent had fallen, 26 percent had died standing, 7 percent were buried under treefalls, and 37 percent had decomposed entirely in thirteen years, leaving no trace. Diana Lieberman et al., "Forest Dynamics at La Selva Biological Station, 1969–1985," in *Four Neotropical Rainforests*, ed. A. H. Gentry (New Haven, CT: Yale University Press, 1990), 509–21. Mortality was approximately balanced by recruitment over a sixteen-year period, based on stem density, basal area, and biomass.
4. Gary Hartshorn, "Tree Falls and Tropical Forest Dynamics," in *Tropical Trees as Living Systems*, ed. P. B. Tomlinson and M. Zimmermann (New York: Cambridge University Press, 1978), 617–38. In the La Selva plots, the rate of new gap formation ranges from 0.74 percent to 1.26 percent of the plot area per year. Stand turnover, based on rates of canopy gap formation, is estimated at 80–135 years. Diana Lieberman et al., "Mortality and Stand Turnover," 915–24.
5. Gary Hartshorn, "Neotropical Forest Dynamics," *Biotropica* 12 (Suppl.) (1980): 23–30. Of 320 tree species in La Selva, 155 (48 percent) are classified as shade intolerant and depend on some form of canopy opening for regeneration. The proportion varies by stature: shade intolerance is seen in 63 percent of canopy species, 43 percent of subcanopy species, and only 38 percent of understory species. Very few of the shade-intolerant species require large gaps. Robert L. Sanford Jr., H. Elizabeth Braker, and Gary S. Hartshorn, "Canopy Openings in a Primary Neotropical Lowland Forest," *Journal of Tropical Ecology* 2 (1986): 277–82. Canopy gaps, caused by tree falls and branch falls, are numerous in primary forest; gap size at La Selva ranged from 40 to 781 m^2 (median size, 110 m^2); most gaps are rather small. Milton Lieberman et al., "Canopy Closure and the Distribution of Tropical Forest Trees at La Selva, Costa Rica," *Journal of Tropical Ecology* 11 (1995): 161–77. Canopy closure was estimated above the crowns of 3,224 trees ≥10 cm dbh in 104 species; 90 species (86.5 percent of the assemblage) were distributed at random with respect to canopy closure, 9 occurred in more open conditions than expected by chance, and 5 were found in shadier conditions than expected by chance. As adults, the great majority of tree species behave as generalists.
6. Diana Lieberman et al., "Growth Rates and Age-Size Relationships of Tropical Wet Forest Trees in Costa Rica," *Journal of Tropical Ecology* 1 (1985): 97–109. Median diameter growth rates ranged from 0.35 to 13.41 mm per year. Maximum rates ranged from 0.95 to 14.62 mm per year. Projected lifespan ranged from 52 to 442 years. Mean longevity among the forty-five tree species studied is 190 years. Diana Lieberman and Milton Lieberman, "Forest Tree Growth and Dynamics at La Selva, Costa Rica (1969–1982)," *Journal of Tropical Ecology* 3 (1987): 347–58. Diameter growth behavior varies widely among tree species. Understory species grow slowly and consistently and have short lifespans; subcanopy trees grow slowly but live longer; shade-tolerant canopy species show variable and often rapid growth and are long-lived; and shade-intolerant canopy trees grow rapidly, show little variation, and have short lifespans.
7. Gary S. Hartshorn et al., "Long-Term Dynamics of Tropical Rain Forests in Permanent Inventory Plots, La Selva, Costa Rica (1969–1995), ver. 3," Environmental Data Initiative (2022). https://doi.org/10.6073/pasta/240bf29397facc19984740ee113ab2ed.
8. Leslie R. Holdridge et al., *Forest Environments in Tropical Life Zones: A Pilot Study* (New York: Pergamon, 1971), 6–15. For a description of the Holdridge life zone system, see Gary Hartshorn and Rodolfo Peralta, "Preliminary Description of Primary Forests along the La Selva–Volcan Barva Altitudinal Transect, Costa Rica," in *Tropical Forests: Diversity and Conservation*, ed. F. Almeda and C. M. Pringle (San Francisco: California Academy of Science, 1988), 281–95.
9. Colin Norman, "Virgin Rain Forest Reprieved," *Science* 227 (1985): 273.
10. Keith Hamylton Jones, ed., *Operation Raleigh: Expedition to Costa Rica, 15 February–13 May 1985* (London: Operation Raleigh, 1985): 21–23.
11. Angela Heaney and John Proctor, "Preliminary Studies on Forest Structure and Floristics on Volcán Barva, Costa Rica," *Journal of Tropical Ecology* 6 (1990): 307–20. Information for the first six plots included physiography, forest stature, species richness and composition, and profile diagrams. Rainfall was highest in midslope, at 1,000 m elevation, with 510 cm (204 inches) per year.
12. A review of initial results showed little overlap in species composition among the first six plots, which were located at intervals of around 500 m elevation. Additional plots were therefore established at elevations intermediate to the existing plots, improving coverage and representation of the forest communities on the gradient.
13. Diana Lieberman et al., "Tropical Forest Structure and Composition on a Large-Scale Altitudinal Gradient in Costa Rica," *Journal of Ecology* 84 (1996): 137–52. The 1988–89 inventory of 14 plots from 30 to 2,600 m elevation included 561 tree species in 91 families. Species composition varied continuously with elevation; there was no evidence of floristic zonation. Canopy height ranged from 24 to 47 m, maximum dbh from 67 to 185 cm, density from 425 to 654 stems per ha, basal area from 23 to 43 m2 per ha, and species richness from 29 to 149 species per ha. Diversity and canopy height were greatest

in the foothills, at 300 m, and lowest at the summit, at 2,600 m.

14. Kristina A. Schierenbeck et al., “Population Structure and Genetic Diversity in Four Tropical Tree Species in Costa Rica,” *Molecular Ecology* 6 (1996): 137–44. High genetic variability and low genetic differentiation observed in these species over distances of 1–9 km on the slope of Volcán Barva reflect the effectiveness of pollen and seed dispersal. The populations across multiple plots are essentially panmictic. Genetic diversity is not affected by population density. Lieberman et al., “Tropical Forest Structure,” 137–52.
15. There is a close linear correspondence between elevation and mean temperature, such that one can be substituted for the other. The moist adiabatic lapse rate of temperature on the slope of Volcán Barva is 6.3°C per 1,000 m of elevation (1986 data). The mean daytime temperature at 35 m above sea level is 27.1°C, and at 2,600 m is 10.9°C; the difference is 16.2° over 2,565 m, or 6.3° per 1,000 m.
16. Humboldt’s contributions are reviewed by Jorge Antonio Gómez-Diaz et al., “Humboldt’s Legacy: Explaining the Influence of Environmental Factors on the Taxonomic and Phylogenetic Diversity of Angiosperms Along a Neotropical Elevational Gradient,” *Annals of Botany Plants* 15 (2022): 1–11.
17. Elevational breadth of a species is defined as the difference between the highest and lowest plot in which it is found, independent of the elevation itself; for example, a species with an elevational breadth of 250 m might occur on the lower slope between 500 and 750 m but might also be found higher on the gradient between 1,750 and 2,000 m.
18. Lieberman et al., “Forest Dynamics 1969–1985,” 509–21; Lieberman et al., “Growth Rates and Age-Size Relationships,” 97–109; and Lieberman and Lieberman, “Growth and Dynamics (1969–1982),” 347–58.
19. Lieberman et al., “Tropical Forest Structure,” 137–52.
20. Daniel H. Janzen, “Why Mountain Passes Are Higher in the Tropics,” *American Naturalist* 101 (1967): 233–49. Unlike temperate zones, tropical climates show little seasonality with respect to temperature. Tropical species are thus normally exposed to, and likely to be adapted to, a much narrower range of temperatures than those living in the temperate regions.
21. Based on the lapse rate (6.3°C per 1,000 m elevation), the mean temperature on Volcán Barva decreases 1°C with every 158 m in elevation. A simple, preliminary prediction regarding one consequence of global warming is that the optimum elevation—representing the temperature “sweet spot”—for a given tree species on the Barva slope would be shifted or displaced upslope by 158 m for every 1°C increase in mean temperature.
22. Walter Oberhuber et al., “Growth Trends of Coniferous Species along Elevational Transects in the Central European Alps Indicate Decreasing Sensitivity to Climate Warming,” *Forests* 11 (2020): 132, https://www.mdpi.com/1999-4907/11/2/132. Analysis of tree species’ responses to climate warming at high elevation must consider factors other than species-specific sensitivity to temperature, such as changes in stand density and consequent competition for resources.
23. Rebecca Lindsey and Luann Dahlman, “Climate Change: Global Temperature” (2023), https://www.climate.gov/news-features/understanding-climate/climate-change-global-temperature. Earth’s temperature has risen by an average of 0.8°C (0.14°F) per decade since 1880; the rate of warming since 1981 is more than twice as fast: 0.18°C (0.32°F) per decade.
24. By some estimates, approximately 9,200 species of trees remain undiscovered and unknown to science, of 73,300 total species. The vast majority of these as-yet-undiscovered trees are likely to be in the tropics. Some of these missing species might well lie along the Barva transect. Estimates of global tree species richness from Roberto Cazzolla Gatti et al., “The Number of Tree Species on Earth,” *Proceedings of the National Academy of Sciences U.S.A.* 119 (2022), https://doi.org/10.1073/pnas.2115329119.