Advancements in the understanding of spatiotemporal gradients in tropical landscapes: a Luquillo focus and global perspective

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Background

The Luquillo Mountains have served as a focal point for people since pre-Columbian times. The Taíno Indians in Puerto Rico believed that the spirit of Yuquiyú – god of order, after which El Yunque National Forest (or Luquillo Experimental Forest) is named – dwelled and protected the people from Juracán (the phonetic name given by the Spanish settlers to the god of chaos and disorder believed to control the weather, particularly hurricanes). The chapters in this book illustrate how the Luquillo Mountains continue to serve as a focal point for understanding climate and for using our knowledge to better plan for and 'protect' people from climate-induced disturbances in the future. The juxtaposition of a rise in elevation from sea level to nearly 1100 m over the course of 10 km, the tropical climate, and the location of the Luquillo Mountains on the easternmost of the Greater Antilles, exposed to moisture laden trade winds, gives rise to gradients in rainfall, temperature, and seasonality that have structured ecological systems and human use of the landscape. Assessing the patterns and mechanisms of control along gradients that are often interdependent requires thoughtful analyses from many perspectives, rigorous experimental design, and long-term study. The value in understanding these gradients arises because knowledge is the basis for independently predicting responses to changes in rainfall, temperature, seasonality, storm intensity or frequency, and human use of the landscape.

Gradient analysis uses spatial measures of physical, chemical, and biological properties of the environment to understand the spatiotemporal dynamics of species, biological communities, biogeochemical fluxes, and ecosystem properties. The study of environmental gradients traces its history to the origins of the discipline of ecology (Clements 1904, Gleason 1917, Shelford 1951, Andrewartha and Birch 1954, Odum 1959). Indeed, the relation between environmental gradients and the distribution of organisms and communities is a favorite topic of ecologists and biogeographers, and papers on the subject abound in the literature. Much of this work focuses on environmental gradients that arise in concert with changes in elevation, such as temperature and rainfall (Whittaker 1967). Thus, studies of montane ecosystems are frequent in the literature on environmental gradients, and tropical mountains, because of their high biodiversity compared to those in temperate latitudes, provide an excellent laboratory for examining ecological responses to environmental change.

The chapters in this book take advantage of gradients that exist in the Luquillo Mountains, one of the most intensively studied tropical landscapes in the world (Brokaw et al. 2012). Moreover, the work described in this book furthers the studies of ecological gradients that have been undertaken in other parts of the tropics (Olson 1963, Terborgh 1977, Patton and Smith 1992, Stevens 1992, Lieberman et al. 1996, Schneider et al. 1999, Givnish 2001, 2002, Smith et al. 2001, Ogden and Thorpe 2002, McCain 2005, Presley et al. 2012). The extensive literature on environmental gradients provides a general conceptual framework for studies in the Luquillo Mountains. For example, formulation of an energy-based mechanism that

provided insight into how individuals and species respond to gradients (Hall et al. 1992) stimulated development of a conceptual model for the Luquillo LTER program that uses the concept of gradients to link landscape-scale patterns and processes with disturbance regimes (Willig and Walker 1999, Waide and Willig 2012). In this model, spatial gradients of environmental factors in the landscape are dynamic. Disturbance modifies environmental conditions so that any location in the landscape is subject to a range of environmental conditions over time. The distribution and abundance of individuals and species are determined by the tolerances to this range of conditions. Much of the work reported in this volume has been stimulated by this conceptual model. Yet, the way human actions interact with the environment at all scales (e.g. global warming, urban heat island effect, land use, roads and landslides, and water extraction) make future scenarios difficult to predict.

The elevational and climatic gradients within the Luquillo Mountains and northeastern Puerto Rico provide a natural in situ simulation of climate change, as a difference of about 5°C in mean annual temperature and more 3000 mm in mean annual precipitation occur from the top of the Luquillo Mountains to the coast. Thus, the use or exploration of the elevation gradient as a proxy for climate change can be a practical and informative way to study climate change scenarios, or to conduct experiments based on translocation manipulations. Manipulative experiments along elevation gradients could focus on populations, communities or ecosystem processes, and can be designed to anticipate and understand the effects of warming and drying.

Lessons learned along gradients in the Luquillo Mountains

We understand that climatic variability within the Luquillo Mountains manifests as gradients associated with elevation, slope, aspect, land use history, and disturbances. Previous efforts to explain spatial variability in the Luquillo Mountains have depended strongly on the concept of gradients (Lash-Marshall et al. this volume). Three introductory chapters explore the broader landscape of the Luquillo Mountains, and include analyses and discussions of climate variability (Waide et al. this volume), forest vegetation (Weaver and Gould this volume) and soils (Ping et al. this volume). These chapters reflect the interactions among large-scale climatic drivers, geologic substrates and topographic position on forest composition and soil characteristics. Certainly, together these factors and human modifications of the land can leave a historical legacy on the Luquillo landscape. The chapter on climate (Waide et al. this volume) reviews variation along the elevation gradient and highlights the importance of cyclic storm activity in structuring the ecosystems that are present in the Luquillo Mountains. It also presents preliminary information concerning predicted warming and drying due to large scale climatic factors and introduces the human drivers of deforestation and urbanization as they affect, respectively, evapotranspiration and cloud formation in the upper elevations and temperature due to the urban heat island effect. The discussion of forest vegetation (Weaver and Gould this volume) has at its core the interaction of climate, storm events, and human use of the landscape. The uppermost cloud forests and lowermost mangroves are the least suitable ecosystems for human exploitation, and as such, have been governed principally by climate, hydrologic and substrate characteristics. Forest vegetation at intermediate elevations has been strongly influenced by a complex mix of land governance, shifting land use, active management practices, land abandonment, and secondary succession. Direct and indirect human influences are based on a mix of governmental and non-governmental decisions as well as on individual landowner decisions. The conclusions are that species composition, tree growth, and forests respond predictably over the long term to the controls of climate, substrate, and topography, but human actions can and have superseded these controls to dramatically alter forest composition and structure. It is critical to understand that forests are living landscapes harboring individuals that may be hundreds of years old, whereas human actions and interests are often directed toward outcomes during much shorter time scales (decades). Uncertainties lie less in what future climate brings than in what we want and value from the forested landscape.

Soils in the Luquillo Mountains are formed from two different parent materials (quartz-diorite and andesite). Yet independent of those, aeolian deposits of Saharan dust can change the composition and characteristics of the mineral fractions in soil surface horizons at the top of the Luquillo Mountains (Ping et al. this volume). Changes in texture, for example, can have strong impact on water infiltration, drainage, and conductivity in the clayey sub soils, potentially affecting carbon and nutrient storages throughout the landscape. Given climate change scenarios that predict increased desertification in many African countries, carbon sequestration in the Luquillo Mountains can be an important indicator of change. Ultimately, the study of gradients in the Luquillo Mountains helps to understand the vulnerability of systems to climate variability and can serve as a motivation to elevate the discussion of policy-level linkages among social-ecological factors, desertification, and global climate change.

The work reported in this volume is organized around analysis of gradients at different scales, and includes perspectives based on organisms, ecosystem processes, and the broader landscape. Organismal responses were examined with respect to two different gradients – elevation (Cantrell et al. this volume, Richardson and Richardson this volume, and Willig et al. this volume) and urbanization (Vázquez-Plass and Wunderle this volume) – each is geo-

graphic or spatial in nature. Organismal responses to such spatial gradients arise via direct and indirect mechanisms. For example, in montane areas, temperature and precipitation vary with elevation in predictable ways (Waide et al. this volume). Direct effects on the biota in response to variation in such abiotic conditions may include phenotypic changes (e.g. body size, physiognomy) as well as demographic changes that ultimately affect abundance and distribution. Indirect effects arise because species in the biota form a network of interspecific interactions (e.g. predation, competition, and mutualism) that molds variation in phenotypic characteristics and abundance. This is particularly relevant for heterotrophic organisms (e.g. herbivores and decomposers) that are strongly affected by the abundance and phenotypic characteristics of the plants on which they depend for energy, nutrients, and habitat. Importantly, it is a considerable challenge to distinguish elevationally induced direct effects of abiotic gradients on heterotrophic organisms from the elevationally induced indirect effects that arise from variation in plant species, such as those represented by distinctive forest zones or forest types.

Although they employed different designs, Cantrell et al. (this volume), Richardson and Richardson (this volume), and Willig et al. (this volume) used a non-manipulative approach to distinguish direct responses by the biota to gradual abiotic gradients from the indirect responses by the biota to forest types. Litter invertebrates responded more clearly to differences in litter associated with forest types than to elevational variation in abiotic characteristics (Richardson and Richardson this volume), whereas terrestrial gastropods responded more clearly to gradual environmental variation associated with elevation than to differences among forest types (Willig et al. this volume). Differences in soil microbial communities were strongly linked to differences among forest types, but were associated with elevational variation in moisture and temperature as well (Cantrell et al. this volume). Ecological understanding would be advanced significantly by manipulative experiments that involve the transplant of litter or soils along the elevation gradient or that modify precipitation or temperature at scales relevant to invertebrate and microbial communities.

Anthropogenic modification of landscapes in northeastern Puerto Rico has resulted in considerable variation in environmental attributes (Weaver and Gould this volume) that can be recognized as distinctive habitat types (forest, exurban, suburban, and urban). This variation has had complex effects on the avifauna (Vázquez-Plass and Wunderle this volume), with distinctive responses by endemic (lower abundances and richness in urban areas) and non native (higher abundances and richness in urban areas) components of the biota. Nonetheless, total avian richness and abundance generally increased with urbanization. It is unclear whether urban and suburban populations, especially of resident insectivores, granivores, and

omnivores, are self-maintaining or rescued from local extinction via movement of individuals from more forested areas into human-modified landscapes. Such source dynamics have considerable implications for conservation, especially if human populations expand in distribution and density, and decrease the extent or quality of forested areas in the landscape.

In this book, we examined the spatial and temporal heterogeneity of nutrient cycling along a climate gradient that is associated with elevation. The Luquillo Mountains – like many tropical mountains – are characterized by a nutrient cycle in which nutrients are tightly cycled within the surface soil and biomass because the underlying substrates are highly weathered and thus nutrient poor (Bruijnzeel 1991, Buss et al. 2010). Consequently, nutrient inputs in rainfall play a central role in the study of nutrient cycling in the tropics. In the Caribbean Islands in particular, soils can receive significant nutrient inputs from African dust and volcanic ash (Graham and Duce 1982, Heartsill-Scalley et al. 2007, Muhs et al. 2007). In the Luquillo Mountains, important variations in precipitation chemistry within and among years can be associated with climate variability and the occurrence of tropical storms and hurricanes. Moreover, the influence of maritime aerosols is equally evident from the coast to the top of mountains (Medina et al. this volume). As previously mentioned, Saharan and volcanic ashes are important characterizing elements in the formation of surface soils at high elevation sites in the Luquillo Mountains (Ping et al. this volume). Thus, the long-term effects of changes in and interactions between soil structural properties and the spatial and temporal dynamics of precipitation on soil biogeochemical properties remain unknown. The sensitivity of this montane system to climate change will most likely lead to greater variability in the decay of organic matter (González and Luce this volume), the pattern of soil oxygen concentrations (Silver et al. this volume) and the accessibility of nutrients for plant uptake. Optimal leaf traits differ along the elevational gradient in response to resource availability, herbivory and frequency of disturbance in the Luquillo Mountains (Harris et al. this volume). Thus, trade-offs exist in terms of nutrient allocation between photosynthesis and leaf longevity that could ultimately determine the species distributions in the Luquillo landscape (Harris et al. this volume). The tight temporal coupling of soil O_2 concentrations and rainfall suggests that these montane ecosystems are likely to be very sensitive to climate change. Shifts in the timing and amount of rainfall are likely to alter redox dynamics, nutrient retention and loss, and greenhouse gas emissions. Future research should explore both direct and indirect effects of precipitation change on soil redox dynamics, vegetation structure, and biogeochemical cycling.

Across the landscape of the Luquillo Mountains, simulation models integrate empirical measures of physical drivers in a framework that incorporates our understanding of fundamental biophysical processes to predict distri-

butions of organisms as well as biogeochemical storages and fluxes (Lash-Marshall et al. this volume). Simulations have generated a number of predictions that have been substantiated with field data, including spatial and seasonal patterns of environmental conditions; cloud cover; storage and flux of soil organic carbon; actual evapotranspiration; soil moisture; distribution of dominant tree species; and responses of vegetation and carbon balance to hurricanes. Studies in this volume have facilitated the testing of hypotheses such as the Maximum Power hypothesis (Odum and Pinkerton 1955) in which the simulation of gross primary productivity, respiration, and net primary productivity along the elevation gradient suggests that mid-elevation environmental conditions in the Luquillo Mountains are optimal for conversion of sunlight to biomass (Harris et al. this volume), as predicted by the Maximum Power hypothesis. Although patterns along gradients can be predicted by simulation under static conditions, alteration in environmental conditions by disturbance may modify patterns over long time periods. That is, disturbance can decouple environmental and elevational gradients. Since the Luquillo Mountains have a history of extensive natural and anthropogenic disturbance, patterns predicted by simulation may only be apparent at large scales.

The distribution of disturbances and their effects do not parallel the physical and biotic gradients that exist in the Luquillo Mountains. Consequently, this complicates predictions of plant distribution and ecosystem characteristics. Landslide abundance, for example, is not closely related to elevation and its associated abiotic and biotic gradients in the Luquillo Mountains (Shiels and Walker this volume). Landscape-level differences in the distribution of landslides affect large-scale gradients of soil nutrients, slope, temperature and light as well as drainage patterns and canopy patchiness. Biotic responses to landslides reflect large-scale environmental gradients as well as gradients established within each landslide, including light, temperature, soil moisture and nutrients, and seed rain. A similar argument can be made for other types of disturbance such as hurricanes. Thus, prediction of distributions of species, communities, and ecosystem characteristics can be quite complicated and challenging, especially without comprehensive knowledge of the spatial and temporal extent of disturbances (Willig and Walker 1999, Waide and Willig 2012).

Future research directions

As we further the study of gradients in tropical landscapes, the quantification of the linkages between aspects of biodiversity and abiotic or biotic environmental characteristics associated with elevation or urbanization will provide deeper mechanistic understanding of the controls on the structure and functioning of ecosystems. This quantification requires 1) the development of a synoptic network of sites at which suites of abiotic and biotic characteristics, including biodiversity, are measured in tandem, and 2) the implementation of manipulative experiments to decouple effects of environmental drivers that are confounded along gradients. Also, a fuller consideration of the effects of spatial heterogeneity and variation, especially that induced by disturbance, on various dimensions biodiversity (e.g. taxonomic, functional, genetic, or phylogenetic dimensions) would inform understanding of interactions between patch-generating phenomena, such as hurricanes, landslides, or land-use policies and local conditions that affect movement of individuals or source-sink dynamics. These approaches are particularly relevant to the future, as alterations in climatic characteristics and disturbance regimes associated with global change will likely alter the mapping of abiotic and biotic characteristics in geographic space, with profound consequences to cross-scale interactions and the spatiotemporal dynamics of biodiversity that ultimately affect the provisioning of critical ecosystem services.

Key considerations for future studies

1) Because human populations continue to expand spatially and increase in density, especially in the tropics, research on urbanization gradients is paramount. Moreover, it is critical to recognize that organismal responses to particular gradients must be interpreted within the context of the composition and configuration of associated landscapes, as these mosaics can have profound effects on source-sink dynamics and the likelihood of local extinction.
2) Because of evolutionary and functional constraints, species respond to gradients in different ways, and do so in a scale-specific manner. Consequently, concerted efforts are required to explore biotic responses at the individual-, population-, or community-level by key organismal groups of producers, consumers, and decomposers to the same environmental gradients.
3) Microbes are diverse and essential contributors to ecosystem processes. Consequently, a more mechanistic understanding of how environmental variation affects the dynamics of different microbial assemblages, and how variation in the composition of such assemblages controls decomposition processes and nutrient cycling is critical for long-term sustainability and management of ecosystems that are threatened by global change.
4) The soils in the Luquillo Mountains experience high precipitation and rapid fluctuations in oxygen availability. Soil oxygen and associated redox-dynamics are closely linked to patterns in N, Fe, P, and C cycling in these tropical forest soils.
5) Precipitation chemistry in the Luquillo Mountains is affected by long-range transport of inorganic salts. Yet the correlation between dust deposition and ion composition in bulk rainfall remains to be established.

6) Surveying the presence and amount of palm fronds within different forests in Puerto Rico can increase the understanding of the amounts of woody debris within and among forests types. Within the sierra palm forest, palm fronds compose a significant portion of litter and woody debris that cover the ground. Palm fronds fulfill a similar functional role to that of woody debris and litter, buffering variation in soil surface temperature and moisture, providing nutrients and habitat for ground-dwelling decomposing organisms, stabilizing soil, and enhancing carbon storage.

7) Improved and more accessible simulation models could improve understanding of the effects of projected trends such as increased frequency of extreme events, the study of which is not amenable to field experiments. Future models need to be developed in a context of developing ecological theory and related hypotheses, and at scales relevant to the processes under study.

8) The view that net energy is an appropriate proxy for fitness provides an experimental approach that is scalable across levels of biological organization and allows for an integration of evolutionary and ecological principles. Future field and modeling studies should incorporate measures or estimates of optimum conditions for acquisition of energy as part of their theoretical framework.

9) Accurate predictions of species composition and time to recovery after a landslide remain challenging because of the multiple factors that influence plant colonization and succession. A coordinated approach to understanding the relative effects of these factors requires standardized methods, aggregation of existing and new data, and powerful multivariate approaches, including simulation modeling. Moreover, additional attention to the cumulative effect of successive disturbances is required to understand landscape patterns.

10) Plant succession after a landslide has been well studied, but differences in succession across elevational gradients are less well understood. Additional long-term studies of variation of successional pathways and rates across gradients are necessary.

11) Sustainable management of coupled human and natural systems, such as those in the Luquillo Mountains, requires more integrated collaboration between social scientists and biophysical scientists, especially as it relates to the valuation of critical ecosystem services and products that are likely to be affected by global change and expanding human populations.

Finally, a coordinated effort to expand collection of meteorological data and to improve the quality of such data is a fundamental necessity for understanding the effect of future climate change. Long-term records of Saharan dust deposition in the Caribbean Islands are needed, particularly if we want to understand the effects of human activities, climate variability and desertification in these tropical islands.

References

Andrewartha, H. G. and Birch, L. C. 1954. The distribution and abundance of animals. – Univ. of Chicago Press.

Brokaw, N. et al. 2012. A Caribbean forest tapestry: the multidimensional nature of disturbance and response. – Oxford Univ. Press.

Bruijnzeel, L. A. 1991. Nutrient input–output budgets of tropical forest ecosystems: a review. – J. Trop. Ecol. 7: 1–24.

Buss, H. et al. 2010. Phosphorus and iron cycling in deep saprolite, Luquillo Mountains, Puerto Rico. – Chem. Geol. 269: 52–61.

Clements, F. E. 1904. The development and structure of vegetation. – Nebr. Univ. Bot. Surv. 7: 1–175.

Givnish, T. J. 2001. On the causes of gradients in tropical tree diversity. – J. Ecol. 87: 193–210.

Givnish, T. J. 2002. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. – J. Ecol. 86: 999–1020.

Gleason, H. A. 1917. The structure and development of the plant association. – Bull. Torrey Bot. Club 43: 463–481.

Graham, R. C. and Duce, R. A. 1982. The atmospheric transport of phosphorus to the western North Atlantic. – Atmos. Environ. 16: 1089–1097.

Hall, C. A. S. et al. 1992. A geographically-based ecosystem model and its application to the carbon balance of the Luquillo Forest, Puerto Rico. – Water Air Soil Pollut. 64: 385–404.

Heartsill-Scalley, T. et al. 2007. Disturbance and long-term patterns of rainfall and throughfall nutrient fluxes in a subtropical wet forest in Puerto Rico. – J. Hydrol. 333: 472–485.

Lieberman, D. et al. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. – J. Ecol. 84: 137–152.

McCain, C. M. 2005. Elevational gradients in diversity of small mammals. – Ecology 86: 366–372.

Muhs, D. R. et al. 2007. Geochemical evidence for African dust inputs to soils of western Atlantic islands: Barbados, the Bahamas, and Florida. – J. Geophys. Res. Atmos. 112: F02009.

Odum, E. P. 1959. Fundamentals of ecology. – W. B. Saunders.

Odum, H. T. and Pinkerton, R. C. 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. – Am. Sci. 43: 331–343.

Ogden, R. and Thorpe, R. S. 2002. Molecular evidence for ecological speciation in tropical habitats. – Proc. Natl Acad. Sci. USA 99: 13612–13615.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. – Ecology 44: 322–331.

Patton, J. L. and Smith, M. F. 1992. mtDNA phylogeny of Andean mice: a test of diversification across ecological gradients. – Evolution 46: 174–183.

Presley, S. J. et al. 2012. Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: a comparison of bats, rats, and birds. – Global Ecol. Biogeogr. 21: 968–976.

Schneider, C. J. et al. 1999. A test of alternative models of diversification in tropical rainforests: ecological gradients vs. rainforest refugia. – Proc. Natl Acad. Sci. USA 96: 13869–13873.

Shelford, V. E. 1951. Fluctuations of forest animal populations in east central Illinois. – Ecol. Monogr. 21: 183–213.

Smith, T. B. et al. 2001. Refugial isolation versus ecological gradients. – Genetica 112: 383–398.

Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. – Am. Nat. 140: 893–911.

Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. – Ecology 58: 1007–1019.

Waide, R. B. and Willig, M R. 2012. Conceptual overview: disturbance, gradients, and response. – In: Brokaw, N. et al. (eds), A Caribbean forest tapestry: the multidimensional nature of disturbance and response. Oxford Univ. Press, pp. 42–71.

Willig, M. R. and Walker, L. R. 1999. Disturbance in terrestrial ecosystems: salient themes, synthesis, and future directions. – In: Walker, L. R. (ed.), Ecosystems of disturbed ground. Elsevier, pp. 747–767.

Whittaker, R. H. 1967. Gradient analysis of vegetation. – Biol. Rev. 42: 207–264.