Chapter 5
The Luquillo Experimental Forest: A Neotropical Example of the Interaction Between Forest Conservation and Long-Term Ecological Research

Ariel E. Lugo

Abstract The origins of the Luquillo Long Term Ecological Research Program are traced through four historical trends that still influence research activity in Puerto Rico's Luquillo Mountains: (1) A history of identifying lands for protection and their designation for public uses; (2) A history of governmental and non-governmental institutions acting with the foresight to pursue scientific research for the benefit of economic development and the will to support scientific activity; (3) The uninterrupted progression of scientific activity through projects and programs that cumulatively developed a knowledge base that supported succeeding projects and programs; (4) The excellence of the individual scientific talent that participated in research in this location over the last 200 years. These historical trends took place within the context of four time intervals: (1) Discovery and colonization of Puerto Rico (1493 to 1898); (2) The negotiation of the Paris Treaty in 1898, which transferred Puerto Rico to the United States of America and led to the Scientific Survey of Puerto Rico (1913 to 1957); (3) Development of tropical forestry and ecosystem-level research through the establishment of the USDA Forest Service Tropical Forest Experiment Station in 1939 and the funding of radio-ecological and ecological research by the Atomic Energy Commission and the Department of Energy from 1963 to 1988 (1939 to 1988); (4) Funding of multiple research programs, including the Luquillo LTER, by the National Science Foundation (1989 to the present). This history demonstrates how advancing scientific understanding of tropical ecosystems benefited science, society, and the conservation of Neotropical natural resources.

Keywords LTER program · Long-term ecological research · Disturbance ecology · Tropical ecology · Radiation ecology · USDA Forest Service · Social-ecological research · Puerto Rico · International Institute of Tropical Forestry

A. E. Lugo (✉)
International Institute of Tropical Forestry, USDA Forest Service, Río Piedras, Puerto Rico
e-mail: ariel.lugo@usda.gov

R. B. Waide, S. E. Kingsland (eds.), *The Challenges of Long Term Ecological Research: A Historical Analysis*, Archimedes 59,
https://doi.org/10.1007/978-3-030-66933-1_5

5.1 Introduction

In this essay, I explore the historical roots of the Luquillo Experimental Forest Long -Term Ecological Research Program (LUQ LTER) to illustrate a successful example of the integration of local ecological research and the conservation[1] of a complex Neotropical forest. The historical roots of the LUQ LTER are as many and as intertwined as are the roots of tabonuco (*Dacryodes excelsa*) tree unions in the Luquillo Mountains (Fig. 4.6 in Lugo and Scatena 1995). These historical roots connect the Luquillo Mountains and the LUQ LTER to the early human inhabitants of Puerto Rico,[2] Spanish conquistadors, early natural history research scientists, the emergence of radiation ecology and ecosystem-level ecology in the tropics, the integration of the subfields of population and community ecology, and the systematization of long-term ecological research. Moreover, the roots of the LUQ LTER are solidly connected with the emergence of the New York Botanical Garden as a premier scientific organization in the United States of America, with the origins of the United States Department of Agriculture (USDA) Forest Service, and even the early history of the Ecological Society of America. Much of this institution building activity early in the twentieth century occurred simultaneously with the development of the field of modern ecology (Golley 1993; Kingsland 2005). Those involved in the new research and conservation organizations and emerging scientific fields of study accumulated a knowledge base upon which LUQ LTER scientists could develop new paradigms about tropical forest resilience and restoration management (Lugo et al. 2012; Brokaw et al. 2012a).

None of the rich history of ecological research and conservation in the Luquillo Mountains would have been possible without the talent and collaboration of pioneering educators at the University of Puerto Rico, and the support of the colonial government of Puerto Rico and its legislature. The key players in this history were Nathaniel Lord Britton and his wife Elizabeth Gertrude Britton, Raphael Zon, Carlos Eugenio Chardón Palacios, Howard Thomas Odum, and Frank H. Wadsworth. These main actors were associated with a distinguished and substantial cast of supporters that included Gifford Pinchot, Henry Allan Gleason, the Vanderbilt family, Eugene P. Odum, José Marrero, Leslie R. Holdridge, and many others. Key institutions in this history include the New York Botanical Garden, the University of Puerto Rico, the USDA Forest Service, the government of Puerto Rico and its legislature, and the US Atomic Energy Commission. The roles that these actors and organizations played in the history of the LUQ LTER will become evident in the narrative that follows.

---

[1] I use 'conservation' and 'management' interchangeably, as both concepts involve notions of 'use' and 'preservation' based on scientific information (Lugo 1989).

[2] For several decades after the United States of America invaded Puerto Rico, the island was identified as Porto Rico. I use Puerto Rico throughout, except when citing official documents or publications.

5.2 Legacies Before the *Scientific Survey of Porto Rico and the Virgin Islands*

The Luquillo Mountains attracted the attention of humans for millennia. The Taínos considered the mountains a "sacred and spiritual landscape" (Walker 2014, p. 26) and the inspiration for their *cemi*, which portrays the mountains in the form of an animal (Walker 2014, p. 18). The earliest date given by Wadsworth (1970) for the exploration of the Luquillo Mountains was 1513, when Diego Columbus began searching for gold. Spanish conquistadors harvested tropical timbers and contributed to the deforestation of the island during the eighteenth and nineteenth centuries. They mined the Mameyes River in the Luquillo Mountains during the first half of the nineteenth century. Formal management on these mountains began as a result of forest policies originating in Spain and applied to the Caribbean during the second half of the nineteenth century (Domínguez Cristóbal 2000). In 1876 King Alphonse XII of Spain promulgated *La Ley de Montes*, a law that established forest management on all Spanish colonies in the Caribbean (Domínguez Cristóbal 2000). At this time not only was the *Inspección de Montes de Puerto Rico* (Puerto Rico's Forest Service) established, but also portions of the Luquillo Mountains where the LUQ LTER was to be established were designated as a reserve dedicated to the conservation of its timbers and waters. Professional foresters trained in Spain were assigned the conservation of the reserve, and the inventory of forests began (Domínguez Cristóbal 2000).

While all this forestry activity was brewing on the island, the transfer of Puerto Rico from the Spanish empire to the emergent American empire was imminent, the result of the Paris Treaty of December 10, 1898 between the United States of America and the government of Spain. On the mainland United States, New York City in particular, a group of influential botanists were working to establish a research organization in the city (Mickulas 2007). The group was led by a husband-wife team (Nathaniel and Elizabeth Britton) that later became the first scientific partnership to conduct research in the Luquillo Mountains. However, before the dawn of the twentieth century, they were busy designing and establishing the New York Botanical Garden as a scientific organization meant to be the United States of America's version of the Royal Botanic Gardens at Kew, London, England (Kingsland 2005; Mickulas 2007). The New York Botanical Garden was incorporated in 1891 and in 1896 began operations. In 1898 and 1899, the Garden sent plant collectors to Puerto Rico, and they returned with 8000 specimens (Kingsland 2005). Amos Arthur Heller, who returned to Puerto Rico in 1900, and 1902 to 1903, led these collecting trips (Santiago Valentín 2005). Heller collected island-wide, including in the Luquillo Mountains.

At the turn of the twentieth century, Puerto Rico lacked self-government and the President of the United States of America appointed most of its government officials. All the activities in the island by the USDA Forest Service and its predecessor agencies and by Britton's Scientific Survey were performed with the knowledge and strong collaboration of the Insular Government and Legislature. An example of

local government influence on the federal government was through the relationship between Governor Rexford G. Tugwell and the President of the United States of America. The appointment of USDA Forest Service Chief Ferdinand Silcox benefitted from the friendship with Governor Tugwell, who recommended him to the President for the position (Tugwell 1947).

The American colonization of Puerto Rico led to a burst of scientific activity, including the botanical collectors from the New York Botanical Garden, and botanical and zoological collectors from Puerto Rico and Europe. The identity and contributions of these collectors and natural historians are itemized by Wadsworth (1970), and in every one of the 19 volumes of the *Scientific Survey of Porto Rico and the Virgin Islands*. The United States of America Fisheries Commission sponsored the first organized scientific exploration of the Luquillo Mountains. They sent the steamer *Fish Hawk* to Puerto Rico to study the aquatic resources of the island. The steamer sailed the same month that the Paris Treaty was signed (December 1898), arrived in San Juan on January 2, 1899, and remained in Puerto Rico until late February 1899. This ship spent 52 days circumnavigating the island and adjacent cays and 38 days of actual fieldwork while visiting all available ports (Evermann 1899). They produced detailed maps of the San Juan and Guánica Bays, studied the mollusks of the island, produced beautiful color plates of fish species, and visited with island naturalist and physician Agustín Stahl in Bayamón. Stahl was the island's first internationally known scientist and the first to write an insular flora (Santiago Valentín et al. 2015).

The *Fish Hawk* expedition also surveyed fisherman and described in some detail the fisheries industry of Puerto Rico, including the techniques used for fishing. Among the inland sites they visited, was El Yunque (the Luquillo Mountains), thought to be the tallest mountain in Puerto Rico. There, they studied what they identified as the Luquillo River, which I surmise was the Mameyes River, and described the pool and ripple habitats and the shrimp that the LUQ LTER has studied continuously since 1988 (Crowl et al. 2012).

Robert T. Hill, an employee of the United States Geological Survey, spent a month in Puerto Rico to examine the forest conditions of the island (Hill 1899), including those of the Luquillo Mountains. He also arrived in January 1899, but probably after the arrival of the *Fish Hawk*. Gifford Pinchot transmitted Hill's report to the Secretary of Agriculture to be published as a Bulletin of the Forestry Division that he headed. As a geologist, Hill noticed the importance of soils and geological formations to the flora of the island, and described problems of erosion and deforestation. In 1905, John C. Gifford, working as a consultant for the USDA Bureau of Forestry (previously known as the Forestry Division), visited the Luquillo Mountains for the purpose of studying the forestry situation of the island and making forest management recommendations. His nine recommendations represent positive steps towards professional conservation of forestlands in Puerto Rico, the Virgin Islands, and the Luquillo Mountains (Gifford 1905).

The University of Puerto Rico was established in 1903, and in 1908 became a land grant college, which allowed for the establishment of the College of Agriculture in Mayagüez in 1911. Both campuses were engaged with the Scientific Survey of

Britton. Several stations of the Universities' Agriculture Experiment Station were strong collaborators of the Scientific Survey. The Río Piedras Station in particular supported the ecological survey by Henry A. Gleason and provided support to Mel T. Cook, the co-author of the ecological study. Early in the twentieth century the University of Puerto Rico hosted offices and nurseries of the Puerto Rico Forest Service and the USDA Forest Service from which reforestation programs were managed. Today, the USDA Forest Service International Institute of Tropical Forestry is located on the grounds of the Agriculture Experiment Station of Río Piedras.

Between November 1911 and May 1912, Louis S. Murphy (1916), Forest Examiner of the USDA Forest Service (previously known as the Bureau of Forestry), studied the forestry problems of Puerto Rico under an agreement between the USDA and the governor and Board of Commissioners of Agriculture of Puerto Rico. His report asked for an expansion of the authority of the Commissioners of Agriculture so that the management of forests and the establishment of an Insular Forest Service be delegated to them.[3]

Around the same time in Washington, D.C., Raphael Zon was leading the Office of Special Investigations in Forest Economics of the USDA Forest Service. Zon had left his native Russia in 1896, and after studying for two years in Belgium and England he emigrated to the USDA in 1898, coincident with the acquisition of Puerto Rico by the United States (Rudolf 1957). After completing a degree in forestry at Cornell University in 1901, he joined Gifford Pinchot's Bureau of Forestry (later the USDA Forest Service) in the U. S. Department of Agriculture. He was among those who established the *Journal of Forestry* and served as its editor-in-chief for six years. Zon was Chief of the Office of Silvics (1907), led the Office of Special Investigations in Forest Economics (1920) and was Director of the Lakes States Forest Experiment Station in St. Paul, Minnesota (1923). He was the right hand of Gifford Pinchot at the USDA Forest Service, and was responsible for recommending the establishment of the Forest Research Experiment Stations and Experimental Forests and Ranges, which Pinchot approved on May 6, 1908. The Luquillo LTER would later benefit from both designations.

Zon collaborated with William N. Sparhawk, Senior Forest Economist of the USDA Forest Service, in the compilation of the first global report of the status of forests, including those of Puerto Rico (Zon and Sparhawk 1923). This publication summarized available information about the forests of the island and was foundational for developing local forestry policy. All these events resulted in the establishment of a strong coalition between federal and state governments, including the University of Puerto Rico. This coalition has remained strong into the present in its support of the LUQ LTER.

Britton played a dual role in Puerto Rico. On the one hand, he directed and played a scientific role in the *Scientific Survey of Porto Rico and the Virgin Islands*

[3] By this time, the Puerto Rico Forest Service established by the Spanish Government was no longer operating. In 1917, the Puerto Rico Legislature established the current Puerto Rico Forest Service.

(from now on Scientific Survey), and on the other hand he promoted forestry, conservation, and education in Puerto Rico, taking advantage of his position and opportunities to express his opinions to the public. Britton's proposals (discussed in more detail below) for conserving forest cover in Puerto Rico, increasing the area of protected lands, expanding research activity, and incorporating professional forest management practices were a synthesis of all the knowledge and practices that had accumulated by the procession of technical visitors and interventions since the Spanish era, augmented by excursions by professionals affiliated with the US Government and American universities and institutions (Britton 1919a). This wealth of information was about to be greatly multiplied by the Scientific Survey and together formed one part of the technical basis upon which the LUQ LTER was conceived and eventually established. The other part includes the studies that took place after the Scientific Survey. Both parts of the technical roots of the LUQ LTER are discussed next.

5.3 The *Scientific Survey of Porto Rico and the Virgin Islands*

History and Scientific Content of the Survey On the evening of November 19, 1912, the Executive Council of the New York Academy of Sciences received a proposal from Britton to conduct a Scientific Survey of Puerto Rico (Baatz 1996). The Survey was designed to contribute to the economic development of Puerto Rico in terms of forestry, agriculture, and mineral exploration (Fig. 5.1) The *Scientific Survey of Porto Rico and the Virgin Islands* was a seminal research program of the New York Botanical Garden, as it gained a national and international reputation in the sciences. Top scientific talent from the New York Botanical Garden and other American institutions participated in the Scientific Survey.

To the promise of this science-based development, the Puerto Rico legislature contributed funding and in-kind support such as security by the Insular Police, and staff and facilities from the University of Puerto Rico, including its Agriculture Experiment Station (Britton 1930). Examples of participating Agriculture Experiment Station staff included Mel T. Cook on the ecology of the island and Carlos Eugenio Chardón Palacios on the fungi.

Chardón was born in Ponce and educated in Ponce, Mayagüez, and Cornell University. He is considered the first Puerto Rican mycologist, and began his career at the Agriculture Experiment Station in Río Piedras. He was the appointed Commissioner of Agriculture and Labor of Puerto Rico between 1923 and 1931. In 1931, Governor of Puerto Rico, Theodore Roosevelt III, appointed Chardón Chancellor of the University of Puerto Rico. His Plan Chardón resulted in the establishment of the Puerto Rico Reconstruction Administration, which he headed. This organization was a critical contributor to the training and development of agricultural technicians and the construction of conservation infrastructure in public forest reserves, including the Luquillo National Forest. After a period of time in exile from

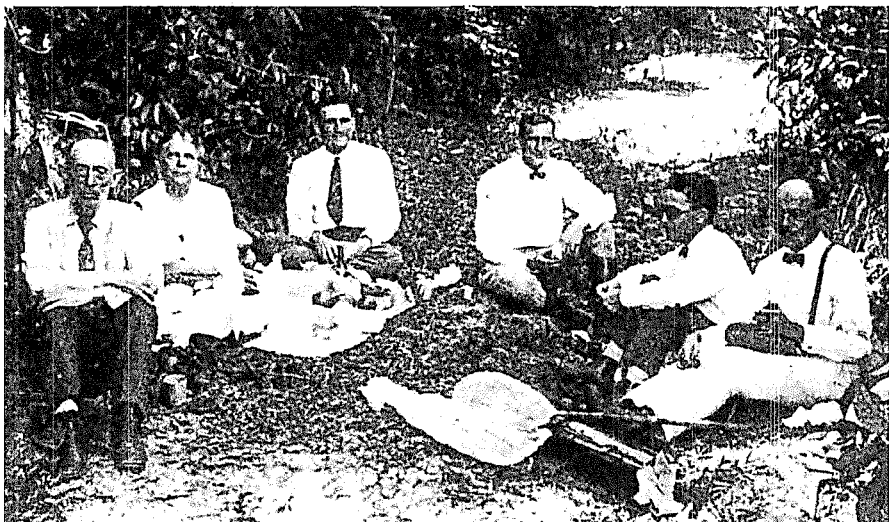

Fig. 5.1 Scientists having lunch on the Guaynabo road leading to the San Juan Aqueduct early in 1924. Left to right: Nathaniel and Elizabeth Britton, Carlos Chardón (Agriculture Commissioner), W. P. Kramer (Puerto Rico Forest Service and Supervisor of the Luquillo National Forest), E. E. Dale and John S. Dexter (professors at the University of Puerto Rico). (From Kramer 1924)

Puerto Rico, he returned to direct the Puerto Rico Land Authority (1940) and the Tropical Agricultural Institute in Mayagüez (1942). His partnership with Britton began while he was a scientist at the Agriculture Experiment Station, and continued through his career as Commissioner of Agriculture and Labor and Chancellor of the University of Puerto Rico.

Chardón used his influence to secure funding for the Scientific Survey from the legislature of Puerto Rico (Baatz 1996). Among the original group of collaborators of the Scientific Survey (a list that was augmented dramatically over the subsequent decades) were the federal and insular Agriculture Experiment Stations, the American Museum of Natural History, the New York Botanical Garden, scientific departments of Columbia University, and the government of Puerto Rico.

The Scientific Survey covered all groups of plants and animals including algae, as well as the paleontology, meteorology, archeology, botany, plant ecology, and geology of the island. Among the prominent scientists that contributed to the Scientific Survey were Howard Augustus Meyerhoff (geologist), Arthur Hollick (paleobotanist), Harold Elmer Anthony (mammalogist), Alexander Wetmore (ornithologist), Percy Wilson (botanist), Karl Patterson Schmidt (herpetologist), John Treadwell Nichols (ichthyologist), John Alden Mason (archaeological anthropologist), Fred J. Seavers (mycologist), and many others. Elizabeth Britton also participated in the Scientific Survey. Crum and Steere (1957) recognized her collections of mosses in Puerto Rico as the largest in existence at the New York Botanical Garden. Scientists of the Scientific Survey developed tools such as geologic maps, and maps of suggested geographic locations for ports, mineral explorations, and natural

resources assessments, to name a few. The results of the Scientific Survey are published in a 19-volume publication series (each with up to four parts) of the New York Academy of Sciences.

The Scientific Survey and the USDA Forest Service When Britton was elected to the National Academy of Sciences in 1917, his inaugural speech was on the subject of Forestry in Puerto Rico. For that speech, he developed a proposed forest management policy for the island, a proposal that he sent to the governor of Puerto Rico. At the time, Emory Murray Bruner, who was the Forest Supervisor of the USDA Forest Service Luquillo Forest Reserve, also led the Puerto Rico Forest Service as Chief Forester. The incumbent USDA Forest Service Forest Supervisor supervised the activities in both insular and federal forests (Wadsworth 2014). Britton's proposal was successful, and from then on, he worked closely with Bruner and those who followed him.[4] Britton also provided botanical advice to USDA Forest Service employees in Puerto Rico.

Britton used his influence with Gifford Pinchot, USDA Chief Forester, to support the designation of the Luquillo Forest Reserve as the Luquillo National Forest in 1907. Britton and Pinchot had known each other for many years, and both had strong ambitions to develop botany as a science and to develop educational institutions that would provide training for future botanists. In the early twentieth century, Britton and Pinchot were part of an elite group of scientific leaders who not only advocated for the expansion of American science, but with their personal wealth and connections were in a position to see their ambitious visions realized. As the New York Botanical Garden opened its doors in 1900, Pinchot was busy helping to establish, with his family's financial support, a school of forestry at Yale University. When the Carnegie Institution of Washington was founded in late 1901, it turned to Britton and Pinchot for advice on how it should develop its own programs in botanical research. During President Theodore Roosevelt's administration, Pinchot established the Forest Service in 1905, served as the first USDA Chief Forester until 1910, and became known as a prominent conservationist and advocate of scientific management of forests (Pinchot 1947).

The Luquillo National Forest was renamed Caribbean National Forest in 1935 and El Yunque National Forest in 2007. Since the pioneering work of Zon at the turn of the twentieth century, the USDA Forest Service supported the close relationship between science and conservation. In 1956, the USDA Forest Service proclaimed the totality of the Caribbean National Forest in Puerto Rico as an Experimental Forest, recognizing that management activities in such a complex environment by necessity are experiments that require a research approach. For the next 18 years starting in 1955, Wadsworth, Director of the Institute of Tropical Forestry, led both the management and research programs of the USDA Forest Service in Puerto Rico. Today, El Yunque National Forest still has the same boundary as the Luquillo

[4] William P. Kramer (1922–1931), Thomas R. Barbour (1931–1935), E. Worth Hadley (1935–1943), Arthur Upson (1943–1951), and Henry B Bosworth (19551–1953) followed Bruner over the next 36 years.

Experimental Forest (LEF), but the conservation of the forest is the dual responsibility of the management (National Forest System) and research (Research and Development) arms of the USDA Forest Service.

Britton also advocated for more protected lands on the central mountains of Puerto Rico (Mickulas 2007). In response to his advice, in 1924 the Puerto Rico government gave one of the first indications of official interest in forest conservation with the recommendation that trees in upper watersheds be protected (Little and Wadsworth 1964).

Henry A. Gleason and the Ecology of Puerto Rico In 1919, Britton announced the appointment of Henry Gleason as the first assistant to the Director in Chief of the New York Botanical Garden (Britton 1919b). Gleason obtained his PhD from Columbia University in 1906, based on research done at the New York Botanical Garden, which served as Columbia's botany department. Gleason gained fame as an ecologist for his plant succession work that led him to challenge the prevailing views of Frederic Clements (Clements 1928).

Clements had advanced the idea that plant communities developed toward a single climax community, with a distinctive and predictable species composition that ultimately depended on the climate. His conception of the plant community was that it was like a "complex organism", developing, as a single organism would, toward a given endpoint. Gleason, in a now-classic article published in 1926 called "The individualistic concept of the plant association," proposed to the contrary that species behaved individually, not as parts of a larger "complex organism." They arrived in a region individually, according to their tolerance of the environmental conditions, and assembled into communities composed of species. The pattern of assembly could occur in different ways, depending on local conditions, and as a result, he concluded, two regions that were similar in climate and physiography might have very different plant associations. Gleason defended his individualistic concept from an attack by George E. Nichols of Yale University (Egerton 2015) during a meeting of American ecologists attending the Fourth International Congress of Plant Sciences at Cornell University. A famous picture of attendants to that conference shows Zon and Gleason standing near each other. Eighty-seven years after Gleason's paper, scientists at the LUQ LTER were still debating the relative importance of Clementsian vs. Gleasonian patterns of community organization up the elevational gradient of the Luquillo Mountains (Willig et al. 2013).

The same year that Gleason published his individual species classic he also published *Plant Ecology of Porto Rico* (Gleason and Cook 1926). The collaborators for this work were the New York Botanical Garden, the University of Puerto Rico Agriculture Experiment Station, and the Puerto Rico Agriculture and Labor Department. Chardón, then Commissioner of Agriculture and Labor, Francisco López Domínguez, Director of the Insular Experiment Station, and Britton, Director of the New York Botanical Garden, provided leadership support. Clara Livingston, Puerto Rico's first female aviator and friend of Amelia Earhart, was among a large group of local cooperators of the study. William P. Kramer and Charles Z. Bates of the USDA Forest Service helped in the selection of sites to visit and provided

personal guidance to the authors. Fieldwork was from January 18 to April 30, 1926. Over 90 years later, Gleason and Cook's work remains the most comprehensive description of Puerto Rican native plant communities (Lugo 1996).

Mentoring and Collaboration as Keys to Scientific Success Britton used a mentoring process in which he paired continental and insular scientists in collaborative work that strengthened the insular institutions and augmented human scientific power for the Scientific Survey. An example is the visit of Fred Jay Seaver, a New York Botanical Garden mycologist and editor of the journal *Mycologia* between 1909 and 1947. At the suggestion of Britton in 1923, the government of Puerto Rico invited Seaver to visit the island and spend time exploring with Elizabeth and Nathaniel Britton. Simultaneously, Chardón, a Puerto Rican mycologist, was teamed with Seaver to write the definitive work on the fungi of Puerto Rico as part of the Scientific Survey (Seaver and Chardón 1926).

Collaboration was an asset that Britton modeled and which contributed to the development of science and forest conservation in Puerto Rico. This collaborative style was in display in his address at the Muñoz Rivera Park in San Juan on November 1929. The occasion was the planting of a *Stahlia monosperma* tree, an endemic tree named after Stahl, Puerto Rico's first natural scientist, who had died in 1917 (Britton 1930). In short three pages, Britton acknowledged Kramer, who in 1922 had replaced Bruner as Forest Supervisor and Chief Forester and had grown the tree from seed, reviewed the ecology of *Stahlia* and other native tree species, advised on the proper upkeep of the growing seedling, highlighted the work of Stahl, mentioned the previous planting of a mahogany tree in the Bayamón Plaza to also honor Stahl's work, acknowledged the work of Chardón, and used the occasion to review the problems of water and soil quality associated with island deforestation and the need for reforestation and a forestry policy. Britton also acknowledged the work of reforestation of the USDA Forest Service and asked that everyone collaborate with those efforts. Britton finally thanked and credited the insular governor for his support for reforestation.

Final Outcome of the Survey At the end of the Scientific Survey in the mid-1940s, Puerto Rico had available a solid base of scientific information and expertise to manage its natural resources and advance many scientific fields.[5] Puerto Rico was also notable as the Neotropical location with the most comprehensive foundational knowledge about its natural resources. Many decades later, the Scientific Survey continued to inspire as the island's scientists celebrated its 80th anniversary by updating knowledge of its various original topics (Figueroa Colón 1996). Studies following the Scientific Survey, such as those discussed below, were poised to use available scientific knowledge for more effective research because they did not have to develop basic information and could directly address pressing conservation and research issues.

[5]The last publication was dated 1957, but was part of volume 7.

5.4 Two Evolving Lines of Research: Tropical Forestry and Radio-Ecological Research

After the Scientific Survey, the historical path to the LUQ LTER bifurcated into two independent but interacting pathways: that of the USDA Forest Service and other federal agencies in Puerto Rico, and the establishment of radio-ecological research at the University of Puerto Rico's Nuclear Center. I will discuss these two paths independently.

5.4.1 USDA Forest Service Tropical Forest Experiment Station

In 1939, research activity in the Luquillo Mountains was formalized through the establishment of the USDA Forest Service Tropical Forest Experiment Station, a unit that was designated in 1955 as the Institute of Tropical Forestry, and in 1992 as the International Institute of Tropical Forestry (from now on the Institute). The Institute was established because land restoration efforts by the USDA Forest Service were failing throughout the island. Officials recognized that forestry knowledge based on temperate zone experience was not sufficient to address the ecological issues in the tropics, where scientific understanding of forests was insufficient (Wadsworth 1995). Over the next 50 years the Institute developed successful research, application, and dissemination programs in tree dendrology, wood products, tropical silviculture, and tree propagation. Institute scientists applied newly acquired knowledge in reforestation projects and tree plantation establishment. They screened hundreds of native and introduced tree species for suitability for planting, and developed demonstration projects on land rehabilitation under a variety of tropical climates and soils. In the absence of tropical forestry schools in the Neotropics, the Institute conducted many tropical forestry trainings with regional participation, helped organize forestry schools in several countries, and edited and published a regional journal (the *Caribbean Forester*) to disseminate research findings in support of forest conservation.

Since its establishment, the Institute has been a consistent collaborator with all significant scientific activity in the Luquillo Mountains. Its scientists have continuously participated in the international science arena, particularly in the Neotropics, where they have influenced tropical forestry activities as well as the development of knowledge in support of forest conservation. Leslie R. Holdridge was the first scientist of the Institute, but by 1931 he had already started research activity in the Luquillo Mountains. He initiated a tree dendrology project, conducted fieldwork, supervised part of the initial botanical work, and wrote two preliminary volumes of the trees of Puerto Rico. Holdridge later became known for his Life Zone System for the delimitation of world plant formations (Holdridge 1967), a system used by scientists of the LUQ LTER and countless others around the world to classify the climates of the world.

Frank Wadsworth (Fig. 5.2) was another Institute scientist. His USDA Forest Service career epitomizes the merging of forest research and forest management activities with the objective of advancing the conservation of a complex tropical forest. At the beginning of his Forest Service career in 1938, Wadsworth worked under Gustav Adolph Pearson, Chief Silvicultural Scientist at the Southwestern Forest and Range Experiment Station at Fort Valley, Arizona. Wadsworth was transferred to Puerto Rico when he married Pearson's daughter, Margaret "Peggy" Pearson, and they arrived on the freighter *S.S. Maiden Creek* in January 1942. Wadsworth was appointed to the Tropical Forest Experiment Station as a replacement for Leslie Holdridge, who was taking an assignment in Haiti. Wadsworth, a silviculturist, faced many forestry challenges in Puerto Rico, called "the stricken land" by governor Rexford G. Tugwell (1947). His six-decade career as a tropical forester is legendary and described from his own perspective in Wadsworth (2014).

During a field campaign, Wadsworth was the cabin mate of Elbert Luther Little, Jr. Little became the Leading and National Dendrologist of the USDA Forest Service and in the 1950s they teamed up to describe the trees of Puerto Rico. The

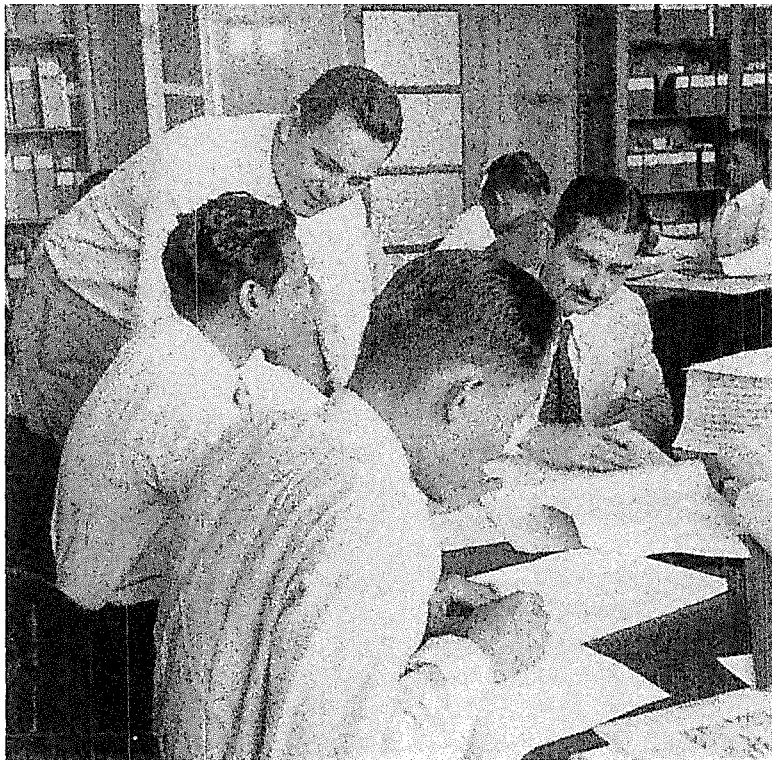

Fig. 5.2 Frank Wadsworth (standing) circa 1960s, teaching to an international tropical forestry course at the Institute of Tropical Forestry of the USDA Forest Service. (From the historical archives of the International Institute of Tropical Forestry, USDA Forest Service)

completion of *Common Trees of Puerto Rico and the Virgin Islands* (Little and Wadsworth 1964), took five years from 1950 to 1955. Before publication in 1964, the manuscript was translated to Spanish and revised slightly in 1962. One of their main sources of information was the flora of Puerto Rico that was published by the Scientific Survey (Britton and Wilson 1923–1930). The information gathered by the Scientific Survey was critical to the systematization of forestry and long-term ecological research in the region. In addition, the New York Botanical Garden and the United States National Museum collaborated, identifying species and sharing herbarium specimens. Other important collaborators were the Division of Forests, Fisheries, and Wildlife of the Puerto Rico Commonwealth, and the Agriculture Experiment Station of the University of Puerto Rico.

Marrero translated to Spanish the *Common Trees of Puerto Rico and the Virgin Islands* (Little et al. 1967), a project sponsored by the College of Agriculture and Mechanical Arts of the University of Puerto Rico and the University's Agriculture Experiment Station and Agriculture Extension Service. The volume was elegantly produced with the addition of the beautiful and botanically accurate watercolors of Mrs. Frances W. Horne. Mrs. Horne, wife of University of Puerto Rico at Mayagüez professor Charles E. Horne, attended field trips with Britton, learned to identify the plants, and used to accompany herbarium specimens sent to the New York Botanical Garden with her watercolors. Roy O. Woodbury, plant taxonomist at the Agriculture Experiment Station, became a co-author in the second volume of the *Trees of Puerto Rico and the Virgin Islands* (Little et al. 1974), which contained the tree species not included in the first volume by Little and Wadsworth (1964) and was published with a new title. Many individuals and institutions collaborated with the elaboration of the second volume of the work and are acknowledged in the book. These two volumes describe all tree species in the island (native and non-native) and provide information essential for the conservation of forests and tree species, information that was foundational for the LUQ LTER.

The publication of *Trees of Puerto Rico and the Virgin Islands* is a milestone of federal government activities in Puerto Rico. Other federal agencies in Puerto Rico added to the wealth of scientific materials that contribute to the conservation of all the island's natural resources. For example, the Soil Conservation Service (now Natural Resources Conservation Service) described the soils of the island (Roberts 1942); the US Geological Survey did the same with the geology and geomorphology by developing geological and topographical quadrangles at a scale of 1:250,000 for the whole island, and gauging rivers and aquifers island-wide; and the Weather Bureau (now the National Weather Service) did so with the climate (e.g., Colón Torres 2009).

A significant technical problem facing Wadsworth as he focused on tropical silviculture was dealing with tropical trees that did not produce annual tree growth rings, as they did in Arizona where he had started his professional career in forestry. Without the benefit of annual tree growth rings, it was impossible to determine the age of trees and their rates of growth. He understood that he needed repetitive measurement of tree allometry over long time periods to estimate tree growth rates. Much as he had done under the supervision of Pearson in Arizona, Wadsworth

tagged some 15,000 trees between 1943 and 1946. Wadsworth grouped the trees into permanent plots that by themselves alone, established long-term ecological research in the Luquillo Mountains. The tree growth plots were representative of the major forest types in the Luquillo Mountains and provided the first insights into the productivity of mature Neotropical forests (Briscoe and Wadsworth 1970) and on how hurricanes affected forest structure (Crow 1980). They were also the first step towards long-term measurements of forest structure and functioning in the Neotropics. When coupled to the ecosystem level work of Odum that I discuss below, the long-term behavior of the tree growth plots of Wadsworth provided the intellectual foundation for the first LUQ LTER proposal in 1980.

Through his activities as both manager and scientist, Wadsworth was responsible for the development of research infrastructure within the LEF, infrastructure that was vital to the success of the LUQ LTER. A few examples include the 1949 designation of the Baño de Oro Research Natural Area, containing the best examples of the historical primary forests of Puerto Rico (Weaver 1994); development of wood volume tables for critical species and forests, the first step towards the carbon cycling work advanced later by Odum and the LUQ LTER; development of road and trail infrastructure used by scientists today; establishment of tree plantations and an arboretum with iconic tropical timber species such as teak, mahogany, and Caribbean pine; management of forest stands; rehabilitation of degraded lands; and many other tropical forestry research initiatives. Marrero, a silviculturist at the Institute, was Wadsworth's partner and collaborator in many of these activities beginning with their overnight stays at what was to become the El Verde Field Station, establishment of long-term tree growth plots, and planting of millions of trees throughout the Luquillo Mountains and Puerto Rico (Marrero 1950).

Wadsworth signed the Special Use Permits to the US Atomic Energy Commission (AEC) to run the El Verde Radiation Experiment (Radiation Experiment from now on). He also permitted the Federal Agricultural Research Station to test defoliants on tropical forests,[6] Harvard University's Arnold Arboretum to conduct a seminal ecological and taxonomic study of the elfin forest at *Pico del Oeste* (Howard 1968), and the University of Puerto Rico to continue research at El Verde post-Radiation Experiment, a permit that enabled the LUQ LTER. Wadsworth was also responsible for the dedication of the El Verde Field Station, used later by Odum for the Radiation Experiment and by the LUQ LTER as its field headquarters. He facilitated the work of Odum and collaborated with the research through site selection, research history (Wadsworth 1970), and contribution to the understanding of tree growth and yield in the tabonuco forest (Briscoe and Wadsworth 1970).

[6] This permit was terminated when the site was found to be unsuitable.

5.4.2 *The El Verde Radiation Experiment*

In 1962, Howard Teas, a scientist at the Puerto Rico Nuclear Center, and Howard T. Odum (Fig. 5.3) wrote the original proposal for the Radiation Experiment. Odum was one of the most influential ecologists of the twentieth century. His father Howard W. Odum, a sociologist at the University of North Carolina at Chapel Hill, influenced him, as did his brother Eugene P. Odum, and his doctoral mentor, G. Evelyn Hutchinson (under whom he did his doctoral dissertation on the biogeochemical cycle of strontium at Yale University). Odum applied a holistic approach to all the ecosystems that he studied, including Texas bays, tropical coral reefs, mangroves, freshwater springs, cypress wetlands, and tropical forests. During the Second World War, Odum visited Puerto Rico for the first time as a meteorologist, and in the 1950s he conducted studies in the mangroves of Puerto Rico and the forests of the Luquillo Mountains. His contributions to tropical ecology are summarized in Lugo (1995a, 2003, 2004).

Under the Atoms for Peace Program of the Administration of President Dwight D. Eisenhower, the University of Puerto Rico had established the Puerto Rico Nuclear Center in 1957 with facilities in Río Piedras and Mayagüez. The University of Puerto Rico became a leader in Latin America in the field of nuclear energy both for medical and ecological applications. The Radiation Experiment at El Verde (1963–1967) was a collaboration between the University of Puerto Rico, the USDA Forest Service, and the Atomic Energy Commission. Oak Ridge National Laboratory in Tennessee was particularly influential, as it administered the funds for the Radiation Experiment for the AEC and provided scientific and technical support to the study.

Fig. 5.3 Howard Thomas Odum in 1963, when he was leading the radiation experiment at El Verde, Puerto Rico. (From the historical archives of the International Institute of Tropical Forestry, USDA Forest Service)

Teas and Odum's proposal was to the Division of Biology and Medicine of the AEC. In developing the proposal, Teas and Odum used the results of the Scientific Survey and the research of the Institute. The Radiation Experiment started in 1963 under Odum's leadership, who became part of the scientific staff of the Puerto Rico Nuclear Center. His office was located in the small space under the stairs leading to the second floor of the Nuclear Center's Río Piedras building at the Medical Center campus.

The Radiation Experiment (Fig. 5.4) attracted many scientists from mainland United States and European Universities and, from National Laboratories, as well as students, faculty, and staff from Puerto Rican universities and government agencies. Even the Puerto Rico Electric Power Authority (known then as *Autoridad de las Fuentes Fluviales*) collaborated by providing the helicopter that lowered the radiation source to the concrete pad from which it irradiated the forest for nearly three months. One participant scientist was William C. Steere, who was the only scientist to have participated in both the Scientific Survey (Crum and Steere 1957) and the Radiation Experiment (Steere 1970). At the time that he studied the effects of radiation on Bryophytes, Steere was Director of the New York Botanical Garden, the position held by Britton at the turn of the century.

The Radiation Experiment was conceived at a time when scientists and engineers were making rapid strides in the development of nuclear energy but the consequences of radiation exposure for organisms and communities was not clear (Bugher 1970). Research was needed to help clarify how nuclides moved through the environment and learn how sensitive organisms and ecosystems were to radiation exposure. Moreover, John N. Wolfe of the AEC's Division of Biology and Medicine was calling for greater emphasis on human ecology at a landscape scale with a focus on the interaction of whole ecosystems with technologically oriented humans (Wolfe 1970). Available research in the arctic and temperate zone was demonstrating high sensitivity to radiation in arctic communities and pine forests in the eastern United States (Wolfe 1970). Wolfe proved to be a visionary as he visualized the need for ecosystem-oriented, long-term studies through networks of sites as the way to develop sufficient understanding of ecological phenomena in a changing world. In his own words (p iv): "It does not seem unreasonable to suggest that massive ecological studies such as those at El Verde be federally funded and carried out in every biotic province of the continent on a continuing basis. Such endeavors would provide base lines and would answer many questions before disturbances occurred." In short, he anticipated the LTER program.[7]

Odum was among the first to ask ecosystem-level questions about the vulnerability of tropical forests to gamma radiation and suggested that the Radiation Experiment would begin to answer fundamental questions about what we call today the resilience of tropical forests. Dealing with this issue of resilience to disturbances

[7] In 1908, Zon established in the USDA Forest Service the first of a network of Experimental Forests and Ranges with similar national scope and scientific objectives (Lugo et al. 2006).

Fig. 5.4 T
Experimer
radioactive
oval metal

was one
research

The fi
circumst
At the na
uses of a
the Puert
applicati
Center, t
dealing v
Rico, to

Fig. 5.4 The radiation source used to irradiate the wet forest at the El Verde sector of the Luquillo Experimental Forest. The two-ton lead container at the center of the concrete base contains the radioactive Cesium source, which when in operation, would be magnetically hoisted to below the oval metal structure at the top of the aluminum shaft. (From Odum 1970c)

was one of the themes that found its way to the LUQ LTER and became the central research topic of LUQ LTER for decades.

The funding of the Radiation Experiment benefitted from several institutional circumstances that made Puerto Rico attractive for hosting the study (Bugher 1970). At the national level, the AEC had been tasked with all matters related to peaceful uses of atomic energy. At the insular level, the University of Puerto Rico established the Puerto Rico Nuclear Center, which was tasked with developing nuclear energy applications for the benefit of Puerto Rico's economy. In addition to the Nuclear Center, the Commonwealth trained a new cadre of scientists and technicians for dealing with atomic energy and also established an atomic reactor in Rincón, Puerto Rico, to explore the potential for the generation of electricity for the island. The

Puerto Rico Nuclear Center focused on public health applications of nuclear energy, nuclear energy development, and marine and terrestrial environmental issues.

The Radiation Experiment was located in the terrestrial division of the Puerto Rico Nuclear Center. This institutional investment by the Commonwealth made it feasible for the AEC to locate the Radiation Experiment in Puerto Rico. Also, the intention of using nuclear explosions to open a new transoceanic canal in the Republic of Panama (Golley et al. 1975), favored Puerto Rico as a venue for this research because of its tropical location and the need to understand how tropical environments would respond to radiation effects as well as how nuclides would move in wet tropical conditions. Moreover, Puerto Rico had a unique level of foundational knowledge on tropical systems given the information about natural resources accumulated before, during, and after the Scientific Survey.

The timing of the funding for ecological research in the Puerto Rico Nuclear Center by the AEC also coincided with the development of new ways of thinking in the ecological field, a field that had its early development during the time the New York Botanical Garden was exerting scientific leadership in the United States of America (Kingsland 2005). The two ecological fields that were developing nationally in the 1950s and 1960s were the field of radiation ecology and the field of ecosystem-level ecology, neither of which had a tropical focus at their outset. Golley (1993) and Kingsland (2005) provide details on the connections among the AEC, the emergence of modern ecology, and the development of the ecosystem concept. In all these matters, Odum and his brother E. P. Odum were active participants. Of particular note in this regard was their joint study of a Pacific coral reef located in the Eniwetok Atoll that had been subjected to radionuclide fallout (Odum and Odum 1955). This study was an early example of ecosystem-level research with many lessons regarding the functioning of an ecosystem studied from both the population and community levels of complexity.

Odum's involvement in the Radiation Experiment assured that the El Verde Field Station would become a facility that hosted the visits of many scientists active in the discussion of the major ecological issues of the time. The Odum brothers and collaborators such as Golley, Richard Wiegert, and J. Frank McCormick were leaders within the Ecological Society of America (Egerton 2015). Their joint efforts at El Verde were reminiscent of the collaborative activities at the beginning of the century between scientists of the New York Botanical Garden and the USDA Forest Service during the origins of the Scientific Survey. All these historical developments would prove to be critical for the success of the LUQ LTER because the Luquillo Mountains in general, and the El Verde sector in particular, became known as centers of cutting edge research within the scientific community, both nationally and internationally.

The work at El Verde also transcended tropical ecological research, achieving international interest, including historical threads that lead to the projection of United States of America power over Latin America (Baldivieso 2016).

Odum's work and approach to scientific research was similar to that of Britton and Wadsworth, as these men had a strong sense of mission, welcomed collaboration, mentored scientists, and they all attracted dozens of scientists to Puerto Rico to advance the study and understanding of its natural resources. The notion of coupling

forest research to forest conservation was also shared by Odum, as evidenced in his early writings (e.g., Odum 1962) and the strong presence of management issues in the Odum and Pigeon (1970) volume, which contains all the results of the Radiation Experiment between 1963 and 1970.

To the chagrin of some scientists, Odum prevented participants in the Radiation Experiment from publishing the results of their studies in journals. Instead, all contributions were published in a single volume edited by Odum and Robert F. Pigeon, Technical Editor at Oak Ridge National Laboratory. The book, titled *A Tropical Rain Forest: A Study of Irradiation and Ecology at El Verde, Puerto Rico*, is known among its users as *the rain forest book*, *the green giant,* or the *green bible*. Its impressive size (4.9 kg, 1644 pages, and 111 chapters) either encourages or discourages its use, depending on the user's intentions. The AEC published the volume, which received broad recognition for its comprehensive analysis of a tropical ecosystem, including positive reviews in major research journals. Its contents established a model for ecosystem-level studies of complex tropical forests. The volume also serves as an archive of field data and location of measurements for future reference.

The Radiation Experiment yielded numerous insights about the structure and functioning of tropical forests, insights that were useful to LUQ LTER scientists when developing the LTER proposal. A few examples suffice. The carbon cycle of the tabonuco forest was documented in detail during the Radiation Experiment. Part of the innovation involved was the early measurements of gas exchange rates of plants and soil in the field (Odum et al. 1970a), including the use of a giant cylinder to measure the metabolism and carbon balance of the whole forest (Odum and Jordan 1970). Odum and Lugo (1970) used forest floor microcosms to explore the issue of carbon enrichment of the atmosphere when respiration processes exceed photosynthesis rates. The coupling of the El Verde forest with global phenomena was done through the study of nuclide cycling and accumulation in forest epiphytes (Odum et al. 1970b). Microbial ecology studies drew attention to their high turnover and critical role in decomposition processes and nutrient cycling (Odum 1970a). Autecological studies of tropical forest species showed fundamental differences in life history strategies of pioneer and non-pioneer tree species (McCormick 1995). These population studies, conducted in the context of whole forest functioning, contributed to breaking down the false dichotomies between population and community-level approaches to ecology.

In his memoirs, Wadsworth (2014) recounts a lunch encounter with Odum. They were sitting on a log on the forest floor within tabonuco forest at El Verde. Their lunch discussion focused on all the perils encountered by tree seedlings on their way to canopy domination. This conversation epitomizes the fundamental research and management question that both individuals dedicated a lot of creative time to answering through research and application. Wadsworth's interest was in the development of seedlings into dominant trees with high quality wood volume, while Odum's interest focused on the ecological factors regulating the self-organization involved as seedlings developed into dominant members of the mature forest. This

encounter of two of the most influential scientists on the island at that time, symbolizes the merging of science and conservation in the Luquillo Mountains.

When the Radiation Experiment ended with Odum's departure to the University of North Carolina at Chapel Hill in 1967, research continued on a second phase dealing with the movement of radionuclides through the forested landscape. Jerry R. Kline (1967–1968) and Carl Jordan (1968–1969), assisted by George E. Drewry led this phase of the study. Drewry had started with Odum in 1963 and acted as head of the El Verde Field Station. By 1970, Richard G. Clements and Drewry provided leadership to the program through its transition due to changes in the national funding landscape. In 1974, the AEC was abolished and substituted in part by the Energy Research and Development Administration, which continued to fund ecological research at El Verde. The Puerto Rico Nuclear Center was converted into the Center for Energy and Environment Research in 1976. In 1977, the Department of Energy was established and continued funding of ecological research at El Verde until the site was designated an LTER site by the National Science Foundation (NSF) in 1988. The transition under Clements culminated by 1980, when the research evolved into the Tropical Rainforest Cycling and Transport Program. This program focused on studies of succession, nutrient cycling, and animal ecology. After Clements, Laurence J. Tilly and Douglas P. Reagan led the research program followed by Robert B. Waide, who led the transition to the LUQ LTER.

5.5 The Luquillo Long-Term Ecological Research Program

Before the establishment of the LUQ LTER, Gerald Bauer, a USDA Forest Service forester, and Institute Project Leader Ariel E. Lugo spent several days in the National Forest searching for suitable locations to establish a watershed research program. They settled on three adjacent watersheds along the Bisley road. The USDA Forest Service constructed the road in the 1930s with labor from the Civilian Conservation Corps who followed an existing oxen trail (Scatena 1989). The oxen trail and road were used for a variety of purposes including transporting people and forest products to Sabana, the site where the National Forest Ranger had his home and office. Today, the Institute's Sabana Field Research Station is located at this site where it provides support to the LUQ LTER. Odum used part of the Bisley road to access the site of his 1950s biomass and metabolism study (Odum et al. 1970c). The three watersheds became the Bisley Experimental Watersheds, a long-term research program initially led by Institute scientist Frederick N. Scatena (Scatena 1989). The watersheds became the windward site that complemented the leeward El Verde site as the two main LUQ LTER study sites.

Funding for the LUQ LTER was secured in 1988 through a grant from the NSF to the University of Puerto Rico and the Institute. While funding from the NSF was significant and long-term, the LUQ LTER has always matched the NSF funding with substantial contributions from the University of Puerto Rico and the USDA Forest Service. The LUQ LTER has had functional similarities with the Scientific

Survey in that it is a multiagency collaboration where all participants contribute funds and scientists to the research program. Moreover, like the Scientific Survey, the LUQ LTER attracts the additional collaboration of many scientists and institutions from Puerto Rico, mainland United States, and internationally. As discussed above, the Institute's research program also operated on a similar philosophy, as did the Radiation Experiment. The high level of collaboration of the major ecological and forestry research and management programs in the Luquillo Mountains is one of the fundamental reasons why science and forest management has advanced so much in Puerto Rico and why the research and management programs have fed from each other to achieve excellence individually and through their synergy. Moreover, the LUQ LTER is connected to a national network of similar sites with similar missions: "to learn to protect and manage ecosystems, their diversity, and services" (Egerton 2015, p. 121).

The outcomes of the Radiation Experiment provided a framework for ecosystem-level studies in the LUQ LTER, a focus rare in other tropical sites at the time. The LUQ LTER was therefore in a good position to advance the understanding of tropical forests from ecosystem and community-level perspectives. For example, Reagan and Waide (1996) compiled the most detailed available analysis of the food web of an entire working tropical community because they had more than a decade of field research at El Verde to allow their comprehensive description and analysis of the complex community, and because the taxonomy and biology of the organisms were well known and dating back to results published in the Scientific Survey. Another synthesis effort used to boost research interest in the LEF and to support the drafting of NSF proposals was the summary of the research history and opportunities in the LEF (Brown et al. 1983). This publication became highly cited by LUQ LTER scientists and was latter updated (Harris et al. 2012).

The LTER program started in 1980 with James Callahan directing the program at the NSF. Luquillo scientists were unsuccessful in obtaining funding from NSF in 1980 and 1981. In 1987, when the NSF call for proposals invited submissions from tropical sites, the Luquillo proposal was partially funded. They received full funding in the 1988 competition. During the time the LUQ LTER proposals were being developed in the early 1980s, it was common for ecologists to identify themselves as population or community-level ecologists. This dichotomy was a source of tension among those scientists who assumed that these two parallel approaches to ecology had independent contributions to make to the understanding of tropical forests. This notion was initially accepted by the LUQ LTER, but was abandoned as participating scientists became more familiar with each other's work.

The LUQ LTER strategy for developing the research program at the Luquillo Mountains was to be inclusive and incorporate as much help as possible in the design of the research approach. They insured breadth of ideas by establishing an outside advisory committee that over time included such scientists as Odum, Wiegert, Jordan, Mathew Larsen, Gene E. Likens, Frank H. Bormann, Sandra Brown, and others. Scientists from other LTER programs were also invited to help in the design of the LUQ LTER. These scientists included Frederick J. Swanson

(Andrews LTER), David R. Foster (Harvard Forest LTER), Bruce Haines (Coweeta LTER), and Kristiina and Daniel Vogt (Andrews LTER).

To build strong bonds among all LUQ LTER scientists, weeklong meetings were held in natural settings suitable to scientific discourse and social interactions. One such meeting at a rustic facility at El Verde looking out over the forest was a memorable experience to all participants, and resulted in a tightly knit and scientifically unified group of scientists who understood each other's research and collaborated for decades to come. By the time that LUQ LTER published the book *A Caribbean Forest Tapestry; The Multidimensional Nature of Disturbance and Response* (Brokaw et al. 2012a), the focus for understanding tropical forests had evolved from a population and community ecology approach to an integrated approach based on the multidimensional nature of ecosystems. Such merging of the two sub-fields of ecology built on the results of the Radiation Experiment and represented one of many groundbreaking intellectual advances that resulted from the LUQ LTER.

Over a 30-year period the LUQ LTER has had numerous positive social and ecological outcomes. The passage of hurricane Hugo in 1989 over LUQ LTER sites led to better understanding of how disturbances affect tropical forest functioning (Lugo 2008) and exposed the accepted canopy gap-dynamics paradigm for explaining tropical forest regeneration as inadequate to explain the dynamics of forests exposed to hurricane winds (Lugo and Zimmerman 2002). Equally important to forest conservation and research, notions of ecosystem resilience, initially articulated by Odum (1970b), predominated during the LUQ LTER research synthesis (Waide and Willig 2012; Brokaw et al. 2012b). The results of this research falsified the prevailing paradigm that assumed tropical forests to be fragile (Farnworth and Golley 1974; Lugo 1995b; Sodhi et al. 2007).

In Puerto Rico, the LUQ LTER is a model for island-wide forest studies and a place where large numbers of underserved students (from Kindergarten to postdoctoral) train and learn about science, the tropics, and conservation. After the passage of hurricanes Irma and María in 2017, the research lessons after hurricane Hugo became critical to the design of management activities such as evaluating hurricane effects on trees, streams, and landslides. Luquillo LTER scientists had learned about the nature of forest response mechanisms through observation, measurement, and experimentation (Shiels and González 2014), and this knowledge proved useful for guiding post hurricane management actions.

Through the 200-year research history discussed here, Puerto Rico and the Neotropics have benefitted from the work of highly trained and talented scientists who spent time in the island and contributed to the development of new scientific talent, insular institutions, programs, and scientific and management activities. The progression of knowledge over time has followed a logical pathway starting with observation and spiritual expression among Taíno people, and ending with complex multi-scale research that spans from microbial to global scales with equal spiritual expression about the wonders of natural phenomena. The search for knowledge throughout this long period of research included exploration, inventory, and exploitation; taxonomic and natural history studies; forestry and silviculture research designed for assuring wise use of resources; and population and ecosystem-level

studies involving experimentation to better understand and conduct forest conservation activities.

In the twelfth century, Bernard of Chartres introduced the notion of the progressive improvement of knowledge and how present generations benefit from the past as if standing on the shoulders of giants. Such is the case of the success of the LUQ LTER. Its accomplishments are rooted in 200 years of human investment in trying to understand the magic of the Luquillo Mountains. Therefore, in the temporal progression of events, the LUQ LTER is just another stage in the passing of the baton from the Taíno to tomorrow (Robinson et al. 2014).

5.6 Roads Taken and Not Taken: LUQ LTER in the Anthropocene

In his memoirs, Wadsworth (2014) included a section titled *frustrated visions* where he outlined missed opportunities at different times of his career. All careers and programs have such lost opportunities that in no way undermine accomplishments but that are important to learn from. The lost opportunities of LUQ LTER reflect a difference between the programs led by Britton, Wadsworth, and Odum, who were strong leaders operating independently under institutionally empowering missions, and the LTER Program, a national network of sites with strong top down constraints on participating sites. Many consider the fact that LTER scientists develop proposals to advance science as evidence of a bottom up approach. This is only partially true because top down control in the LTER is exerted through the framing of the required five core areas of research emphasis; required administrative and educational functions such as centralized data management and schoolyard programs; and the requirement to re-visit the research questions every six years as well as shifting objectives and approaches required by NSF.

Constraints imposed by NSF have benefits, such as advances in data management in ecological research, and comparative research across latitudes and ecosystem types. A strong justification for top down control in a long-term research network is the limitation of funds, which are barely sufficient to maintain core programs at participating sites, given that new research avenues require additional funding sources. The risk of a top down approach is in limiting creativity and individual initiatives when new avenues of research that conflict with program priorities are called for. As I discuss below, securing additional research funding sources outside the scope of LTER to study the Luquillo Mountains mitigates the limitations of the top down direction on ecological research of the LTER program.

Under the strong science leadership of Britton, Wadsworth, and Odum, past research programs in Puerto Rico were capable of exploring non-conventional topics such as Britton's exploration of forestry policy, Wadsworth's ecological approach to forestry, or Odum's application of computer simulations to advance system-level understanding of forests. In short, new research questions and new research

directions naturally emerge from long-term ecological research. This also happened in the LUQ LTER. For example, scientists realized the importance of environmental gradients driving ecological processes in the Luquillo Mountains (González et al. 2013) and thus the need to study lowland forests, including secondary and emerging novel forest ecosystems (Lugo 2009). They also discovered the importance of past land use history to understanding present forest structure and species composition (Thompson et al. 2002), and the need to approach ecological systems from a social-ecological perspective (Muñoz Erickson et al. 2014). Moreover, new scientific frontiers were greatly expanding the ecological approach to include microbial, hydro-ecological, and geological scales that transcended traditional ecological scales of study. However in the context of the LTER, scientists did not have the same flexibility that Britton, Odum and Wadsworth had for exploring additional lines of research.

Given the above, LUQ LTER missed two opportunities: (1) not expanding research into lowland secondary and novel forests, and (2) not exploiting its momentum towards social-ecological research. These research topics conflicted with the traditional ecological focus of the LTER on mature forests and with the siloed-organization within NSF, which prevented a social-ecological approach to LTER research, with the exception of two urban ecology LTERs: the Central Arizona Phoenix, and the Baltimore Ecosystem Study.[8] In response to emerging research opportunities and LTER's resistance to the new topics of research, the LUQ LTER scientists were successful in articulating these new avenues of research activity through other funding sources. They received funding from other NSF programs to address new research questions about the ecosystems of the Luquillo Mountains, while the NSF and the USDA Forest Service funded social-ecological research and research on secondary novel forests outside the Luquillo Mountains. Unfortunately, the LTER Program was not designed for such dramatic expansion of research focus, and to save the LTER designation for the LUQ LTER, the scientific activity had to split according to other NSF Program objectives and research themes. By not addressing these developing lines of research and synthesis opportunities, the road was open to other organizations and research groups to fill the void, a process that strengthens ecological research island-wide, but does so outside the scope of LUQ LTER.

A positive outcome of roads not taken was that students and collaborators of senior LUQ LTER scientists are filling gaps left by the LTER program (e.g., Cusack 2013; Atkinson and Marín Spiotta 2015; Abelleira Martínez 2010; Muñoz Erickson et al. 2014) while some LUQ LTER scientists conduct significant research activity outside the scope of the LTER (e.g., María Uriarte, Grizelle González, Whendee Silver, Tana Wood, William McDowell). New research programs have arisen within the Luquillo Mountains with strong overlap with the LUQ LTER. Examples are the Tropical Responses to Altered Climate Experiments (TRACE; funded by the Department of Energy and the USDA Forest Service), the Luquillo Critical Zone

[8] NSF recently withdrew the Baltimore Ecosystem Study from the LTER network.

Observatory (LCZO, funded by NSF), and The Next Generation of Ecosystem Experiments (NGEE-Tropics, funded by the Department of Energy).

The LUQ LTER initially attempted to develop social-ecological research in the Luquillo Mountains and surrounding areas and it intended to expand this research focus in an upcoming renewal proposal. However, during the review process, the NSF LTER Program Manager strongly advised the LUQ-LTER principal investigators not to pursue social-ecological research within the scope of the LTER. At that time, the USDA Forest Service hired Tischa Muñoz Erickson, one of the pioneer scientists that were pursuing this research in collaboration with the LUQ LTER.[9] Muñoz Erickson assembled a transdisciplinary group that was funded through the Urban Long-Term Research Area (ULTRA) program with funds from NSF and USDA Forest Service. They focused on an urban watershed, the Río Piedras River Watershed (sanjuanultra.org), and the Institute established an International Urban Field Station in Río Piedras to support this research. The San Juan ULTRA evolved into a network of cities throughout the Neotropics and the temperate zones under the Urban Resilience to Extreme Events Sustainability Research Network managed by the Arizona State University. The NSF funded this network of cities, and the Institute's International Urban Field Station added cities in the Dominican Republic to further develop this line of research.

As research activity within the Luquillo Mountains multiplied, it became obvious that coordinating such a diversity of research programs, even in the small geographic area of Puerto Rico and the Luquillo Mountains, is a challenge. Coordination was necessary to ensure the forest conservation benefits from the results of new lines of research inquiry, and to prevent loss of information needed to advance knowledge about tropical forests. This has led to a third road not taken by the LTER, which is not integrating federal research in the Luquillo Mountains. Unfortunately, the different groups of scientists that participate in this diversity of research activity meet separately and have limited interaction with scientists from other groups studying the same forest stands. This results in loss of information for groups of scientists and loss of synergy among research groups that represent different NSF funding silos. The conservation benefits of the scientific synergy between different approaches to the study of the Luquillo Mountains are also lost.

Irrespective of the above, the LUQ LTER is blazing new trails regarding the study of Neotropical forests. These include the study through experimentation of the mechanisms of forest response to hurricanes, studies of the effects of droughts on wet forests, studies of gradients up the Luquillo Mountains, and studies of soil and microbial ecology. These are all understudied areas of research that are at present gaps in the understanding of tropical forest functioning. The long-term understanding of the forests of the Luquillo Mountains is particularly important in the Anthropocene Epoch, when changing environmental conditions challenge the adaptability of these forests. Moreover, the increased role and importance of people

[9] Others within LUQ LTER included Charles A.S. Hall, William H. McDowell, Jess K. Zimmerman, and Ariel E. Lugo.

in the Anthropocene also challenge forest managers that must deal day to day with uncertainty.

Although historical forests represent a small and shrinking proportion of the forests in Puerto Rico and the tropical world, they represent the forest type with the greatest complexity of all forest types, particularly more so than the simpler novel forests that predominate in Puerto Rico (Lugo and Helmer 2004) and are increasingly abundant in the world (Hobbs et al. 2013). Understanding and interpreting that complexity will require every advantage scientists can muster, and once again, the impressive information produced by the LUQ LTER and its predecessors will come into play to assure success and help the scientists support forest conservation in an age of environmental uncertainty. The remaining challenge is to integrate and make LTER studies relevant to the rest of the Anthropocene world.

Acknowledgments This work was conducted in collaboration with the University of Puerto Rico. Gisel Reyes and Jorge Morales assisted with the literature search. Mariela Ortiz is the graphic artist responsible for a timeline, and Sarah Stankavich, and Grizelle González contributed to the timeline of events. Carlos Domínguez Cristóbal, Kathleen McGinley, Tischa Muñoz Erickson, Robert B. Waide, and Sharon E. Kingsland reviewed and improved the manuscript. Patrick C. Kangas shared documents and a draft of the chapter on the El Verde Radiation Experiment of his upcoming book on the history of radiation ecology, and Helen Nunci helped with the production of the manuscript. Sylvia Zavala and Jorge Morales obtained the photos that illustrate the manuscript and their descriptions.

References

Abelleira Martínez, O.J. 2010. Invasion by native tree species prevents biotic homogenization in novel forests of Puerto Rico. *Plant Ecology* 211: 49–64.

Atkinson, E.E., and E. Marín Spiotta. 2015. Land use legacy effects on structure and composition of subtropical dry forests in St. Croix, US Virgin Islands. *Forest Ecology and Management* 335: 270–280.

Baatz, S. 1996. Imperial science and metropolitan ambition: The scientific survey of Puerto Rico, 1913-1934. *Annals of the New York Academy of Sciences* 776: 1–16.

Baldivieso, C. 2016. *Irradiating Eden: The El Verde experiment and the Atomic Energy Commission's nuclear prospecting in Latin America, 1954–1970.* M.A. thesis, University of Maryland, Baltimore County, Baltimore, Maryland.

Briscoe, C.B., and F.H. Wadsworth. 1970. Stand structure and yield in the tabonuco forest of Puerto Rico. In *A Tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, B79–B89. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Britton, N.L. 1919a. History of the survey. In *Scientific survey of Porto Rico and the Virgin Islands*, vol. 1, 1–10. New York: New York Academy of Sciences.

———. 1919b. Dr. Henry Allen Gleason, appointed first assistant. *Journal of the New York Botanical Garden* 20: 39–40.

———. 1930. The planting of a *Stahlia* on Arbor Day in Porto Rico. *Journal of the New York Botanical Garden* 31: 45–47.

Britton, N.L., and P. Wilson. 1923–1930. Descriptive flora-Spermatophyta. Botany of Porto Rico and the Virgin Islands, Vols. 5, 6. In *Scientific survey of Porto Rico and the Virgin Islands*. New York: New York Academy of Sciences.

Brokaw, N., T.A. Crowl, A.E. Lugo, W.H. McDowell, F.N. Scatena, R.B. Waide, and M.R. Willig, eds. 2012a. *A Caribbean forest tapestry: The multidimensional nature of disturbance and response*. New York: Oxford University Press.

Brokaw, N., J.K. Zimmerman, M.R. Willig, G.R. Camilo, A.P. Covich, T.A. Crowl, N. Fetcher, B.L. Haines, D.J. Lodge, A.E. Lugo, R.W. Myster, C.M. Pringle, J.M. Sharpe, F.N. Scatena, T.D. Schowalter, W.L. Silver, J. Thompson, D.J. Vogt, K.A. Vogt, R.B. Waide, L.R. Walker, L.L. Woolbright, J.M. Wunderle Jr., and X. Zou. 2012b. Response to disturbance. In *A Caribbean forest tapestry: The multidimensional nature of disturbance and response*, ed. N. Brokaw, T.A. Crowl, A.E. Lugo, W.H. McDowell, F.N. Scatena, R.B. Waide, and M.R. Willig, 201–271. New York: Oxford University Press.

Brown, S., A.E. Lugo, S. Silander, and L. Liegel. 1983. Research history and opportunities in the Luquillo experimental Forest. In *General technical report SO-44*. New Orleans: USDA Forest Service, Southern Forest Experiment Station.

Bugher, J.C. 1970. Project foreword. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, vii–viii. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Clements, F.E. 1928. *Plant succession and indicators: A definitive edition of plant succession and plant indicators*. New York: Hafner Press.

Colón Torres, J.A. 2009. *Climatología de Puerto Rico*. San Juan: La Editorial de la Universidad de Puerto Rico.

Crow, T.R. 1980. A rainforest chronicle: A 30-year record of change in structure and composition at El Verde, Puerto Rico. *Biotropica* 12: 42–55.

Crowl, T.A., N. Brokaw, R.B. Waide, G. González, K.H. Beard, E.A. Greathouse, A.E. Lugo, A.P. Covich, D.J. Lodge, C.M. Pringle, J. Thompson, and G.E. Belovsky. 2012. When and where biota matter, linking disturbance regime, species characteristics, and dynamics of communities and ecosystems. In *A Caribbean forest tapestry: the multidimensional nature of disturbance and response*, ed. N. Brokaw, T.A. Crowl, A.E. Lugo, W.H. McDowell, F.N. Scatena, R.B. Waide, and M.R. Willig, 272–304. New York: Oxford University Press.

Crum, H.A., and W.C. Steere. 1957. The mosses of Porto Rico and the Virgin Islands. In *Scientific survey of Porto Rico and the Virgin Islands*, volume 7, part 4, 395–599. New York: New York Academy of Sciences.

Cusack, D.F. 2013. Soil nitrogen levels are linked to decomposition enzyme activities along an urban-remote tropical forest gradient. *Soil Biology & Biochemistry* 57: 192–203.

Domínguez Cristóbal, C.M. 2000. *Panorama histórico forestal de Puerto Rico*. San Juan: Editorial de la Universidad de Puerto Rico.

Egerton, F.N. 2015. *A centennial history of the ecological society of America*. Boca Raton: CRC Press, Taylor & Francis Group.

Evermann, B.W. 1899. Summary of the scientific results of the Fish Commission expedition to Porto Rico. In *Investigations of the aquatic resources and fisheries of Porto Rico by the United States Fish Commission Steamer Fish Hawk in 1899*, xi–xv. Washington, DC: United States Fisheries Commission.

Farnworth, E.G., and F.B. Golley, eds. 1974. *Fragile eco-systems: Evaluation of research and applications in the Neotropics*. New York: Springer.

Figueroa Colón, J.C., ed. 1996. The scientific survey of Puerto Rico and the Virgin Islands: An eighty-year reassessment of the island's natural history. *Annals of the New York Academy of Sciences* 776: 1–273.

Gifford, J.C. 1905. The Luquillo Forest Reserve, Porto Rico. *Bulletin of the U.S. Department of Agriculture*, Bureau of Forestry, no. 54. Washington, DC: Government Printing Office.

Gleason, H.A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7–26.

Gleason, H.A., and M.T. Cook. 1926. Plant ecology of Porto Rico. In *Scientific survey of Porto Rico and the Virgin Islands*, vol. 7, 1–173. New York: New York Academy of Sciences.

Golley, F.B. 1993. *A history of the ecosystem concept in ecology: More than the sum of the parts*. New Haven: Yale University Press.

Golley, F.B., J.T. McGinnis, R.G. Clements, G.I. Child, and M.J. Duever. 1975. *Mineral cycling in a tropical moist forest ecosystem*. Athens: University of Georgia Press.

González, G.G., M.R. Willig, and R.B. Waide. 2013. Ecological gradient analyses in a tropical landscape. *Ecological Bulletins* 54: 7–250.

Harris, N.L., A.E. Lugo, S. Brown, and T. Heartsill-Scalley, eds. 2012. *Luquillo Experimental Forest: Research history and opportunities*. Washington, DC: U.S. Department of Agriculture, EFR-1.

Hill, R.T. 1899. Notes on the forest conditions of Porto Rico. *Bulletin of the Division of Forestry*, no. 25: Washington, DC: U.S. Department of Agriculture.

Hobbs, R.J., E.S. Higgs, and C.M. Hall, eds. 2013. *Novel ecosystems: Intervening in the new ecological world order*. West Sussex: Wiley-Blackwell.

Holdridge, L.R. 1967. *Life zone ecology*. San José: Tropical Science Center.

Howard, R.A. 1968. The ecology of an Elfin Forest in Puerto Rico, 1. Introduction and composition studies. *Journal of the Arnold Arboretum* 49: 381–418.

Kingsland, S.E. 2005. *The evolution of American ecology, 1890–2000*. Baltimore: Johns Hopkins University Press.

Kramer, W.P. 1924. El bosque del acueducto. *Revista de Agricultura de Puerto Rico* 12: 315–323.

Little, E.L., and F.H. Wadsworth. 1964. *Agriculture handbook 249: Common trees of Puerto Rico and the Virgin Islands*. Washington, DC: USDA Forest Service.

Little, E.L., F.H. Wadsworth, and J. Marrero. 1967. *Árboles comunes de Puerto Rico y las Islas Vírgenes*. San Juan: Editorial de la Universidad de Puerto Rico.

Little, E.L., R.O. Woodbury, and F.H. Wadsworth. 1974. *Trees of Puerto Rico and the Virgin Islands*, Agriculture handbook 449. Vol. 2. Washington, DC: USDA Forest Service.

Lugo, A.E. 1989. Biosphere reserves in the tropics: An opportunity for integrating wise use and preservation of biotic resources. In *Proceedings of the symposium on biosphere reserves, Fourth World Wilderness Congress*, ed. J.W.P. Gregg, S.L. Krugman, and J.D. Wood, 53–67. Atlanta: US Department of Interior, National Park Service.

———. 1995a. Contributions of H.T. Odum to tropical ecology. In *Maximum power: The ideas and applications of H.T. Odum*, ed. C.A.S. Hall, 23–24. Niwot: University Press of Colorado.

———. 1995b. Management of tropical biodiversity. *Ecological Applications* 5: 956–961.

———. 1996. Ninety years of plant ecology research in Puerto Rico. *Annals of the New York Academy of Sciences* 776: 73–88.

———. 2003. Obituary: Professor H.T. Odum (1924-2002). *Tropical Ecology* 44: 267–268.

———. 2004. H.T. Odum and the Luquillo Experimental Forest. *Ecological Modelling* 178: 65–74.

———. 2008. Visible and invisible effects of Hurricanes on forest ecosystems: An international review. *Austral Ecology* 33: 368–398.

———. 2009. The emerging era of novel tropical forests. *Biotropica* 41: 589–591.

Lugo, A.E., and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190: 145–161.

Lugo, A.E., and F.N. Scatena. 1995. Ecosystem-level properties of the Luquillo Experimental Forest with emphasis on the Tabonuco Forest. In *Tropical forests: Management and ecology*, ed. A.E. Lugo and C. Lowe, 59–108. New York: Springer.

Lugo, A.E., and J.K. Zimmerman. 2002. Ecological life histories. In *Agriculture handbook 721: Tropical tree seed manual*, ed. J.A. Vozzo, 191–213. Washington, DC: USDA Forest Service.

Lugo, A.E., F.J. Swanson, O. Ramos-González, M.B. Adams, B. Palik, R.E. Thill, D.G. Brockway, C. Kern, R. Woodsmith, and R. Musselman. 2006. Long-term research at USDA's Forest Service's experimental forests and ranges. *Bioscience* 56: 39–48.

Lugo, A.E., R.B. Waide, M.R. Willig, T.A. Crowl, F.N. Scatena, J. Thompson, W.L. Silver, W.H. McDowell, and N. Brokaw. 2012. Ecological paradigms for the tropics: Old questions and continuing challenges. In *A Caribbean forest tapestry: The multidimensional nature of disturbance and response*, ed. N. Brokaw, T.A. Crowl, A.E. Lugo, W.H. McDowell, F.N. Scatena, R.B. Waide, and M.R. Willig, 3–41. New York: Oxford University Press.

Marrero, J. 1950. La reforestación de tierras degradadas de Puerto Rico. *Caribbean Forester* 11: 16–24.

McCormick, J.F. 1995. A review of the population dynamics of selected tree species in the Luquillo Experimental Forest, Puerto Rico. In *Tropical forests: Management and ecology*, ed. A.E. Lugo and C.A. Lowe, 224–257. New York: Springer Verlag.

Mickulas, P. 2007. *Britton's botanical empire: The New York Botanical Garden and American botany, 1888–1929*. New York: The New York Botanical Garden Press.

Muñoz Erickson, T.A., A.E. Lugo, and B. Quintero. 2014. Emerging synthesis themes from the study of social-ecological systems of a tropical city. *Ecology and Society* 19: 23.

Murphy, L.S. 1916. Forests of Puerto Rico: Past, present, and future and their physical and economic environment. *Bulletin of the US Department of Agriculture*, no. 354. Washington, DC: U.S. Department of Agriculture.

Odum, H.T. 1962. Man and the ecosystem. In *Lockwood conference on the suburban forest and ecology*, 57–75. New Haven: The Connecticut Agricultural Experiment Station.

———. 1970a. Rain forest structure and mineral-cycling homeostasis. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, H3–H52. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

———. 1970b. Summary: An emerging view of the ecological systems at El Verde. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, I191–I289. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

———. 1970c. The AEC rain forest program. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, C3–C22. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Odum, H.T., and C.F. Jordan. 1970. Metabolism and evapotranspiration of the lower forest in a giant plastic cylinder. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, I165–I189. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Odum, H.T., and A. Lugo. 1970. Metabolism of forest-floor microcosms. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, I35–I56. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Odum, H.T., and E.P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs* 25: 291–320.

Odum, H.T., and R.F. Pigeon, eds. 1970. *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Odum, H.T., A. Lugo, G. Cintrón, and C.F. Jordan. 1970a. Metabolism and evapotranspiration of some rain forest plants and soil. In *A tropical rain forest: A Study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, I103–I164. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Odum, H.T., G.A. Briscoe, and C.B. Briscoe. 1970b. Fallout radioactivity and epiphytes. In *A tropical rain forest. A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, H167–H176. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Odum, H.T., W. Abbott, R.K. Selander, F.B. Golley, and R.F. Wilson. 1970c. Estimates of chlorophyll and biomass of the Tabonuco Forest of Puerto Rico. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, I3–I19. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Pinchot, G. 1947. *Breaking new ground.* Washington, DC: Island Press.

Reagan, D.P., and R.B. Waide, eds. 1996. *The food web of a tropical rain forest.* Chicago: University of Chicago Press.

Roberts, R.C. 1942. USDA Series 1936, No. 8.: Soil Survey of Puerto Rico. Washington, DC: US. Government Printing Office.

Robinson, K., A.E. Lugo, and J. Bauer, eds. 2014. *Passing the baton from the Taínos to tomorrow: Forest conservation in Puerto Rico. FS-862.* San Juan: USDA Forest Service International Institute of Tropical Forestry.

Rudolf, P.O. 1957. R. Zon, pioneer in forest research. *Science* 125 (3261): 1283–1284.

Santiago Valentín, E. 2005. Amos Arthur Heller's Puerto Rico plant collecting itineraries of 1900 and 1902-1903 and their utility for the historical study of endangered plants. *Brittonia* 57: 292–294.

Santiago Valentín, E., L. Sánchez-Pinto, and J. Francisco-Ortega. 2015. Domingo Bello y Espinosa (1817-1884) and the new taxa published in his *Apuntes para la flora de Puerto-Rico. Taxon* 64: 323–349.

Scatena, F.N. 1989. *An introduction to the physiography and history of the Bisley experimental watersheds in the Luquillo Mountains of Puerto Rico.* General Technical Report SO-72. New Orleans: USDA Forest Service, Southern Forest Experiment Station.

Seaver, F.J., and C. Chardón. 1926. Mycology. In *Scientific survey of Porto Rico and the Virgin Islands*, vol. 8. New York: New York Academy of Sciences.

Shiels, A.B., and G.G. González. 2014. Tropical forest responses to large-scale experimental hurricane effects. *Forest Ecology and Management* 332: 1–135.

Sodhi, N.S., B.W. Brook, and C.J.A. Bradshaw. 2007. *Tropical conservation biology.* Malden: Blackwell Publishing.

Steere, W.C. 1970. Bryophyte studies on the irradiated and control sites in the rain forest at El Verde. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, D213–D225. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Thompson, J., N. Brokaw, J.K. Zimmerman, R.B. Waide, E.M. Everham III, D.J. Lodge, C.M. Taylor, D. García Montiel, and M. Fluet. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12: 1344–1363.

Tugwell, R.G. 1947. *The stricken land: The story of Puerto Rico.* Garden City: Doubleday.

Wadsworth, F.H. 1970. A review of past research in the Luquillo Mountains. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, B33–B46. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

———. 1995. A forest research institution in the West Indies: The first 50 years. In *Tropical forests: Management and ecology*, ed. A.E. Lugo and C. Lowe, 33–56. New York: Springer Verlag.

Wadsworth, F. 2014. *A forestry assignment to Puerto Rico: Memoirs of Frank Wadsworth.* San Juan: Impresos Emmanuelli.

Waide, R.B., and M.R. Willig. 2012. Conceptual overview: Disturbance, gradients, and ecological response. In *A Caribbean forest tapestry: The multidimensional nature of disturbance and response*, ed. N. Brokaw, T.A. Crowl, A.E. Lugo, W.H. McDowell, F.N. Scatena, R.B. Waide, and M.R. Willig, 42–71. New York: Oxford University Press.

Walker, J. 2014. The prehistoric island to 1508. In *Passing the baton from the Taínos to tomorrow: Forest conservation in Puerto Rico*, ed. K. Robinson, J. Bauer, and A.E. Lugo, 17–27. FS–862. San Juan: USDA Forest Service International Institute of Tropical Forestry.

Weaver, P.L. 1994. *Baño de Oro natural area, Luquillo Mountains, Puerto Rico*, Station general technical report SO-111. New Orleans: USDA Forest Service, Southern Forest Experiment Station.

Willig, M.R., S.J. Presley, C.P. Bloch, and J. Alvarez. 2013. Population, community, and metacommunity dynamics of terrestrial gastropods in the Luquillo Mountains: A gradient perspective. *Ecological Bulletins* 54: 117–140.

Wolfe, J.N. 1970. Foreword. In *A tropical rain forest: A study of irradiation and ecology at El Verde, Puerto Rico*, ed. H.T. Odum and R.F. Pigeon, iii–v. Oak Ridge: Division of Technical Information, Atomic Energy Commission.

Zon, R., and W.N. Sparhawk. 1923. *Forest resources of the world*. New York: McGraw-Hill Book Co.