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Foreword

Up, down, and across the mountains: a new look at the Luquillo Mountains

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As they have been doing for hundreds of years, thousands of people move up, down, and across the Luquillo Mountains (LM) every day. The difference over that span of time has been the transportation mode. This continuous exposure of humans to the dramatic diversity of the mountain environment has led to multiple mental models of these mountains. Scientists synthesized these models as paradigms that describe the nature and functioning of the LM ecosystems (Brokaw et al. 2012, Harris et al. 2012) and by the volume of information available, one would think that all topics involving their description have been exhausted. In fact, Odum and Pigeon (1970) already described the dramatic end points of the elevation gradient of the LM, including the presence of the cloud condensation level at 600 m, and Cintrón (1970) measured increases in the size and frequency of leaf stomata along the same elevation gradient.

However, this volume of the Ecological Bulletins (Ecological gradient analyses in a tropical landscape) contains a new look, or better expressed, an in-depth look at the defining characteristics of mountains, i.e. their many biotic and abiotic gradients. The volume builds on past knowledge and mythology. In the 1930s, Leslie Holdridge was an employee of the US Forest Service working in what is now scientifically known as the Luquillo Experimental Forest. Holdridge was the first to realize the importance of the climatic gradient of the LM and he used his experience in Puerto Rico and Haiti to develop the now famous Life Zone System (Holdridge 1947), which depicts the climatic gradients of the world. Two decades before Holdridge, E. M. Bruner, also a US Forest Service employee, noticed the structural gradient of forests in the LM and identified four forest types that covered the elevation gradient (Heartsill Scalley 2012). However, because his interest was management, the four forest types included a dwarf forest, which from a timber perspective represented small trees (up to 20-m height, see picture in Fig. 3a of Weaver and Gould in this volume) unsuitable for timber production. However, 20-m tall trees do not form a dwarf forest but a woodland, later recognized as the elfin forest or elfin woodland by plant ecologists (Howard 1968).

Today, both the Holdridge life zones and the four forest types are fixtures in the literature of the LM, and while the life zone concept remains useful to the understanding of the climatic gradients of the mountains, the four forest types have lost conceptual power (Heartsill Scalley 2012). It turns out that the abundance of tree species along the elevation gradient does not reflect distinct communities such as the ones implied by the four forest types or by the high species dominance that characterize stands in the LM. Instead, the pattern of tree species abundance along the elevation gradient shows species with narrow as well as wide ranges, and even bimodal and multimodal ranges (Fig. 1, and Lash Marshall et al. this volume). This complexity is not surprising given that the LM are characterized by a large number of tree species, topographic catenas (ridge-slope-valley) along the whole elevation gradient each with different dominant species, and frequent natural disturbances, all of which contribute to dramatic compositional changes in vegetation both in space and time. Moreover, as shown in Fig. 2, the same forest type can exhibit a different successional trajectory at the same elevation but in different life zone conditions across (east/west) the mountain gradient. Therefore, the four forest concept must be applied with caution when sampling in the field because these four vegetation types do not reflect the full

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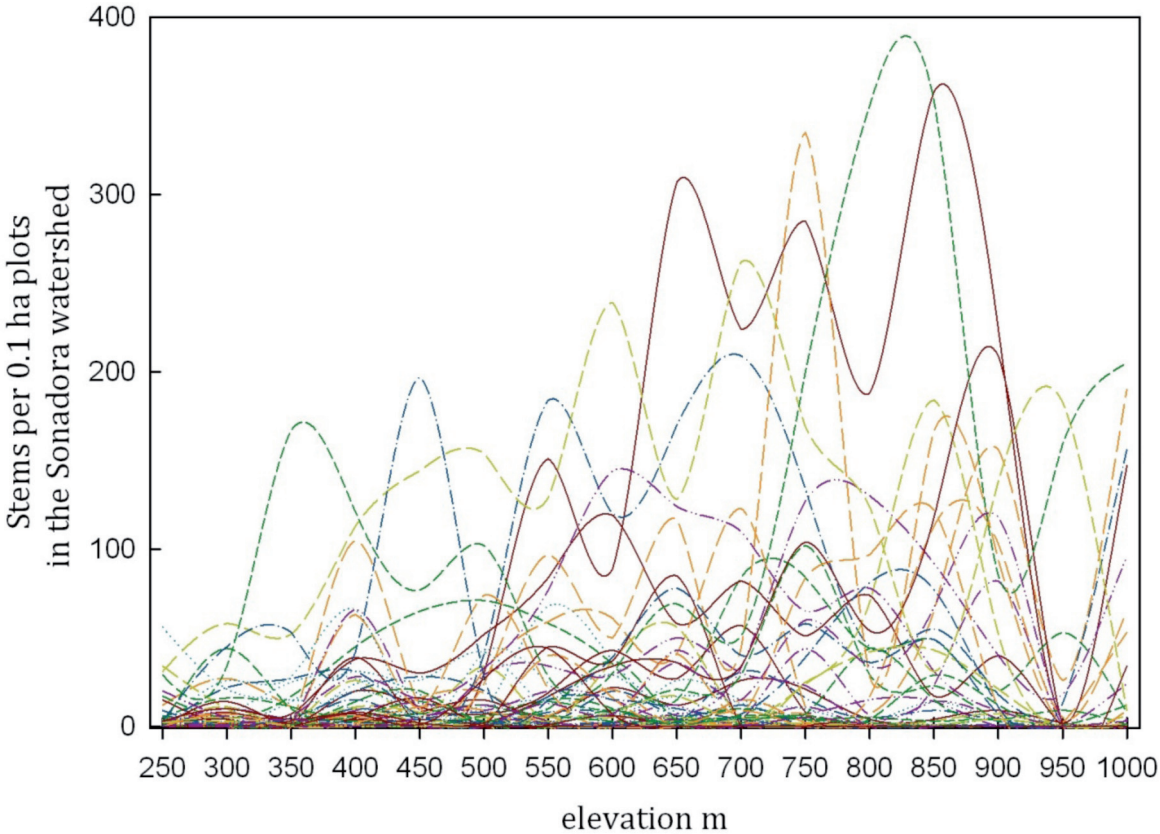

Figure 1. Total number of stems of all tree species measured in 0.1 ha plots across an elevation gradient in the Sonadora watershed, Luquillo Experimental Forest (from Heartsill Scalley 2012). Colored lines represent individual tree species. The list of species can be found at the Luquillo LTER data base 123 available through <http://luq.lternet.edu/>.

complement of vegetation types along the elevation gradient of the LM and they also show variability within each type.

This volume is the first to display the complexity of the biota along the abiotic and biotic gradients that typify the LM. While several of its contributions are still anchored in the old paradigm of the four forest types, most of them break away from that paradigm and describe biotic complexity along other environmental gradients, including elevation, which is a surrogate for multiple variables that change in different directions with elevation change (Medina et al., Waide et al. this volume). Examples of these other gradients covered in this volume are spatial and temporal gradients within landslides (Shiels and Walker this volume), soil REDOX gradients (Silver et al. this volume), and urban to natural gradients (Vázquez Plass and Wunderle this volume), an analysis about avian fauna that will surprise many. Some organisms appear to be influenced by a combination of factors (biotic and abiotic) or by vegetation. For example, litter invertebrates exhibited different responses and adaptations along the same climatic gradient but in different types of litter and plant associations: palm and broadleaved forests, illustrating the importance of secondary factors to the response to climatic gradients (Richardson and Richardson this volume). Microbial communities also responded strongly to forest type and less so to abiotic factors (Cantrell et al. this volume).

The volume contains new angles to the study of tropical mountain gradients that merit attention. It includes analyses of leaf properties (Harris and Medina this volume), and several lesser-known groups of organisms. For example, soil organisms and organisms in bromeliads (Richardson and Richardson this volume), gastropods (Willig et al. this volume), woody debris (González and Luce this volume), soil carbon and nutrient gradients (Ping et al. this volume) and ecological functioning gradients due in part to changes in REDOX but also because microbial functional groups (fungi and bacteria) show divergent elevation gradients in the LM and responded differently along the gradient (Cantrell et al. this volume).

An elevational analysis of the balance between photosynthesis and respiration lead to the conclusion that the net power flow of forests is maximized at just below the cloud condensation level (Harris et al. this volume). Intermediate elevations (between 500 and 700 m have ap-

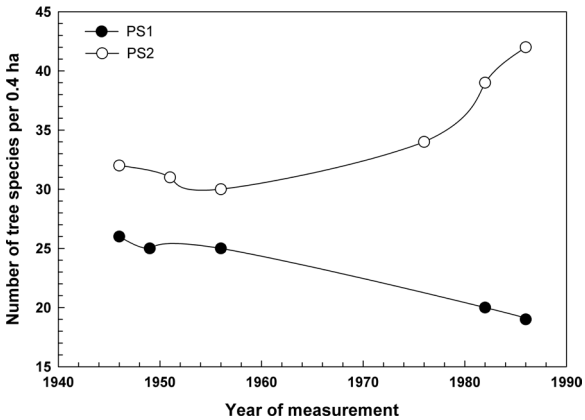

Figure 2. Temporal change in the number of tree species in two 0.4 ha plots in palm brakes at the Luquillo Experimental Forest. The plot PS 1 was in the windward and the plot PS 2 on the leeward side of the LEF at the same elevation of 700–750 m above mean sea level (Lugo et al. 1995).

peared in previous analyses as locations where trends with elevation peak, i.e. the complexity of vegetation (Brown et al. 1983), or where tree species richness per unit area decreases (Gould et al. 2006, Heartsill Scalley 2012). What is so unique about those elevations? The most obvious factor to consider is the cloud condensation level, which make the forest types above 600 m wetland forests (Frangi 1983) and in the Holdridge system, atmospheric associations (cloud forests) because they appear driven by atmospheric phenomena such as additional cloud water and nutrient inputs.

The cloud condensation level looms heavy over those that interpret the relationship between the biota and elevation in the LM. This phenomena has not been the subject of specific analyses by any of the chapters in this volume, although several manuscripts do report effects on gradients at this elevation. For example, rainfall conductivity and ion ratios sharply decrease above the cloud condensation level (Medina et al. this volume). Soil oxygen decreases dramatically in the forests above the cloud condensation level compared to forests below (Silver et al. 1999, Silver et al. this volume). Given the effects of soil oxygen on ecosystem functioning and species composition, and that we do not have clear understanding of the mechanisms that account for the patterns observed along elevational gradients, it is clear that there is plenty of room for future gradient analyses in these mountains. To assure more progress in the future I visualize scientists adding GPS and wireless sensors to their field kits so that a tighter relationship can be established between organisms and their environment. For the time being, this volume takes us up, down, and around the mountain in a way that no previous publication has done for these LM or any other mountain in the tropics. It opens a new avenue of analysis and exposes the reader to many surprises along the way.

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