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Using gradient analysis to simulate the spatial structure and function of the Luquillo Experimental Forest

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A transition to a gradient-based systems approach to scientific research in the Luquillo Experimental Forest (LEF) has yielded a new ability to understand the patterns of variability in abiotic conditions and the resultant structure and function of the LEF ecosystems. The location and topography of the Luquillo Mountains result in strong elevational gradients of temperature, soil moisture, microtopography, solar radiation and other physical characterizations. These gradients offer an exceptional opportunity to understand the response of species to environmental conditions across spatial and temporal scales through the use of spatial simulation models. We know now that the four forest type classification does not capture the biotic reality of the gradual transitions of vegetation and environmental gradients with elevation. We review the evolution of the increasing use of gradients in research in the LEF, and provide evidence that ecosystem structure and function are responding to gradients in environmental conditions based on a series of empirical studies and spatial simulation models of structure and function. Based on these studies, we believe that the gradients perspective is an appropriate conceptual framework for investigating the biota of this ecosystem and provides a strong basis for understanding their relation with the physical environment of the LEF over the long term.

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In ecology, gradient analysis and related frameworks have been used as tools for investigating the link between environmental conditions and the distribution of vegetation. More explicitly, gradients have played a longstanding and increasingly important role in our understanding of the structure and function of the Luquillo Experimental Forest (LEF) in the Luquillo Mountains of northeastern Puerto Rico. Environmental gradients represent characteristics that vary from low to high across a landscape, and that can include abiotic (e.g. temperature, light, moisture) or biotic (e.g. predation, competition, dispersal) parameters. Abiotic gradients have been used most often and most explicitly to help understand vegetation distributions over elevational changes in mountains, in response to frequently large temperature and rainfall gradients (Whittaker 1967), They have also been used to explain continental-scale distributions of species (Iverson et al. 1998). A transition to a gradient-based systems approach to scientific research in the LEF has yielded a new ability to understand the patterns of variability in abiotic conditions and the resultant structure and function of the LEF ecosystem across space and time.

The evolution of the use of gradients in ecology

As early as the mid-nineteeth century, Joakin Schouw (1822) and Alphonse de Candolle (1860) were examining the influence of temperature, soil moisture, and light on plant distribution, linking vegetation to local abiotic parameters. These linkages were expanded through the development of the Holdridge Life Zone Classification System, which summarizes spatial distributions of climax vegetation types based on gradients of climate (Holdridge 1947). The gradient-based classification system of Leslie Holdridge provided a means for describing observed vegetation along latitudinal and elevational gradients, but did little to explain how the observed vegetative assemblages were generated by associated abiotic gradients.

In the early twentieth century, gradients became prominent in one of the best-known debates in the ecological literature, that between Frederick Clements and Henry Gleason. Clements, who described vegetation distribution as discrete community units of reinforcing species (Clements 1904, 1936), was challenged by Gleason's individualistic theory of community structure, where vegetation at any single location is a collection of individuals of different species, each responding in its own way to environmental conditions (Gleason 1917, 1926). Clements' community theory dominated ecology until the 1950s when Robert Whittaker (1956, 1960) and Whittaker and Niering (1965) tested the hypothesis that plant species occurred as explicit communities by sampling vegetation extensively along the elevational gradient in the Smoky and later Siskiyou and Santa Catalina Mountains. Whittaker's methodology involved a direct gradient analysis, and along with research by John Curtis (1959) and Robert McIntosh (1967), supported Gleason's theory. Their results have driven the acceptance and continued use of gradient analysis in ecology (Austin et al. 1984), although not all gradient analyses have supported Gleason's perspective (Lortie et al. 2004).

There have been numerous other investigations related to species' distributions and the physical conditions of their environments (Brown 1984, Chapin et al. 1987, Stevens 1989, Lieberman et al. 1995, Murphy et al. 2006, etc.) and a gradients approach has played an important role in deciphering a number of ecological relations including nutrient cycling (Cox et al. 2002), understanding the carbon balance of plants (Mooney 1972, Bunce et al. 1979) and determining the energy costs and gains of a species along a gradient (Hall et al. 1992a, Harris 2006). Bunce (1979) and Hall et al. (1992a), in particular, have provided an energy-based mechanism for understanding how individuals respond to physical and biotic gradients, and how these relations generate species distribution and abundance.

Gradient analysis and the Luquillo Experimental Forest

Study site

The LEF, established in 1956, represents 11 330 ha of forest ranging from 100 to 1075 m in elevation in the Luquillo Mountains (Brown et al. 1983). Located at 18°N, 65°W in the path of northeasterly trade winds from the Atlantic Ocean, this montane ecosystem is characterized by relatively large changes in environmental conditions along the elevational gradient including precipitation, temperature, moisture and other parameters. These are basically driven by orographic effects as the moisture-laden oceanic air is pushed up the elevational gradient (Brown et al. 1983). These abiotic gradients, particularly the variation along elevation of temperature and moisture, provide the basis for the structure and function of the LEF ecosystem.

History of gradient analysis in the LEF

Understanding the structure and function of ecosystems has become an important, even dominant focus of research in the LEF over time. The LEF is certainly not the first location where gradients have been used in ecology, but it appears to be the first place in the tropics (or tropical montane ecosystem) and has played an important role in the development of measurement techniques and theories of structure and function. The earliest use of gradients in the LEF was the use of elevation to describe the four general forest types of the mountain (Wadsworth 1951, Gould et al. 2006). These forests are commonly referred to as tabonuco, colorado, palm and elfin forest, as outlined by Wadsworth (1951). This general taxonomy, representing a community type description of vegetation structure, has been used by most investigators at the LEF (White 1963, Odum et al. 1970, Brown 1983, Weaver 1986, Weaver and Murphy 1990, Lugo et al. 1995, Waide et al. 1998).

The majority of the earlier work in the LEF focused on forest properties within a zone of elevation or forest type, rather than investigating properties of a species or community along the elevational gradient (White 1963, Crow 1980, Brown et al. 1983, Weaver 1986, Basnet 1992). For example, the early years of scientific investigation under the National Science Foundation Long-Term Ecological Research Program focused on the description of and experiments in the Luquillo Forest Dynamics Plot, located at low to mid elevation within tabonuco forest (Basnet 1992, Johnson 1992, Scatena et al. 1996, McDowell 1998, Schellekens et al. 1999, Thompson et al. 2002, Drew et al. 2009) or within a particular forest type (Lugo et al. 1987, Guariguata 1990, Olander et al. 1998). A more direct descriptive linkage between these forest types and environmental factors was the use of the traditional Holdridge Life Zone Classification System to classify portions of the LEF into subtropical wet, subtropical rain, lower montane rain, and lower montane wet forest. Based on elevation-dependent temperatures, rainfall and the ratio of rainfall to evapotranspiration in the LEF (Brown et al. 1983), this system described reasons for the patterns of vegetation and physiognomy found in the four forest types (Ewel et al. 1973).

Over time, the gradient concept has come to replace the forest-type classification for better understanding of vegetation associations in the LEF (Gould et al. 2006, Heartsill Scalley 2012), including forest recovery rates (Aide et al. 1996), community composition (Barone et al. 2008), tree density (Weaver and Murphy 1990), and vegetation distribution patterns (Weaver and Murphy 1990, Gould et al. 2006, Lash 2008). Gradient analysis has been used to derive elevational variation in abiotic conditions, such as rainfall (García-Martinó et al. 1996), as well as the mechanism for biotic conditions, such as soil oxygen and biogeochemistry (Silver et al. 1999). At a larger scale, gradient conditions have been shown to influence forest structure and function at the species (Weaver 2000, González et al. 2007) and ecosystem level (Wang et al. 2002a, b, 2003, Wu et al. 2006a, b, Brown et al. 2008, Lash 2008). More recently, the focus of research has transitioned to utilizing single or multiple gradients as a way to explain patterns of distribution, abundance and function over larger space, continuing to build on the linkage between environmental gradients and ecosystem structure. These, and corresponding spatial models, demonstrate that the LEF is an entity that can be best thought of as a system that varies more or less continually from the top to the bottom of the mountain.

Spatial modeling of the LEF

Gradient analysis can be especially powerful when explored via spatial algorithms. Such models allow researchers to combine empirical data of biotic responses to a particular environmental condition across spatial and temporal scales. For example, abiotic gradients of air temperature, solar insolation, and rainfall can be used to predict vegetation structure and function across the LEF, as well as functional responses of evapotranspiration, soil moisture, and the decomposition rate of soil organic carbon (SOC). In the following sections, we will highlight spatial models that have been used to predict ecosystem level variation along abiotic gradients and model the biotic structure and function of the LEF.

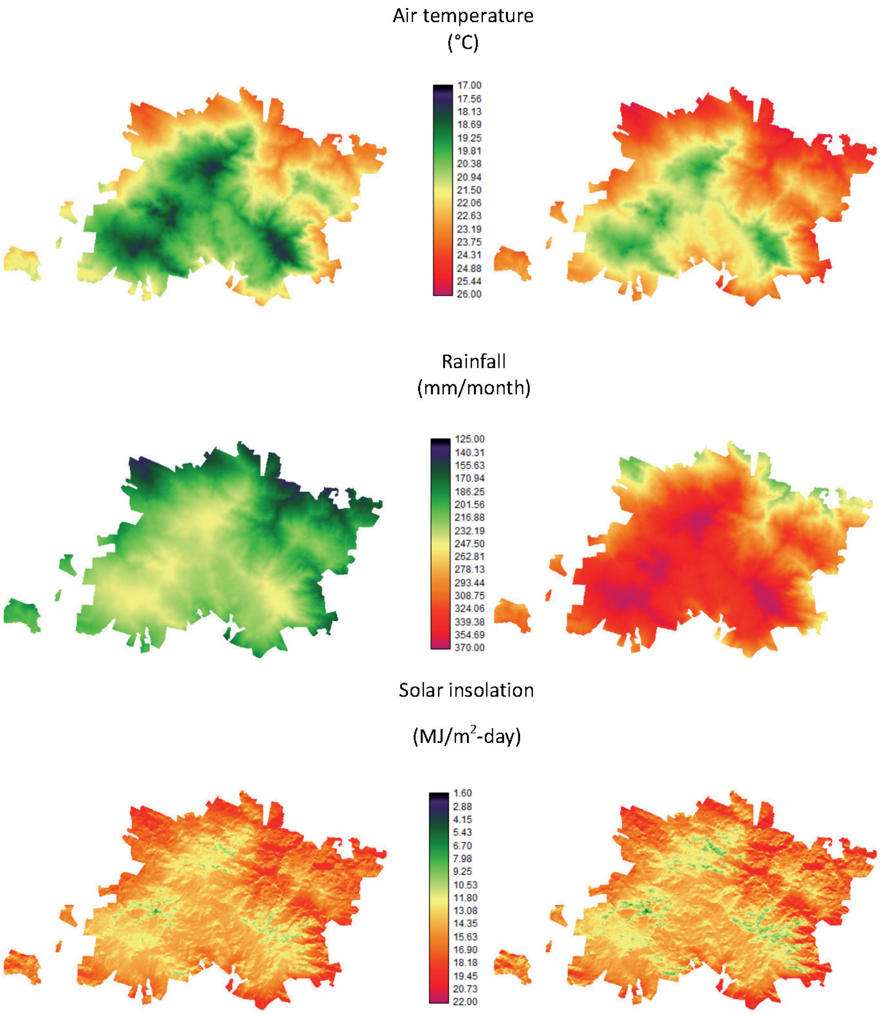

Figure 1. Simulated air temperature (°C), solar insolation (MJ m^{-2} d^{-1}), rainfall (mm $month^{-1}$) in dry and rainy seasons in the LEF, Puerto Rico (Wang et al. 2003). North is to the top of each graphic.

Spatial modeling – abiotic gradients

Simulation models of climatic variables over the entire LEF have generated maps of detailed and explicit spatial and seasonal environmental conditions. The TOPOCLIM (TOPOgraphically driven CLIMate) model yields solar isolation, temperature, relative humidity, and rainfall above the canopy for each hour of the day and each day of the year based on model inputs of elevation, slope, and aspect (Wooster 1989, Marley 1998, Wang et al. 2003). Simulated monthly temperature and daily solar insolation decreased as elevation increased, changing with topographic variation. For example, in a relatively rainy month (e.g. October), air temperature decreases from 26°C at low elevation to 20°C at mountain peaks; and solar insolation decreases from approximately 20 MJ m^{-2} d^{-1} to approximately 8 MJ m^{-2} d^{-1} along the same gradient (Fig. 1, adapted from Wang et al. 2003).

Wu et al. (2006b) developed an independent model of the daily and seasonal variation of cloud cover in the LEF based on elevation, aspect, and slope. Cloud cover increased with elevation (Fig. 2, adapted from Ecological Modeling), with the highest values in the elfin forest. To validate the model output, Wu et al. (2006b) calculated the index of agreement (IoA) between the model simulation and empirical observation at a particular time or particular location. These models generally predict the probability of cloud cover every 100 m in elevation at a particular time with an IoA of 0.560–0.919 and at a certain location over a day with a IoA of 0.940–0.994, indicating a medium to good model simulation at that particular time or location. Due to limited cloud cover data, they were able to corroborate the spatial-temporal model by measuring spatial accuracy only at a particular time and measuring temporal accuracy only at a particular location (Wu et al. 2006b). The model was calibrated using remotely sensed images, including Landsat-TM and Moderate Resolution Imaging Spectroradiometer (MODIS), from which cloud cover was derived.

In addition, modeled probabilities of cloud cover were highest at night and early morning, then decreased in the morning after the sun rose until early afternoon, and increased again from afternoon through night. Cloud cover is a key determinant of carbon, water and energy budgets because clouds are a source of precipitation and can reduce solar radiation and limit photosynthesis, sap flow and transpiration (Graham et al. 2003). By regulating water availability and solar radiation, cloud cover affects the distribution of species along the elevation gradient, especially in elfin forests, which depend on cloud water.

Spatial modeling – biotic gradients

Simulating the variation of abiotic environmental factors has allowed the prediction of biotic factors in the LEF. Hall et al. (1992b) simulated the response of vegetation and the carbon balance with and without hurricane disturbance. Moreover, variables of ecosystem function, such as evapotranspiration and soil carbon content vary with topography and elevation (Wang et al. 2002b, Wu et al. 2006a). Wu et al. (2006a) modeled actual evapotranspiration (aET) as a function of slope, aspect, and elevation. Simulated aET was the highest in the tabo-

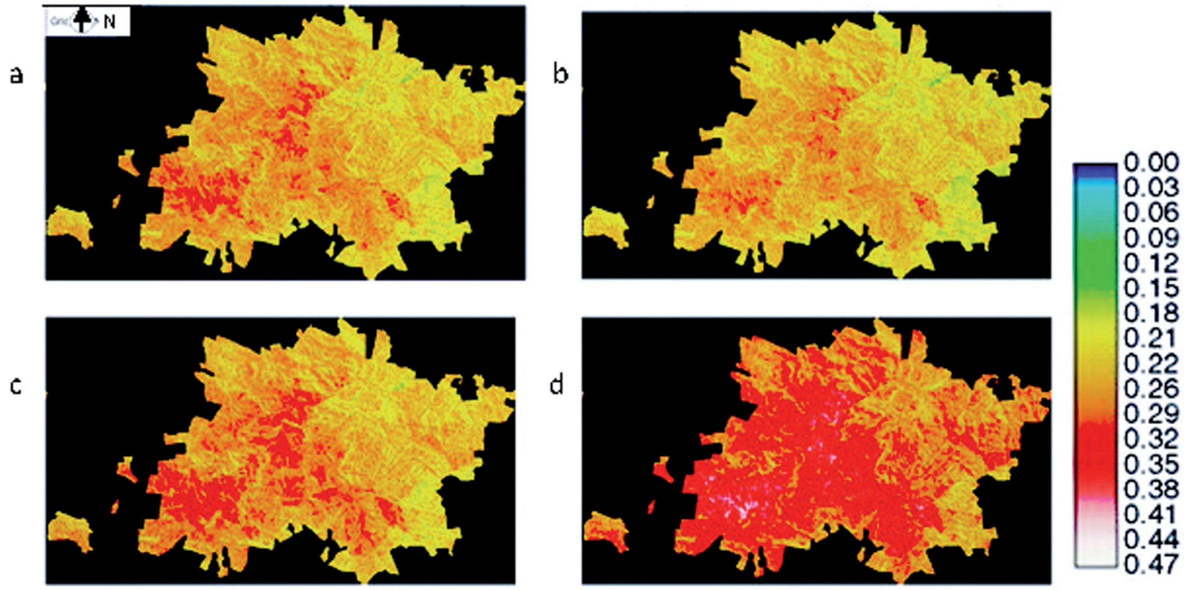

Figure 2. Probability of cloud cover at 9:00 am, 1:00 pm, 5:00 pm, 9:00 pm derived from a generalized linear mixed model with exponential spatial structure on 20 July 2001 calibrated from the MODIS image (Wu et al. 2006b).

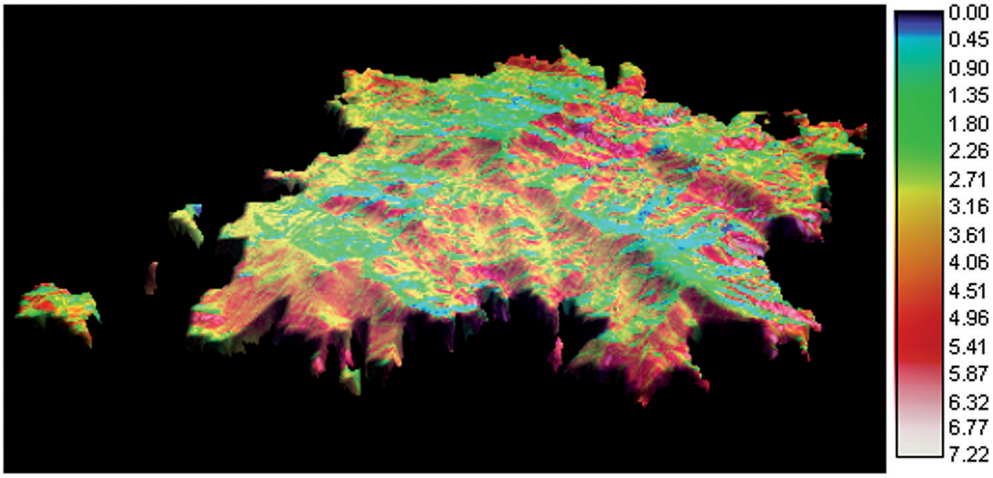

Figure 3. Derived daily average aET in January (Wu et al. 2006a).

nuco forest at low elevations (close to the boundary of the forest) and decreased with elevation (Fig. 3). As the rate of evapotranspiration is driven by solar radiation and vapor pressure deficits in nature and in our model, simulated aET tended to be higher on south slopes and along ridges where available solar radiation and vapor pressure deficit were higher than on north slopes and in the valleys. Trees in the elfin forests appear to be better adapted physiologically to reduced solar radiation by having higher rates of aET than do trees exposed to the same low level of solar radiation but occupying lower elevations. For validation, the simulated values were compared with field measurements of the sap flow velocity of trees using thermal dissipation probes at different elevations and in different forest types. These comparisons had good agreement in forests located at lower elevation but only moderate agreement in the elfin forest at high elevations. The reason for this discrepancy is probably that the sap

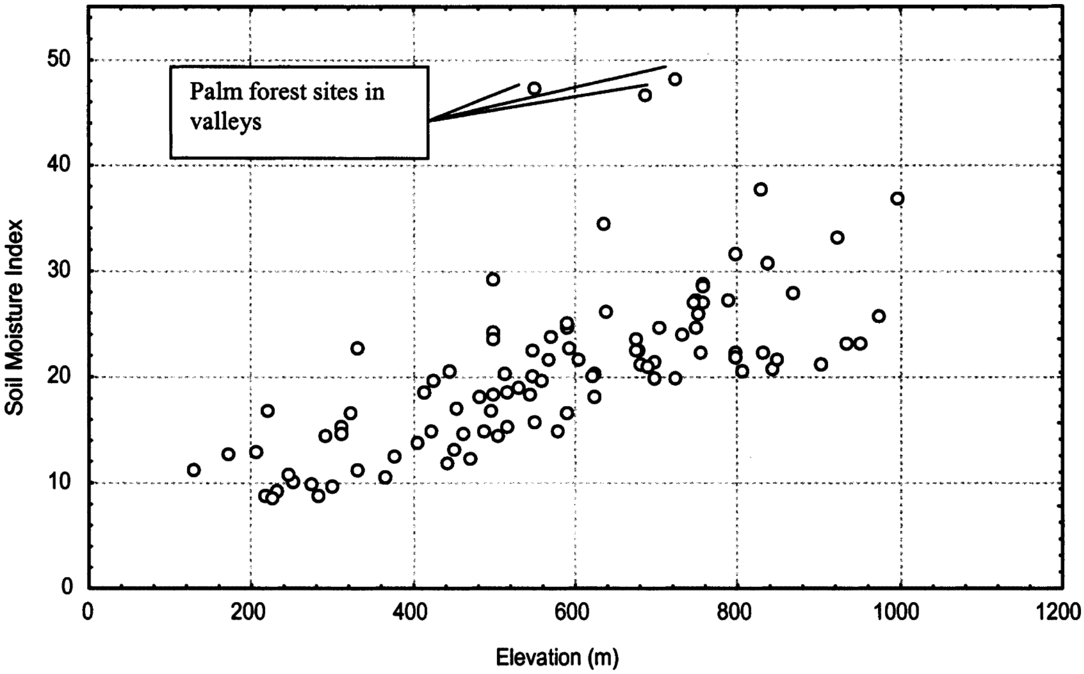

Figure 4. Relation between simulated soil moisture index (SMI), defined here as the ratio of rainfall plus soil available water to potential evapotranspiration (PET) and elevation, in December in the LEF. At a particular elevation, variation in SMI is due to topographic features: valleys tend to have higher SMI than do ridges, especially for palm forest between 500 and 800 m (Wang et al. 2002b).

flow measurements for the small trees in the elfin forests were prone to be more affected by the thermal gradient in the environment compared to the larger trees at lower elevations.

Wang et al. (2002b) developed a model to characterize the storage and flux of soil organic carbon (SOC) to a depth of 30-cm throughout the entire LEF based on topography, elevation, soil, and vegetation. The measured soil moisture (SM) showed considerable spatial heterogeneity over the LEF (Wang et al. 2002b). In general, SOC storage increases from tabonuco forest at lower elevations, to palm and colorado forests at middle elevations, to the highest storage of SOC in the elfin forest near the peaks in the LEF. The simulated soil moisture index (SMI) increases with elevation (Fig. 4) due to more rainfall and less potential evapotranspiration (PET).

The decomposition of soil organic matter (SOM) and the release rates of CO_2 due to decomposition of SOM had strong spatial patterns, each being correlated significantly with elevation. In general, simulated organic matter at cooler locations at higher elevations tend to decompose less rapidly and release less CO_2 per gram of soil over the course of a year than do those at lower elevations (Fig. 5, Wang et al. 2002a). However, these patterns do not always hold true. For example, palm forests have the lowest decomposition fluxes wherever they are located along much of the elevational gradient, presumably due to palm trees being found along steeper and wetter conditions (Wang et al. 2002b). On the other hand, the month-to-month variability in the decomposition flux for each forest type was generally smaller than the differences from one forest type to another. Soils and litter in the tabonuco and colorado forests have a higher CO_2 release per hectare because of higher leaf litter input than do palm or elfin forests, and the variation within-forest-type is smaller than the variation between-forest-types (Wang et al. 2002a).

Simulation models of abiotic conditions generate much higher resolution predictions of ecosystem structure and function then has been possible to measure empirically (Lash 2008), allowing for predictions to be made over a longer time period and to test scenarios on a single dataset (Wu et al. 2006a). Validation of these physical models can be difficult because spatial data are scarce and most was used to generate the models. There are several ways to test the biotic variables, such as using part of the data collected for model generation and part for validation (Wang et al. 2002b).

Spatial modeling – suitability analysis

Ecosystem level models of abiotic and biotic gradients can be integrated with empirical data to simulate the habitat suitability for a particular species of interest. Lash (2008) implemented a direct gradient analysis over 100 10 × 10 m plots along two transects between 450 and 950 m to study the distribution and growth of *Cyrilla racemiflora* along temperature and soil moisture gradients to better understand the conditions that influence their abundance and distribution in the LEF. *Cyrilla racemiflora*, classified in the LEF as the dominant species of the mid-elevational

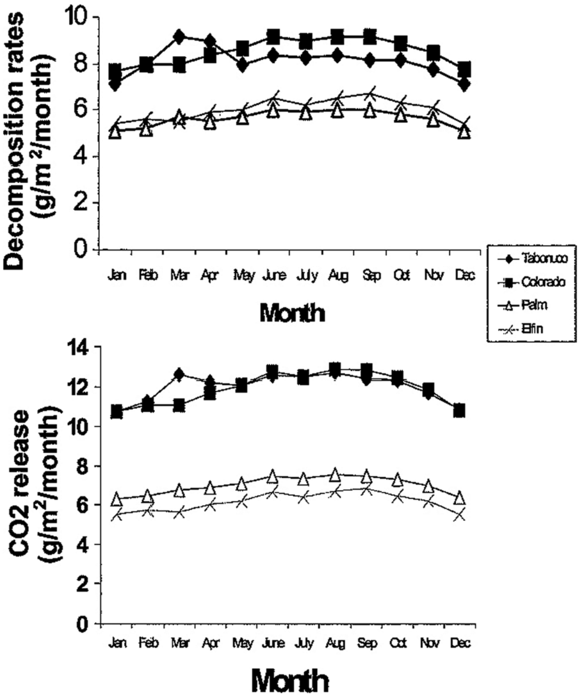

Figure 5. Simulated decomposition rates of soil organic carbon (SOC) (above) and CO_2–C release (below) for tabonuco, colorado, palm and elfin forests in the LEF. Higher elevations tend to have slower decomposition of SOC and release smaller amounts of CO_2. These variations are more pronounced between forest types than within forest variations (Wang et al. 2002b).

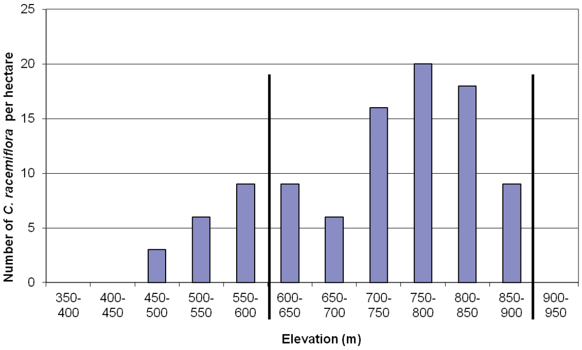

Figure 6. Elevational distribution of *C. racemiflora* in 2007 with the 'traditional' forest-type distributional range of *C. racemiflora* (600–900 m) identified (vertical bars).

(600–900 m) colorado forest, has also been documented in abundance above and below this classified forest type (Weaver 1986, 2000, Drew 1998). The results of this highly targeted field study on the distribution and size of *C. racemiflora* were integrated with previous studies of species' distribution and growth to create a geographic database of spatial coordinates of known locations along an elevational gradient in the LEF (Fig. 6).

A comparison of the actual distribution of *C. racemiflora* and simulation modeling of environmental gradients in the LEF determined that the ideal environmental conditions for *C. racemiflora* is between 22.61 and 22.87°C (Fig. 7) and a saturation potential of 9.97 and 10.75 (Fig. 8). Clearly, not all locations where *C. racemiflora* might be were sampled for this study, but based on 89 sites where individuals were observed between 1946 and 2007, the highest absolute and relative frequency of *C. racemiflora* were found within these conditions.

Lash (2008) developed a model to rank the suitability of conditions within the LEF for this species based on gradients of temperature and soil moisture, under the assumption that the ideal environmental conditions will be where there is the highest number of observed *C. racemiflora*. Based on temperature and soil moisture under present conditions, the model predicted 294 ha of ideal environmental conditions for *C. racemiflora* in the LEF (Fig. 9). Due to limited data on the distribution of *C. racemiflora* outside of colorado forest, these results have not been validated. However, the model results could be validated by sampling in areas predicted to have the most suitable conditions for *C. racemiflora*.

By utilizing a gradients approach to understand the distribution of a particular species within a larger ecosystem, this analysis provided relevant data to inform the future management of this species. For example, Weaver (2001) proposed that the long-term recovery of *C. racemiflora* within the LEF could be influenced by implementing selective thinning to encourage long-term regrowth. Understanding the gradient space of the species could allow for plot selection, as well as aid in determining where *C.racemiflora* are most likely to be located based on known environmental conditions. By expanding research to include sampling sites outside of classical forest types, we are able to understand better the response of an individual species to ecosystem-level conditions.

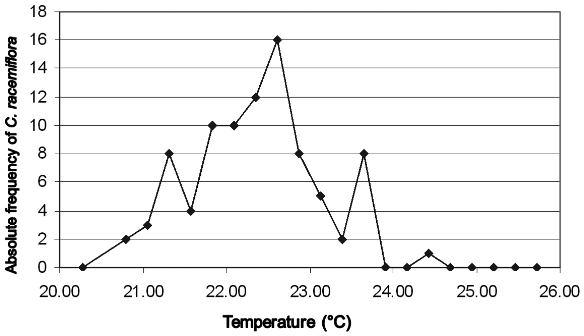

Figure 7. Absolute frequency of *C. racemiflora* along temperature gradients in the LEF.

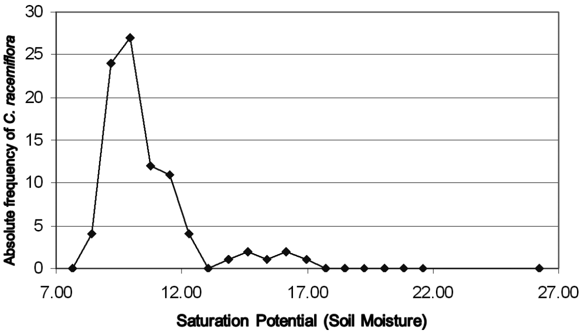

Figure 8. Absolute frequency of *C. racemiflora* along soil moisture gradients in the LEF.

Another example of the utility of the gradients approach is by Brown et al. (2008), who combined a demographic model and a niche-based model to study habitat suitability of an invasive species at multiple spatial scales. Niche-based modeling and gradient analysis address similar issues of species distribution and habitat suitability, but with different tools (Hirzel et al. 2008). Brown et al. (2008) modeled the geographical distribution of suitable habitat in the LEF for *Syzygium jambos,* a pan-tropical invasive tree that occurs throughout Puerto Rico, based on six climatic and biological variables rainfall, temperature, solar radiation, leaf area index, elevation, and canopy cover percentage. The model predicted that the most suitable habitats were at lower elevations occurring at the edges of the northern region of the LEF. In fact, this is where *S. jambos* had already been observed (Fig. 10, Brown et al. 2008). The discrimination capacity of the model (i.e. the area under curve or AUC) was calculated as 0.947, which indicated that the model can discriminate between sites with and without *S. jambos* 95% of the time. The patches with the highest suitability index values were located at the northern edges of the LEF. Based on this model, the evapotranspiration rate was assessed to be the most important environmental variable for determining suitability. Analysis of multiple factors indicated that rainfall and the 1936 canopy cover were the next two most influential variables. Model predictions were only slightly improved when temperature and solar insolation were included. Leaf area index, when used as the sole predictor variable, was not a good predictor of the plant's distribution.

Conclusions

Montane ecosystems present a unique opportunity to study the effects of environmental conditions on individ-

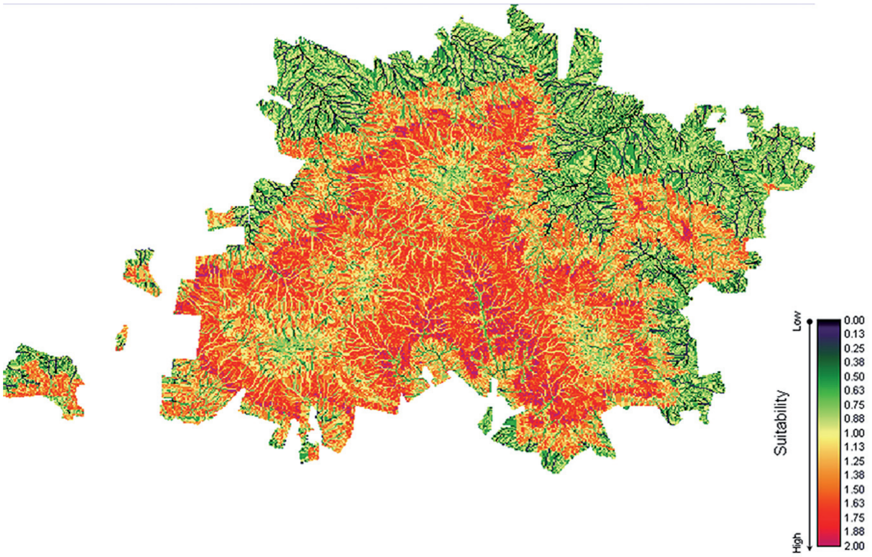

Figure 9. Suitability map for presence of *C. racemiflora* under current temperature and soil moisture conditions in the LEF. Low suitability is based on no presence of *C. racemiflora* and high suitability represents ideal environmental conditions.

ual species or broader scales because of strong gradients in small areas. In the LEF a gradients approach, as demonstrated throughout this volume, has allowed scientists to gain detailed insight into the distribution of conditions and species abundance across multiple spatial and temporal scales. As more research has included the entire mountain, it has become clear that the biological parameters vary gradually with elevation and dynamically with season. Such variations exhibit little evidence of abrupt transitions from one place to another, but instead indicate that the structure and function of the system can be described better using gradients. Most recently, researchers have begun investigating gradients that extend down the mountain into human-dominated regions (Murphy et al. 2010), including gradients of increased human population density and effects. We believe that a gradients approach should have increasing value in the tropics as we attempt to understand and predict the impacts of deforestation, climate change and other disturbance in these regions.

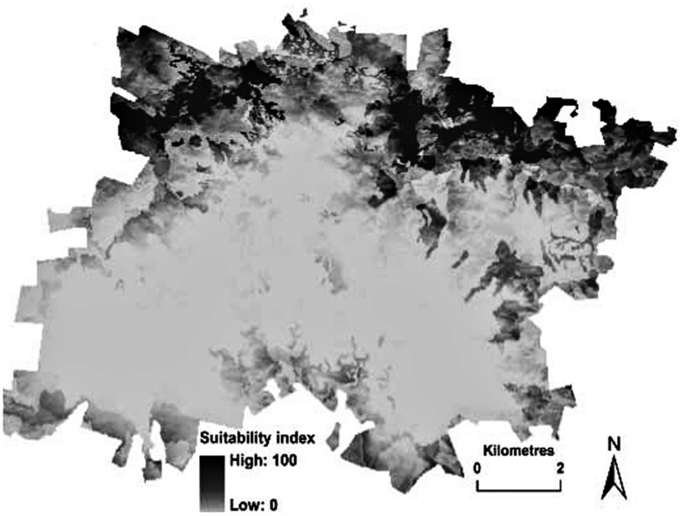

Figure 10. Simulated distribution of environmentally suitable habitats for *S. jambos* in the LEF. A continuous predicted distribution for the species is shown.

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References

Aide, T. M. et al. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. – Biotropica 28: 537–548.

Austin, M. P. et al. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. – Vegetatio 55: 11–27.

Barone, J. et al. 2008. Metacommunity structure of tropical forest along an elevation gradient in Puerto Rico. – J. Trop. Ecol. 24: 525–534.

Basnet, K. 1992. Effect of topography on the pattern of trees in tabonuco (*Dacryodes excelsa*) dominated rain forest of Puerto Rico. – Biotropica 24: 31–42.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. – Am. Nat. 124: 255–279.

Brown, K. A. et al. 2008. Multi-scale analysis to species introductions: combining landscape and demographic models to improve management decisions about non-native species. – J. Appl. Ecol. 45: 1639–1648.

Brown, S. et al. 1983. Research history and opportunities in the Luquillo Experimental Forest. – Gen. Tech. Rep. SO-44, United States Forest Service.

Bunce, J. A. et al. 1979. Role of annual leaf carbon balance in the distribution of plant species along an elevational gradient. – Bot. Gaz. 140: 288–294.

Chapin, F. S. et al. 1987. Plant responses to multiple environmental factors. – BioScience 27: 49–57.

Clements, F. E. 1904. The development and structure of vegetation. – Woodruff–Collins Printing.

Clements, F. E. 1936. Nature and structure of the climax. – J. Ecol. 24: 252–284.

Cox, S. B. et al. 2002. Variation in nutrient characteristics of surface soils from the Luquillo Experimental Forest of Puerto Rico: a multivariate perspective. – Plant Soil 247: 189–198.

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.

Curtis, J. 1959. The vegetation of Wisconsin: an ordination of plant communities. – Univ. of Wisconsin Press.

de Candolle, A. 1860. La distribution geographique de la plants de l'epoque actuelle. – Librarie de Victor Masson Paris.

Drew, A. P. 1998. Growth rings, phenology, hurricane disturbance and climate in *Cyrilla racemiflora* L., a rain forest tree of the Luquillo Mountains, Puerto Rico. – Biotropica 30: 35–49.

Drew, A. P. et al. 2009. Sixty-two years of change in subtropical wet forest structure and composition at El Verde, Puerto Rico. – Interciencia 34: 34–40.

Ewel, J. J. et al. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. – USDA Forest Service Research Paper ITF-18, Inst. of Tropical Forestry.

García-Martinó, A. R. et al. 1996. Rainfall, runoff, and elevation relationships in the Luquillo Mountains of Puerto Rico. Caribb. – J. Sci. 32: 413–424.

Gleason, H. A. 1917. The structure and development of the plant association. – Bull. Torrey Bot. Club 44: 463–481.

Gleason, H. A. 1926. The individualistic concept of the plant association. – Am. Midl. Nat. 21: 92–110.

González, G. et al. 2007. Earthworm communities along an elevation gradient in northeastern Puerto Rico. – Eur. J. Soil Biol. 43: S24–S32.

Gould, W. A. et al. 2006. Structure and composition of vegetation along an elevational gradient in Puerto Rico. – J. Veg. Sci. 17: 653–664.

Graham, E. A. et al. 2003. Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. – Proc. Natl Acad. Sci. USA 100: 572–576.

Guariguata, M. R. 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. – J. Ecol. 78: 814–832.

Hall, C. A. S. et al. 1992a. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. – Oikos 65: 377–390.

Hall, C. A. S. et al. 1992b. 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.

Harris, N. 2006. The carbon balance of a tropical forested ecosystem along an elevational gradient in the Luquillo Mountains, Puerto Rico. – PhD thesis, State Univ. of New York College of Environmental Science and Forestry.

Heartsill Scalley, T. 2012. Vegetation. – In: Harris, N. L. et al. (eds), Luquillo Experimental Forest: research history and opportunities. U.S. Dept of Agriculture, EFR-1, Washington, DC, pp. 64–72.

Hirzel, A. H. et al. 2008. Habitat suitability modeling and niche theory. – J. Appl. Ecol. 45: 1372–1381.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. – Science 105: 367–368.

Iverson, L. R. et al. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. – Ecol. Monogr. 68: 465–485.

Johnson, M. H. 1992. Soil–vegetation relationships in a tabonuco forest community in the Luquillo Mountains of Puerto Rico. – J. Trop. Ecol. 8: 253–263.

Lash, W. G. 2008. Abundance, growth, and reproduction of *Cyrilla racemiflora* as a function of environmental gradients in the Luquillo Mountains of Puerto Rico. – MS thesis, State Univ. of New York College of Environmental Science and Forestry.

Lieberman, M. et al. 1995. Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. – J. Trop. Ecol. 11: 161–177

Lortie, C. J. et al. 2004. Rethinking plant community theory. – Oikos 107: 433–438.

Lugo, A. E. et al. 1987. Leaf production, growth rate, and age of the palm *Prestoea montana* in the Luquillo Experimental Forest, Puerto Rico. – J. Trop. Ecol. 3: 151–161.

Lugo, A. E. et al. (eds) 1995. Tropical forests: management and ecology. – Springer.

Marley, D. P. 1998. Spatial modeling of climate and photosynthesis in the Luquillo Mountains, Puerto Rico. – MS thesis, State Univ. of New York College of Environmental Science and Forestry.

McDowell, W. H. 1998. Internal nutrient fluxes in a Puerto Rican rain forest. – J. Trop. Ecol. 14: 521–536.

McIntosh, R. 1967. The continuum concept of vegetation. – Bot. Rev. 33: 130–187.

Mooney, H. A. 1972. The carbon balance of plants. – Annu. Rev. Ecol. Syst. 3: 315–346.

Murphy, D. J. et al. 2010. The relationship between land cover and the urban heat island in northeastern Puerto Rico. – Int. J. Climatol. 31: 1222–1239.

Murphy, H. T. et al. 2006. Distribution and abundance across the range in eastern North American trees. – Global Ecol. Biogeogr. 15: 63–71.

Odum, H. T. et al. 1970. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. – Atomic Energy Commission.

Olander, L. P. et al. 1998. Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico. – For. Ecol. Manage. 109: 33–49.

Scatena, F. N. et al. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. – Biotropica 28: 424–440.

Schellekens, J. et al. 1999. Modeling rainfall interception by a lowland tropical rain forest in northeastern Puerto Rico. – J. Hydrol. 225: 168–184.

Schouw, J. 1822. Grundtræk til en almindelig plantegeographie. – Gyldendalske Boghandels Forlag.

Silver, W. L. et al. 1999. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. – Biogeochemistry 44: 301–328.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. – Am. Nat.133: 240–256.

Thompson, J. et al. 2002. Land use history, environment, and tree composition in a tropical forest. – Ecol. Appl. 12: 1344–1363.

Wadsworth, F. H. 1951. Forest management in the Luquillo Mountains, I. – Caribb. For. 12: 93–114.

Waide, R. B. et al. 1998. Controls of primary productivity: lessons from the Luquillo Mountains of Puerto Rico. – J. Ecol. 79: 31–37.

Wang, H. et al. 2002a. Spatial and seasonal dynamics of surface soil carbon in the Luquillo Experiment Forest, Puerto Rico. – Ecol. Model. 147: 105–122.

Wang, H. et al. 2002b. Spatial dependence and the relationship of soil organic carbon and soil moisture in the Luquillo experimental Forest, Puerto Rico. – Landscape Ecol. 17: 671–684.

Wang, H. et al. 2003. Modeling the spatial and temporal variability in climate and primary productivity across the Luquillo Mountains, Puerto Rico. – For. Ecol. Manage. 179: 69–94.

Weaver, P. L. 1986. Growth and age of *Cyrilla racemiflora* L. in montane forests of Puerto Rico. – Interciencia 11: 221–228.

Weaver, P. L. 2000. Environmental gradients affect forest structure in Puerto Rico's Luquillo Mountains. – Interciencia 25: 254–259.

Weaver, P. L. 2001. Thinning and regeneration in Puerto Rico's colorado forest, with comments about their effect on the Puerto Rican Parrot. – Caribb. J. Sci. 37: 252–258.

Weaver, P. L. and Murphy, P. G. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. – Biotropica 22: 69–82.

White, H. H. 1963. Variation in stand structure correlated with altitude, in the Luquillo Mountains. – Caribb. For. 24: 46–52.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. – Ecol. Monogr. 26: 1–80.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. – Ecol. Monogr. 30: 279–338.

Whittaker, R. H. 1967. Gradient analysis of vegetation. – Biol. Rev. 42: 207–64.

Whittaker, R. H. and Niering, W. A. 1965. Vegetation of the Santa Catalina Mountains, Arizona. II. A gradient analysis of the south slope. – Ecology 46: 429–452.

Wooster, K. M. 1989. A geographically-based microclimatological computer model for mountainous terrain with application to the Luquillo Experimental Forest in Puerto Rico. – MS thesis, State Univ. of New York College of Environmental Science and Forestry.

Wu, W. et al. 2006a. Spatial modeling of evapotranspiration in the Luquillo Experimental forest of Puerto Rico using remotely-sensed data. – J. Hydrol. 328: 733–752.

Wu, W. et al. 2006b. Predicting the temporal and spatial probability of orographic cloud cover in the Luquillo Experimental Forest in Puerto Rico using generalized linear (mixed) models. – Ecol. Model. 192: 473–498.