

Ecological gradient analyses in a tropical landscape: multiples perspectives and emerging themes

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Seen from space, the Luquillo Mountains stand out on the eastern edge of Puerto Rico like a dark-green eye in the midst of a heterogeneous matrix of fields, forests, roads and cities in the surrounding lowlands (Fig. 1). Intercepting clouds, rain, and Saharan dust as these cross the Atlantic and make landfall in the Caribbean, the peaks of the Luquillo Mountains – El Yunque, El Toro, East Peak, and West Peak – capture resources to sustain coupled human and natural systems. The Luquillo Mountains are not tall by global standards, rising only to just over 1000 m in the short distance from the coast to the peaks, but this moderate elevational relief creates gradients that are expressed in the form and functioning of the landscape. Understanding the way in which species and ecosystems respond to gradients of climate and land use intensity is vital to the sustainability of populations, water resources, and ecosystem services. In the Luquillo Mountains these patterns are expressed in the context of the rich biodiversity of the tropics and the complex interplay of land use, hurricanes, and plant and animal responses to resources and competition. The patterns expressed by the distributions of species and the ecosystem functions that they carry out are dynamic. Understanding the nature of gradients, and responses of species to them, helps to better predict responses to future conditions and ultimately to develop and sustain the kinds of landscapes that support societal interests and human wellbeing.

Reasons abound for the scientific study of mountains from an environmental perspective. Mountains shape regional climatic regimes and effect spatial variation in environmental characteristics in the lowlands (MacArthur 1972, Whiteman 2000, Barry 2008). They make up

about a quarter of the land surface of the planet (Miller and Spoolman 2012), and an equivalent proportion of world's human population lives in mountainous environs (Meybeck et al. 2001). Mountains supply water and make possible the production of hydroelectric power for approximately half of humankind (Messerli and Ives 1997, Viviroli et al. 2003). Consequently they are sometimes referred to as the world's water towers. Moreover, mountains often harbor high biodiversity, e.g. over a third of terrestrial plant species (Barthlott et al. 1996), and are hot spots of endemism, especially in tropical regions (Gradstein et al. 2008). Perhaps most critically, mountains harbor some of the most fragile environments in the world, including tropical cloud forests such as those found in the Luquillo Mountains (Díaz et al. 2003). Dependent on cloud formation and cloud height, the biodiversity as well as ecosystem structure and function of these systems are being significantly altered by land use change at low elevations (Becker et al. 2007) and imperiled by climate change (McCain and Colwell 2011).

Mountains also represent model systems (Garten et al. 1999) for conducting natural experiments (Körner 2003) with an environmental or ecological focus. Because of their global distribution across all continents and latitudes, recurrent broad-scale ecological patterns can be detected with reasonable power, and contrasted between tropical and temperate or humid and arid contexts (Grytnes and McCain 2007, McCain and Grytnes 2010). Moreover, the rapid rate of change in environmental characteristics within relatively short geographic distances provides insight into the mechanisms that mold species distributions and community assembly (Whittaker 1960,



Figure 1. Recent (2010) aerial photo mosaic of Puerto Rico with the outline of the Luquillo Experimental Forest encompassing the peaks of the Luquillo Mountains in northeastern Puerto Rico (top panel). The bottom panel is a view to the northeast from El Yunque Peak in the Luquillo Mountains.

Terborgh 1971) that can then be contrasted among taxa (Presley et al. 2012) or over time (Rowe 2007, Moritz et al. 2008). Indeed, elevational gradients represent substantial changes in temperature, rainfall, cloud interception, soil, and wind exposure, with environmental conditions at the extremes that strongly challenge species tolerances in both evolutionary and physiological contexts (Grubb 1977, Cavalier 1986). Compared to temperate organisms, Janzen (1967) reasoned that tropical organisms should respond more strongly to environmental changes along elevation gradients because, from an evolutionary perspective, such organisms face little intra-annual variation in climate and, therefore, are more sensitive to other forms of environmental variability. If true, then environmental responses to global change drivers on tropical mountains may provide an early indication of what the future holds for many of the world's ecosystems. In addition, human alteration of the earth has accelerated dramatically in the past century (Hannah et al. 1994). A preliminary inventory of human disturbance of world ecosystems has de-

scribed Atlantic forests in the Neotropical region ranking as the most highly disturbed overall (Hannah et al. 1994). The interactions generated by a gradient of anthropogenic uses of the land along topographic conditions makes the analyses of ecological gradients in tropical ecosystems highly complex. To further enhance our understanding of gradient analyses, this book assembles research focused on organismal, community, ecosystem and landscape approaches to the study of tropical ecosystems and presents a comprehensive analysis of one of the best-studied tropical mountains in the world, the Luquillo Mountains in Puerto Rico (Brokaw et al. 2012a).

The setting

Puerto Rico lies at the junction of the Greater and Lesser Antilles in the Caribbean. After his second voyage to the New World, Christopher Columbus purportedly described Puerto Rico to the queen of Spain by crumbling a

piece of parchment to emphasize the dramatic elevational relief of the island (Gannon et al. 2005). A central mountain range runs longitudinally across the island, with peaks approaching the height of the Luquillo Mountains. The Luquillo Mountains, in contrast, are on the northeastern corner of the island and receive the moisture laden trade winds as they cross the Atlantic Ocean. They receive nearly twice the annual rainfall of that received by the Central Mountains at equivalent elevations (Fig. 2). Waide et al. (this volume) describe the climate of the Luquillo Mountains in detail.

Northeastern Puerto Rico represents a heterogeneous landscape, extending from sea level to almost 1075 m at El Toro Peak, all within a distance of approximately 10 km. Both current and historical human and natural factors affect characteristics of the elevational gradient. Land use intensity decreases with increasing elevation and the upper

peaks are protected and managed as the Luquillo Experimental Forest (LEF). Agricultural practices prior to the protection of the LEF continue to have an imprint on species distributions and ecosystem functioning. Elevational variation affects a variety of environmental characteristics such as temperature, precipitation, and productivity, as well as changes in morphological, physiological, population and community characteristics of the biota (Waide and Willig 2012). Moreover, the region is dynamic in time and space (Brokaw et al. 2012b, Scatena et al. 2012) as a consequence of climatic (hurricanes, droughts) and anthropogenic (land use conversion and urbanization) disturbances. Because of global climate change and human demographic trends, the region is likely to experience substantial changes in its disturbance regime (Scatena et al. 2012) with ramifications to the structure, functioning, and human-valued services associated with its constituent ecosystems.

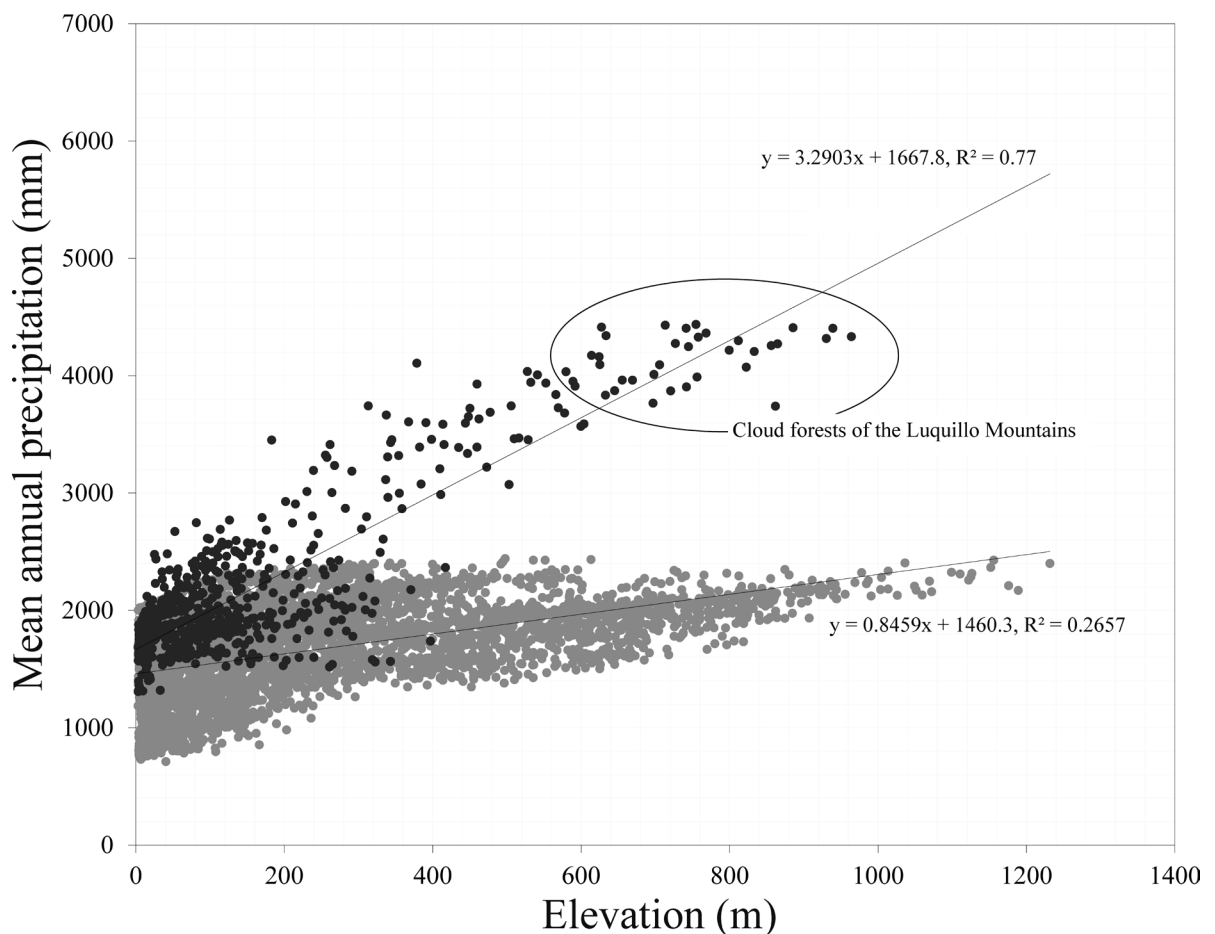


Figure 2. Mean annual rainfall as a function of elevation from a set of randomly sampled, Parameter-elevation Regressions on Independent Slopes Model (PRISM) generated (Daly et al. 2003) climate data. Darker circles are sites in northeastern Puerto Rico, lighter circles are sites throughout the rest of the island. The rainfall gradient is steeper and reaches a higher mean annual value in the Luquillo Mountains than in the equally high Central Mountains of Puerto Rico.

Concepts and constructs

Ecologists have long studied elevational gradients (Whittaker 1960, Terborgh 1971) because they represent non-manipulative or observational experiments in which dramatic changes in climatic characteristics occur over relatively short geographic distance, often resulting in high concentrations (i.e. hotspots) of biodiversity (Mittermeier et al. 1998, 1999, Myers et al. 2000) that is organized into zones (Woldu et al. 1989, Kitayama 1992, Hemp 2006, Martin et al. 2007). This has an important practical advantage: field research to encompass an equivalent quantity of environmental variation as is found along elevational gradients would have to span hundreds of kilometers of latitude. Moreover, due to the short spatial distance along which gradients manifest in mountainous regions, most studies of elevational variation in floras and faunas are not confounded by the existence of multiple species pools or sources of immigration, simplifying interpretations of causative factors.

There are distinct trends in several environmental attributes along the elevational gradient in the Luquillo Mountains. Elevational variability – the way in which environmental characteristics (biotic or abiotic) change with elevation – can assume a variety of forms depending on the underlying mechanisms. Variation with respect to elevation can arise from heterogeneity that is not primarily associated with elevation (Fig. 3, upper left panel) such

as that associated with topographic characteristics (e.g. slope or aspect). For example, Weaver (2010) studied forest structure and tree species composition within lower montane rain forest (tabonuco forest) of the Luquillo Mountains using plots stratified by aspect and topography while differing in elevation. He showed that abundances of 37 species with ≥ 6 occurrences (94 percent of all stems) differed with regard to aspect and topographic features, and that windward plots contained some species associated with wetter sites at higher elevation. Also in the Luquillo Mountains, Richardson et al. (2005) found the abundance of litter invertebrate communities declined significantly in mid- and high-altitude forests. Yet, the differences observed from the lower slopes to the summits, in animal abundance, species richness and the uniformity of communities, were better explained by the contribution of forest composition to the chemical and physical nature of litter and forest heterogeneity, rather than to direct effects of temperature and rainfall. Similarly, Willig et al. (this volume) have shown that abundances of most species of terrestrial gastropod decrease with increasing elevation, as do metrics of taxonomic biodiversity (i.e. species richness, species rarity, species diversity). Because such elevational variation characterized transects that comprised multiple forest types (tabonuco, palo colorado, and elfin forest) as well as a single forest type (palm forest), generally with parallel rates of decline, this fauna was likely responding to environmental aspects that change gradually with eleva-

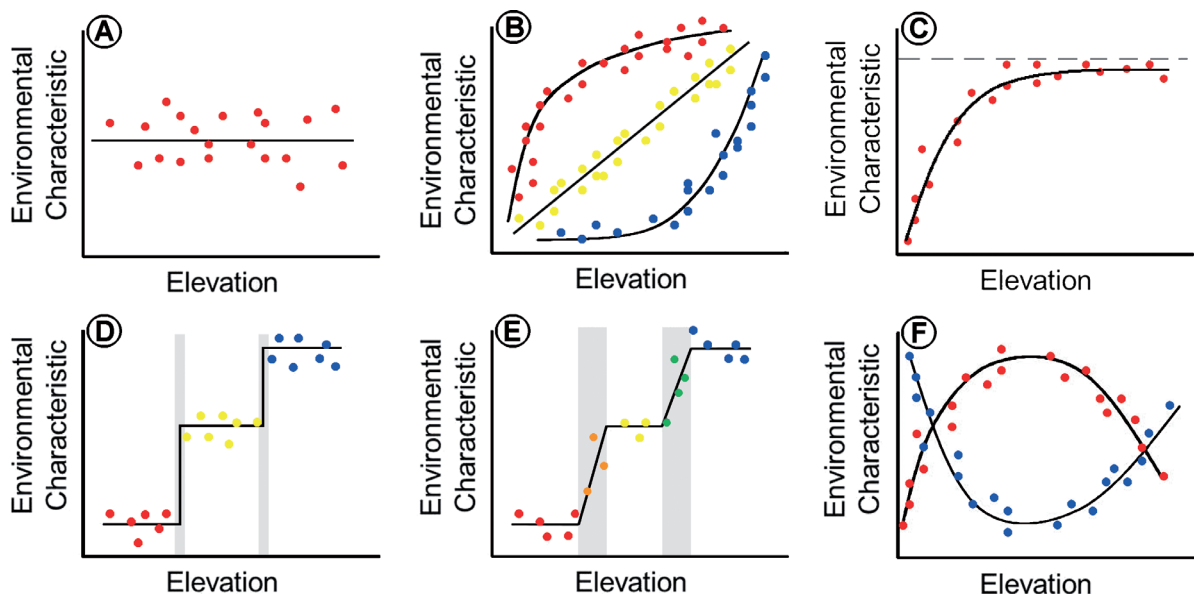


Figure 3. Elevational variation in environmental characteristics can assume a number of idealized forms: (A) stochastic patterns; (B) monotonic patterns in which the rate of increase decreases (red), is constant (yellow), or increases (blue) with elevation; (C) asymptotic increases; (D) step functions with abrupt changes at narrow ranges of elevation; (E) step functions with broad elevational ecotones; and (F) patterns with a distinct mode (red) or pit (blue) at intermediate elevations. Solid lines represent best fit curves describing a relationship between an environmental characteristic and elevation. Boundary zones or ecotones are indicated by vertical grey bars. An asymptote is indicated by a dashed horizontal line. When environmental gradients are explored directly, the driving or independent environmental characteristic is represented by the horizontal axis in place of elevation. See text for details.

tion (e.g. litter production or Ca content of litter) rather than to forest zonation, per se.

Environmental variation can be continuous in form or be represented by step functions. Gradual monotonic increases (or decreases) can be represented by a family of relationships depending on whether the rates of increase (or decrease) vary with elevation (Fig. 3, upper middle panel). For example, resource availability, productivity and diversity have often been described as interrelated, and exhibiting a monotonic decline with increasing elevation (Brown and Gibson 1983, Begon et al. 1996). In the Luquillo Mountains, some characteristics of biogeochemical pools and processes change linearly. For example, litterfall rates decrease linearly with elevation (Weaver and Murphy 1990), whereas the size of soil organic matter pools increases linearly (McGroddy and Silver 2000, Wang et al. 2002). Alternatively, gradual monotonic increases (or decreases) can be represented by asymptotic relationships when upper (or lower) bounds constrain values of environmental characteristics (Fig. 3, upper right panel). When the rate of change switches direction (i.e. has an inflection point) at intermediate elevations, likely as a consequence of trade-offs between pairs of factors that affect the same environmental characteristic (Scheiner and Willig 2005, Fox et al. 2011), patterns emerge that are represented by humps or pits (Fig. 3, lower right panel). For example, Richardson et al. (2000) found the biomass and species richness of invertebrates contained in bromeliads, and the bromeliad biomass per plant, peaked in the intermediate elevation forests of the Luquillo Mountains. In addition, elevational variation may arise as step functions that manifest in two general forms. In the first form, environmental characteristics are constant or vary at random about distinctive plateaus (horizontal lines) that are separated from each other by abrupt steps (vertical lines), giving rise to a staircase pattern (Fig. 3, lower left panel). In the Luquillo Mountains, for example, litter decomposition and soil CO₂ effluxes follow a stepwise trend that suggests thresholds effects (Silver et al. 1999, McGroddy and Silver 2000). In the second form, the distinctive plateaus bound an elevational span in which environmental characteristics change noticeably (e.g. an ecotone) and sometimes rapidly (Fig. 3, lower middle panel). The ability to distinguish between these two types of discontinuous patterns depends on the extent of the ecotone (vertical gray bars). Research in the Luquillo Mountains documents many of these kinds of gradients and infers the mechanistic bases that underlie them, or takes advantage of the distinctive characteristics that arise along the elevational gradient to explore critical scientific issues from basic and applied perspectives.

Highlights of forthcoming research

Although elevational trends in diversity and productivity are well documented, these relationships are often mud-

dled by the complexity and variability within the ecosystems (Richardson et al. 2000). In tropical ecosystems, relatively few studies have concentrated on tree species distributions along gradients (White 1963, Crow and Grigal 1979, Weaver 1991, 2010, Basnet 1992, Gould et al. 2006, Barone et al. 2008). In the Luquillo Mountains, structural and floristic impoverishment increase with elevation (Weaver and Murphy 1990). Leaf area, canopy height, tree diameter, litterfall rates, and mineralization of organic matter decline as elevation increases. From a faunal perspective, González et al. (2007) found that the number of earthworm species significantly increases as elevation and annual rainfall increase and temperature decreases. Richardson et al. (2000) studied the effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities. They found that animal abundance in bromeliads peaked at intermediate elevations. In contrast, Richardson et al. (2005) found the abundance of litter invertebrate communities declined significantly in mid- and high-elevation forests. Consistently, there have been few studies of biomass and body size along elevational gradients (Richardson et al. 2000). In the Luquillo Mountains, Alvarez (1997) studied five species of molluscs and found that one species exhibited no change with increasing elevation, one decreased in size, and three others species were larger. Stewart and Woolbright (1996) found three species of frogs also increased in size with increasing elevation in the Luquillo Mountains up to 750 m.

This volume expands considerations of ecological gradients in the Luquillo Mountains. Constituent chapters include climatic (e.g. precipitation and energy in Waide et al. and Harris et al. this volume, respectively), abiotic (e.g. rainfall chemistry, leaf properties, woody debris, nutrients, carbon stores, soil characteristics and biogeochemistry), and biotic (e.g. microbes, plants, and animal biodiversity) patterns and responses to gradients. These original and synthetic research findings highlight the importance of understanding environmental gradients in molding the structure and functioning of ecological systems. The book also broadens the scope of ecological gradient analyses by studying avian distribution along a gradient of urbanization (Vázquez-Plass and Wunderle this volume); and focusing on landslides as a cause of spatial and temporal gradients at multiples scales in the Luquillo Mountains (Shiels and Walker this volume). Vázquez-Plass and Wunderle (this volume) document how different species, species groups, and dietary guilds of birds respond to urbanization and different measures of developed habitat, pasture and elevation. Shiels and Walker (this volume) examined the effects of elevation on landslide abundance and vegetation recovery, and how gradients and within-landslides can affect patterns of plant colonization and succession. Waide et al. (this volume) define gradient analysis as a conceptual system for examining the distribution, growth, and abundance

of species or biological communities as a function of independently measured physical, chemical or biotic properties of their environment. Within that context, climatic variability within the Luquillo Mountains manifests as gradients that are correlated with elevation, slope, aspect, or land use history. It is further influenced by large-scale movements of air masses, extreme events and regional or global climate change (Waide and Willig 2012). Data from Medina et al. (this volume) support this contention as it reveals that dry deposition constitutes a large fraction of the deposition measured in bulk rainfall in the Luquillo Mountains. In fact, Medina et al. (this volume) reveals a complex interaction of different aerosol sources that cannot be completely elucidated without additional information on atmospheric events such as the Saharan dust or volcanic ashes deposition. Further, Silver et al. (this volume) highlight the sensitivity of montane forests to climate and suggest that redox dynamics may structure ecosystem responses to climate change. Silver et al. (this volume) present a conceptual model of potential patterns in key redox-sensitive biogeochemical processes in a humid tropical forest using both short- and a long-term oxygen records, where the longer term oxygen record (8 yr) is one of the few long data sets known to exist.

Weaver and Gould (this volume) recognize forest structure and composition in northeastern Puerto Rico are heavily influenced by climate, past land use, spatial features, and temporal disturbance conditions. Within this context, Weaver and Gould (this volume) acknowledge that recurrent hurricanes maintain forests in constant flux and that impacts vary by trajectory, storm attributes, and landscape features, all of which influence the amount of forest damage and subsequent recovery of the vegetation along the elevational gradient in the Luquillo Mountains. Similarly, Ping et al. (this volume) find that elevation, through its influence on precipitation and temperature, exerts strong control over the quantity and quality of terrestrial organic carbon stores, and the depth-distribution pattern of carbon, nitrogen and other nutrients. However, Ping et al. (this volume) find only about 35% of the increases in C stores along the gradient can be explained by changes in temperature or rainfall alone; and point to the importance of landscape processes such as landslides, slumps, and alluvial/fluvial activities in contributing to the variation of C stores across the upland forests. González and Morgan (this volume) study woody debris as a potentially large contributor to the carbon pool of these forested terrestrial ecosystems described in the book. González and Morgan (this volume) describe how sites exhibiting high basal area and amounts of aboveground biomass also have larger amounts of down woody debris. Harris and Medina (this volume) is based on one of the few data sets that exist on leaf physiological characteristics of tropical tree species and explore 'leaf economics', a topic relevant to those interested in changes in canopy carbon sequestration across

gradients. Harris and Medina (this volume) show quantitatively that both leaf structure and function differ in response to environmental conditions that vary vertically through the canopy profile as well as across an elevation gradient. This volume also covers organismal gradients associated with elevation via the study of the abundances of microbial functional groups (Cantrell et al. this volume); the relationships between litter invertebrate communities, climate, and forest net primary productivity (Richardson and Richardson this volume); and variation in population, community and metacommunity dynamics of terrestrial gastropods that arise from elevationally induced changes in litter production and Ca content (Willig et al. this volume). Results from Cantrell et al. (this volume) demonstrate an overall decrease in microbial diversity with elevation along the gradient although different microbial groups behave differently; a pattern consistent with Willig et al (this volume) for gastropods and Richardson and Richardson (this volume) for litter invertebrate abundance in bromeliads. Yet, Richardson and Richardson (this volume) describe species richness and animal biomass of bromeliad invertebrates peaking at mid-elevation, confirming to a monotonic pattern reported in other tropical elevation studies.

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