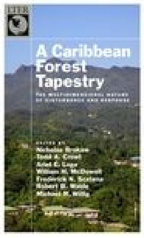

A Caribbean Forest Tapestry: The Multidimensional Nature of Disturbance and Response

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CHAPTER

2 Conceptual Overview: Disturbance, Gradients, and Ecological Response

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Abstract

This chapter examines the causal relationship of physical and climatic gradients to the environmental conditions and resources of the ecosystem. It dwells mainly on the sets of relationships in an abiotic environment, structural environment, biotic environment and disturbance regime. It then distinguishes the varied effects brought by natural variables such as tectonic activity, changes in physiography, and sea level from the regional variables such as topography and global climate through a conceptual model for spatial and temporal dynamics of patterns of Luquillo Mountains.

Keywords: climatic gradients, abiotic environment, structural environment, biotic environment, disturbance regime, physiography, global climate, Luquillo Mountains, spatial dynamics, temporal dynamics

Subject: Plant Sciences and Forestry

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Key Points

- The abundance and distribution of organisms and the attendant ecosystem processes vary across the landscape of the Luquillo Mountains in relation to underlying patterns of spatial heterogeneity and gradients of environmental factors.
- The ecosystems of the Luquillo Mountains are affected by frequent climate-induced disturbances such as treefalls, landslides, tropical storms, and droughts, as well as by human-induced disturbances associated with land use (i.e., agriculture and forest harvest).
- The term “ecological space” refers to multivariate dimensions defined by a suite of environmental characteristics. Disturbances can disrupt or create gradients by altering the mapping of ecological characteristics onto geographic space.
- Because the relationship between geographic space and ecological space is dynamic, the relationship between the physical template and the distribution and abundance of animal, plant, and microbial species cannot be understood without reference to the disturbance regime.
- The resilience of an ecosystem to anthropogenic disturbances might be low because such disturbances often produce severe modifications to the environment, creating novel combinations of environmental characteristics that are outside of the ecological space that was characteristic of the site or which are characterized by the absence of biological residuals.
- p. 43 ↳ Historical factors, as well as contemporary geology, topography, and abiotic or biotic conditions, interact to create spatial variability in ecological characteristics. This variability ultimately determines the abundance and distribution of species in the Luquillo Mountains.

Introduction

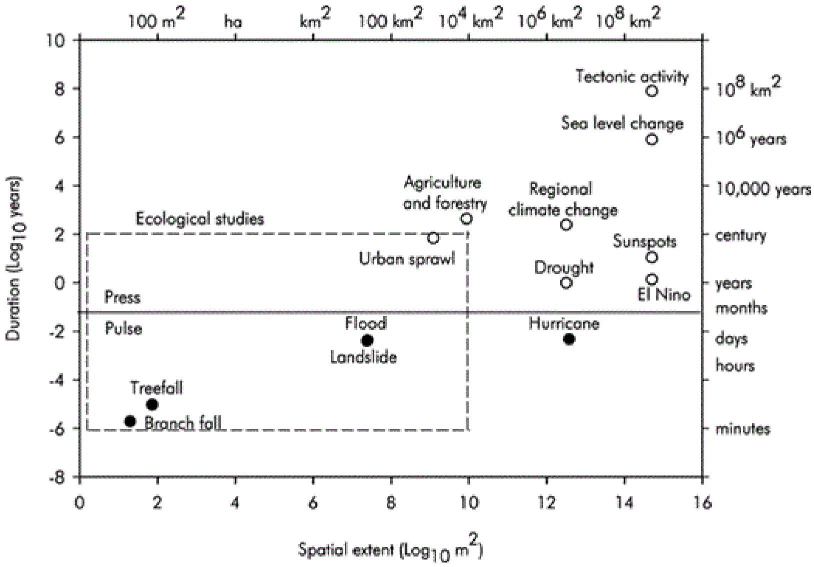
The importance of environmental conditions and resources in determining the distribution and abundance of organisms is a fundamental tenet of ecology (Shelford 1951; Andrewartha and Birch 1954; Maguire 1976; Krebs 1985; Tilman 1988; Smith and Huston 1989). As Lugo et al. point out in chapter 1, spatial gradients in environmental conditions underlie the geographic distribution of ecosystems at global scales and affect the variation within ecosystems at smaller scales. The number of studies of physical and climatic gradients in the ecological literature demonstrates the importance attached to environmental conditions and resources as controls of ecosystem structure and function. Thus, knowledge of the long-term spatial and temporal patterns of environmental factors is critical if one is to understand the dynamics of ecosystems.

The ecosystems of the Luquillo Mountains are affected by frequent disturbances, as defined below and as described in chapter 4. The Luquillo Long Term Ecological Research (LTER) program has focused much effort over the past 20 years on understanding the impacts of two hurricanes, Hugo and Georges, in the context of a disturbance regime that also includes treefalls, landslides, tropical storms, and droughts and which has included human-dominated land uses such as agriculture and forest harvest in the past. This chapter provides an overview of an integrated research framework that incorporates theoretical elements from studies of disturbance and environmental variation.

Field observations supported by experiments and modeling during the past 45 years have led to the formation of an overarching conceptual model for integrating the spatial and temporal dynamics of pattern and process that define the contemporary tapestry of the Luquillo Mountains. In this model, the geological template and the geographic context change slowly over long time scales (figure 2-1) and are driven by processes such as tectonic activity, changes in physiography, and sea level changes. In contrast, regional climate, driven by topography, geography, and global climate, is potentially more dynamic and might change at the scale of centuries or less. Finally, frequent local disturbances provoke dynamism in the system at the annual or decadal scale. Together, geology, topography, regional climate, and disturbance produce heterogeneity or variation in the abiotic environment. The abiotic environment, the disturbance regime, and the regional species pool determine the composition of the biota, which then feeds back to modify the disturbance regime, the structural environment, and the abiotic environment. This last set of relationships

—those among the abiotic environment, the structural environment, the biotic environment, and the disturbance regime—provides the focus for the remainder of this chapter. Definitions of key concepts that relate to these relationships supply critical background for further exploration of these concepts in later
p. 44 chapters. ↳

Figure 2.1



Diagrammatic representation of the temporal and spatial relationships of processes that interact to generate heterogeneity in the ecosystems of the Luquillo Mountains. “Duration” refers to the extent of time over which a process acts. Circles represent the approximate median values for each process in time and space. The horizontal solid line separates press disturbances (open circles), which act over long time periods, from pulse disturbances (solid circles), which act over short periods of time. The dashed box bounds the spatial and temporal extent of most ecological studies in Puerto Rico. The study of the full spatial or temporal extent of some processes requires collaboration with other disciplines (e.g., geology, paleoecology, climatology) or comparative studies using syntopic networks. For example, a full understanding of hurricanes requires information about storms with a wide range of physical characteristics, as well as information about storm impacts under different socioecological conditions. See the text for further explanation.

Components of the Environment of the Luquillo Mountains

The abundance and distribution of organisms, as well as the attendant ecosystem processes, vary across the landscape of the Luquillo Mountains in relation to underlying patterns of spatial heterogeneity and gradients of environmental factors. This variation reflects contemporary, past, and ancient processes operating at multiple spatial and temporal scales (figure 2-1) and results in the abiotic and biotic layers that imbue the current ecological tapestry of the Luquillo Mountains with structure. The abiotic and biotic layers interact within the contexts of geography (surrounding continents and oceans), climate, and regional species pools to determine the spatial and temporal patterns of the ecosystems of the Luquillo Mountains. A complex disturbance regime that includes hurricanes, tropical storms, landslides, and treefalls, as well as
p. 45 anthropogenic disturbances associated with forest management, urbanization, ↳ and other land uses, makes these patterns dynamic and increases the environmental variability. The following overview of environmental patterns and disturbance provides the necessary background for a discussion of ecological space and presages the more detailed treatments of these subjects in chapters 3, 4, and 5.

The Abiotic Environment

Geographic Context and Geologic Template: Changes over Long Time Scales

Puerto Rico lies as a fulcrum between the Greater and Lesser Antilles as a consequence of tectonic movements that have persisted for tens of millions of years and which continue to the present. More specifically, Puerto Rico was formed by volcanic activity and tectonic uplift during the Albian to the upper Eocene (120 to 140 million years ago), followed by erosion and later sedimentary deposition. The same geological processes that created Puerto Rico molded the topographic irregularities of the island, and the local variation in the topography adds heterogeneity to the larger-scale pattern. These ancient and ongoing processes placed Puerto Rico in the midst of oceanic currents, airsheds, and atmospheric fronts, thereby determining to a great extent the prevailing climatic conditions and disturbance regime of the island. Processes such as glacial fluctuations also determined the geographic relationship of Puerto Rico to other islands, continents, and bodies of water. Such historical factors shaped the biogeographic affinities of the island and influence the current biotic composition and richness of Puerto Rico.

Climate and Topography: Changes over Moderate Time Scales

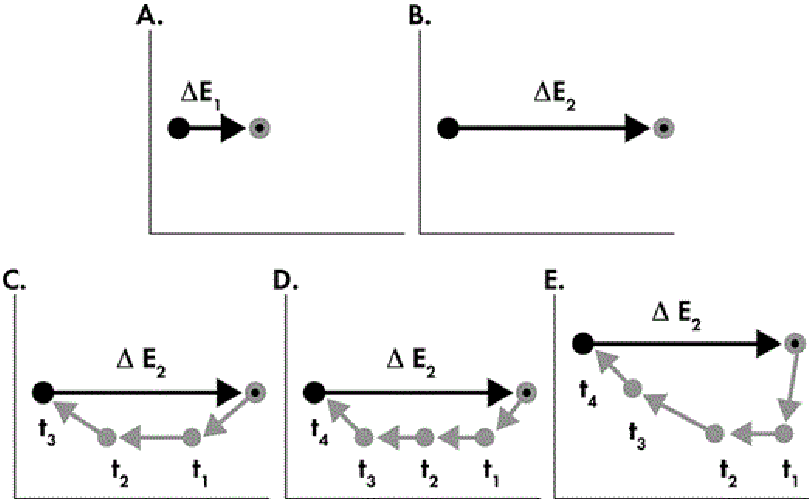
The steep topographic gradient of the Luquillo Mountains (sea level to 1000 m in 8 km) produces landscape-scale variability in the local climate, abiotic characteristics (e.g., soil nutrient levels), and disturbance regime. Across this short spatial extent, the temperature decreases and precipitation increases from sea level to the summit. The direction of the prevailing winds from the northeast creates windward-leeward variation in temperature, rainfall, and windspeeds. Periodic shifts in ocean currents modify the near-shore environment and influence meteorological patterns over the land. Across the smaller scale of land forms, local relief contributes to spatial variation in the abiotic conditions (e.g., pH, oxygen content, soil moisture, temperature, insolation) because of differential exposure to sunlight and flows of water and air from ridges downslope to valleys. The interaction of topography and regional climate creates clouds that frequently shade the upper elevations in the Luquillo Mountains and consequently modify abiotic gradients. Many of the geophysical and geochemical characteristics of soils are determined by the nature of the rock underlying them (e.g., volcaniclastic versus igneous soils). Biogeochemical fluxes of nutrients vary with topography and soil characteristics. The topographic characteristics of the land influence both large-scale disturbances (the effects of hurricanes are more severe on windward sides of mountains) and small-scale disturbances (landslides are most likely to occur on steep slopes; see chapter 4).

Disturbance: Changes over Short Time Scales

Disturbance is a pervasive feature of ecological systems (Pickett and White 1985; Walker and Willig 1999; Willig and Walker 1999) and is a primary driver that produces temporal dynamics in the abiotic and biotic characteristics associated with geographic space. Although disturbance has been defined in a variety of ways (e.g., Sousa 1984), we follow the modified definition of Pickett and White (1985) that was offered by Walker and Willig (1999:3): a disturbance is a relatively discrete event in time and space that alters the structure of populations, communities, and ecosystems, including their attendant processes. Pulse (acute) disturbances are those that transpire over short periods relative to the dynamics of the focal system (e.g., hours, as in hurricanes in a tropical forest), whereas press (chronic) disturbances are those that transpire over longer periods (e.g., months, as in drought in tropical forests). Although the pulse/press dichotomy is a simplification of a continuum of disturbance characteristics, the principal disturbances in the Luquillo Mountains do separate into two classes according to their temporal attributes (figure 2-1). The effects of disturbance are detected as changes in the density, biomass, or spatial distributions of the biota; as alterations in the availability and distribution of resources and substrate; or as alterations in the physical environment. Consequently, disturbance creates patches, affects spatial heterogeneity, and modifies the spatial gradients of environmental factors.

The degree to which ecosystem characteristics remain unaffected by disturbance is referred to as *resistance* (figures 2-2[A] and 2-2[B]). The time required for an ecosystem to return to conditions that are indistinguishable from those prior to a disturbance represents the system's *resilience*. Systems that return more quickly to predisturbance conditions are more resilient than those that return more slowly (figures 2-2[C] and 2-2[D]). Nonetheless, even when two ecosystems are equally resilient, one can undergo more dramatic changes in its ecological characteristics than the other (figures 2-2[D] and 2-2[E]).

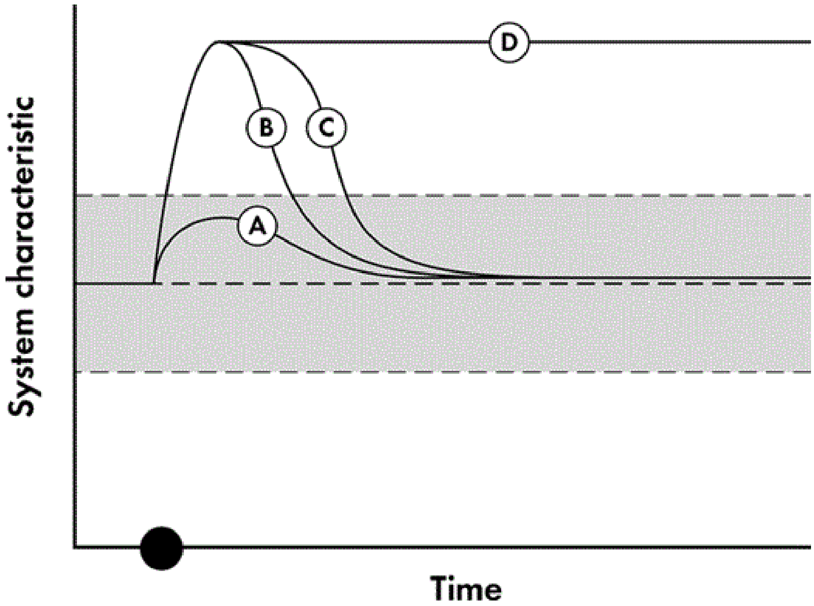
Figure 2.2



Representation of resistance and resilience in ecological space (E) defined by two axes. Each axis can represent aspects of the abiotic (e.g., soil moisture and soil temperature), structural (e.g., foliage height diversity and litter depth), or biotic (e.g., abundances of *Piper glabrescens* and *Piper hispidum*) environment. Change in these ecological attributes as a result of a disturbance (ΔE, illustrated by a solid arrow) quantifies resistance. Panel (A) illustrates a more resistant system (i.e., ΔE_1 is small) than does panel (B) (i.e., ΔE_2 is large). The time needed for a system to return to predisturbance conditions quantifies resilience (number of gray arrows). Panel (C) illustrates a more resilient system (i.e., the time to recovery is short [three time steps]) than does panel (D) (i.e., the time to recovery is long [four time steps]). Although two systems can be equally resilient (i.e., panels [D] and [E] both represent a return to predisturbance conditions in four time steps), secondary succession might evince different trajectories of recovery, with some moving the system to states quite distinct from those of the pre- or even postdisturbance (immediate) environmental conditions (i.e., compare panel [E] to panel [D]).

The combination of resistance and resilience to disturbance produces ecological patterns over time (figure 2-3). In some cases, disturbances can be sufficiently severe as to arrest ecosystem development for extended periods or to prevent the system from returning to predisturbance conditions (Carpenter 2001). Importantly, assessments of stability, resistance, and resilience are each scale dependent. For example, at a small focal scale such as a plot (e.g., square meters), sites might not return to predisturbance conditions with respect to the species composition for long periods, if ever. But at a larger focal scale, such as a watershed (e.g., square kilometers), sites might more quickly return to predisturbance conditions, because the variation among plots within watersheds is amalgamated into the larger spatial unit. Thus, at large scales, systems can be quite stable even if they are markedly unstable or even hypervariable at smaller constituent focal scales. In such situations, the larger system can act as a metacommunity that exhibits metastability (see Wu and Loucks 1995; Ingegnoli 2004).

Figure 2.3



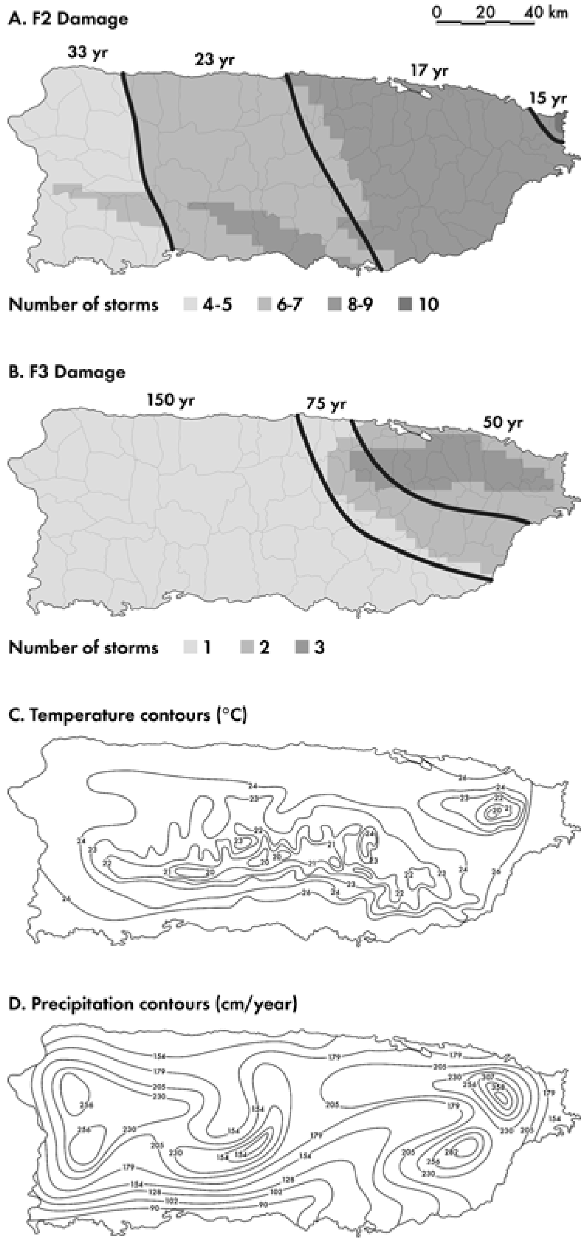
Representation of various idealized types of responses to disturbance. Solid lines represent trajectories of response after a disturbance event (solid circle); the long-term baseline conditions in the absence of disturbance are indicated by the gray shading. Response A is the most resistant, as the system characteristics after disturbance never exceed those of baseline. Responses B, C, and D are equally resistant, but they differ in their resilience. Response B is more resilient than response C, as the system characteristics return to baseline more quickly in the former than in the latter. Response D does not exhibit resilience; the disturbance sufficiently alters the system so that it occupies a new state rather than returning to baseline conditions.

Adapted from Zimmerman et al. (1996).

The Biotic Environment

The composition of the biota of the Luquillo Mountains is determined by a complex combination of factors that act over a wide range of spatial and temporal scales. The insular species pool is regulated largely by the p. 47 biogeographic factors of the island's ↳ size and location, the distance from source biotas, and the colonizing ability of different species. Thus, the biota of Puerto Rico (both present and fossil) lacks many groups of large mammals (Willig and Gannon 1996) and birds (Waide 1996) that are characteristic of mainland tropical forests. Invasions and extinctions continue at a slow-to-moderate pace (e.g., five bird species lost within the past 100 years [Raffaele 1989]) and contribute to species turnover and spatial heterogeneity. On the island, a north-south rainfall gradient and an east-west disturbance gradient (figure 2-4), as well as biotic interactions such as competition, predation, and mutualism, affect the distribution of species. Local variation in the topography, edaphic characteristics, and a multitude of abiotic factors adds heterogeneity to the larger-scale pattern.

Figure 2.4



Disturbance frequency decreases from east to west across Puerto Rico, based on the number of storms from 1886 to 1996. The number of storms that were classified as F2 (extensive blowdowns; panel [A]) or F3 (forests leveled; panel [B]) on the Fujita scale defines damage classes and return intervals for each damage class (modified from Boose et al. [2004]; damage classes redrawn into new map projections with new shading). Spatial variation characterizes temperature (panel [C]) and precipitation (panel [D]) across Puerto Rico (modified from Gannon et al. [2005]; values converted from English to metric system and inserted into contours of the map). The Luquillo Mountains, located in the northeast corner of the island, experience considerable elevational variation in temperature and precipitation (panels [C] and [D]) and lie in one of the most frequently affected areas of Puerto Rico (panels [A] and [C]).

Legacies of human intervention complicate the biogeographic patterns. Habitat modification is severe and widespread in Puerto Rico; at one time, forests occupied less than 5 percent of the island (Birdsey and
p. 48 Weaver 1982). Socioeconomic changes since 1950 have led to gradual reforestation, but new forest ↳ patches accumulate native species slowly and might be dominated at some scales by introduced taxa (Aide et al. 1996; see also chapter 8). Although the introduction and establishment of introduced species have increased the total number of species on the island, some introduced species have also endangered endemic animal diversity. The roof rat (*Rattus rattus*), the small Indian mongoose (*Herpestes auropunctatus*), and the earthworm (*Pontoscolex corethrurus*) are examples of introduced species that have affected the distribution and abundance of native fauna (Willig and Gannon 1996; Zou and González 1997). Active management of the biota encourages the persistence of some species and can determine the bounds of their distributions (e.g., the Puerto Rican parrot, *Amazona vittata* [Snyder et al. 1987]).

The biota responds to abiotic gradients in the Luquillo Mountains and interacts with them to produce observable ecological patterns (see chapter 3). The forest canopy moderates temperature in the understory
p. 49 and traps moisture, whereas openings in the canopy lead to increased sunlight at the forest ↳ floor, which

increases spatial variation in the temperature at the litter layer (Odum et al. 1970; Devoe 1989; Scatena 1990). Fungal mats interconnect dead leaves in the litter and in the canopy, reduce the likelihood of export from terrestrial systems during heavy rains, and enhance the retention of limiting nutrients via their incorporation into biomass (i.e., immobilization) (Lodge and Asbury 1988). Root mats and root grafting among individuals (Basnet et al. 1992) likely stabilize the soil and reduce erosion. Plant species assimilate and concentrate nutrients and trace elements differentially, thereby producing considerable spatial dynamics in biogeochemicals (Scatena et al. 1993). Earthworms mix and aerate the soil and provide routes for the flow of groundwater through the soil (Zou and González 1997). Such mediating influences of the biota are particularly important under the conditions that can result from disturbance (Willig and McGinley 1999).

The distribution of species in the Luquillo Mountains responds to both geological layers and abiotic layers of the current tapestry, and it modifies them in turn. For example, the species composition and physiognomy of plants vary markedly along the elevational gradient in the Luquillo Mountains (Crow and Grigal 1979; Weaver 1991; Gould et al. 2006; also see chapter 3). Cool and wet high elevations support elfin forest, characterized by an intermeshing root mat on the forest floor and small trees festooned with mosses and lichens reaching up to a 3 to 10 m canopy. Lower elevations are warmer and less wet and support tabonuco forest, which is characterized by an extensive litter layer and buttressed trees forming a canopy at 20 to 22 m. Soils at mid- to high elevations that are poorly drained because of the topography support almost pure stands of sierra palm (*Prestoea montana*).

In the Luquillo Mountains, the species richness of most taxa decreases with increasing elevation (Waide et al. 1998), although some groups evince a modal distribution with a maximum in the lowlands (see, e.g., Alvarez 1997). Species appear and disappear along the elevational gradient, and introduced species become less common with distance from human disturbances such as roads (Olander et al. 1998). Variation in the community composition can affect biogeochemical processes, as well as the capacity of the biota to moderate the environment after disturbance. Thus, biotic variability adds a vital layer to the tapestry that is the Luquillo Mountains and increases the complexity of interactions involving the abiotic and biotic environments and the disturbance regime.

Gradients and the Dynamics of Pattern and Process

The proposal that led to the foundation of the Luquillo LTER program (Luquillo LTER 1988) addressed the challenge of linking point and stand data to landscape-scale patterns and processes through simulation modeling: "We propose to develop an explicit scheme for translating geographical information, derived from geographical space, into model parameter space (equivalent to ecological space), using a gradient approach" (p. 14). The term "ecological space," referring to environmental characteristics arrayed along gradients in geographic space, was first used by Minchin (1987) and draws on ideas from Whittaker (1956) and Austin and Cunningham(1981). ↳

p. 50

p. 51 ↳

Our initial use of the idea of ecological space did not acknowledge the complications that disturbance might cause with regard to translating geographic information into model parameters. Disturbance can disrupt or create gradients by altering the mapping of ecological space on geographic space. Six years later, after we had experienced the effects of a major hurricane, a more sophisticated explication of the relationship between geographical location, resource gradients, and disturbance formed the rationale of the second LTER proposal (Luquillo LTER 1994). Five premises derived from our own observations (Hall et al. 1992a, 1992b) and from the literature (Keddy 1991; Gosz 1992) formed the basis for our research approach.

1. The distribution of organisms and associated rates of ecosystem processes are related to a limited number of spatial gradients of environmental factors (e.g., temperature, sunlight, soil moisture, and soil nutrient levels) in the landscape.

2. Each physical position on the landscape (i.e., geographical space) has a representation in n-dimensional gradient space (or ecological space). This representation in ecological space is determined by interactions of geography, geology, climate, topography, disturbance history, and the biota, which collectively determine the conditions along each primary gradient.

3. Disturbance affecting a spatial position in the landscape displaces conditions in ecological space. Disturbance modifies characteristics with respect to many or all environmental factors or conditions, resulting in a new spatial configuration of ecological space. Describing displacements in ecological space potentially allows for a mechanistic understanding and predictions of changes in distributions and rates of processes.

4. An explicit consideration of the association between geographic space and ecological space facilitates the comparison of different types of disturbances. Different disturbance types have characteristic directions of displacement in ecological space. The size and, especially, the intensity of the disturbance influence the magnitude of the displacement in that characteristic direction. The frequency of disturbances, in conjunction with the response time, influences the impact of subsequent disturbances. If a subsequent disturbance (or a new type of disturbance) results in a further displacement before the response to an initial disturbance is complete, new and unique positions in ecological space might result.

p. 52

5. ↳ In this conceptual framework, resistance and resilience to disturbance can be defined and quantified. Resistance is related to the displacement in ecological space for a given disturbance. Resilience is the time required in order to return to the original position (or a position much like the original position) for a given displacement.

Our conceptual approach, and especially its development from an energetic perspective (see below), helped to integrate studies at various levels of biotic organization by providing a framework that was intuitively attractive to population, community, and ecosystem ecologists. The idea of ecological space shared concepts with niche theory (Hutchinson 1958, 1965) and thus provided common intellectual ground across subdisciplines. However, the fundamental niche stays relatively constant over ecological time scales, whereas disturbance can modify ecological space over relatively short periods, leading to community reorganization after disturbance. This conceptual approach integrates studies at various levels of biotic organization and provides a mechanism for synthesis and modeling that is extremely powerful because of its quantitative nature. Understanding gained from this approach is directly applicable to the evaluation of techniques for the ecological management of tropical forests under different disturbance regimes.

Dynamics of Ecological Space and the Biota

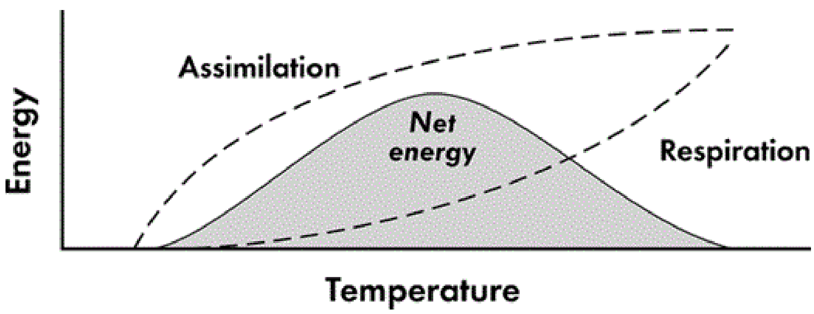
The mechanisms by which the abiotic environment determines the distribution of species, the composition of communities, and the nature of ecosystem processes act on individual organisms. The currency of that interaction is energy. More specifically, the existence of an organism under particular environmental conditions depends on the energy balance of the organism (Shelford 1951; Maguire 1976; Dill 1978; McNab 1980; Kitchell 1983; Root 1988; Covich 2000). The dynamic nature of the determinants of energy balance arises from variation in abiotic factors, including those associated with the disturbance regime. In the following sections, we review these processes from the perspective of the species (niche-based), the disturbance regime (disturbance-based), and the community (succession-based).

Energetic Basis of Organismal Responses to the Environment

Organisms respond to gradients of and heterogeneity in environmental characteristics as a consequence of their morphological, physiological, and behavioral attributes. These attributes essentially determine the fitness for organisms at any location. These concepts are rooted in niche theory (Hutchinson 1958, 1965) and have been amplified in the context of a common currency, namely, energy (Hall et al. 1992b). The presence, abundance, and behavior of a species are linked intimately to the energetic costs and benefits associated with living in a particular geographic position. A species can persist in an area only if the long-term energy gains equal or exceed the costs, thereby facilitating growth and reproduction (Hall et al. 1992b and references therein). The effects of abiotic resources (e.g., low levels or high levels of nutrients), as well
p. 53
as biotic interactions (e.g., the presence of consumers or mutualists), can be incorporated into such ↳ a conceptual model as energetic costs or benefits. For example, in order to survive and persist in an area characterized by low nitrogen availability, an organism must invest in phenotypic characteristics that allow it to accumulate nitrogen, resulting in reduced energy allocation to reproduction. In the absence of mutualism, this tradeoff might narrow the range of acceptable nitrogen levels to a subset of what exists in ecological space. Similarly, the energy used to escape predation, through chemical defenses (e.g., toxins), morphological structures (e.g., thorns or thick cuticles), or behavioral activities (e.g., lunar phobia enacted to avoid visual predators at night), must be diverted from energetic resources that could otherwise be allocated to growth and reproduction. Nonetheless, areas with abundant resources might not support the persistence of a species if the cost of predation is high. Alternatively, the presence of mutualists such as root mychorrizae can reduce the cost of acquiring essential nutrients such as nitrogen or phosphorus, thereby facilitating the persistence and reproduction of a species in a habitat that otherwise would be impossible to thrive in energetically. Energetic tradeoffs exist because the cost of investment in any set of phenotypic characteristics associated with the soma reduces possible investments in reproductive output.

Energetic tradeoffs are particularly relevant for understanding elevational or latitudinal distributions of species because costs (respiration rates) and benefits (assimilation rates) vary with temperature in nonlinear ways (figure 2-5). Respiration is the metabolic cost of executing vital physiological processes. The respiration rate is positively and often exponentially related to the temperature for extensive portions of the thermal gradient (i.e., a Q_{10}-type response). Assimilation rates also increase with temperature, but they do so in a near-asymptotic manner. That is, the rate of increase decreases with increasing temperature (i.e., saturates), essentially reaching zero. The difference between the rates of assimilation and respiration represents the net profit (or loss) associated with life at any point in the thermal gradient. Because of the general shapes of the response curves for assimilation and respiration, the difference results in a net profit curve that is modal or Gaussian in form (figure 2-5). Such net profits are available for allocation to biomass accumulation (growth) or reproduction (figure 2-6). Thus, individuals of a species might be found in environments in which they can (1) subsist only for short periods of time, (2) survive indefinitely but not reproduce (sink habitats), or (3) persist and reproduce beyond replacement (source habitats) (Pulliam 1996). Other biotic or abiotic factors effectively shift the cost or benefit curves, expanding or contracting the thermal range in which individuals maintain source or sink populations.

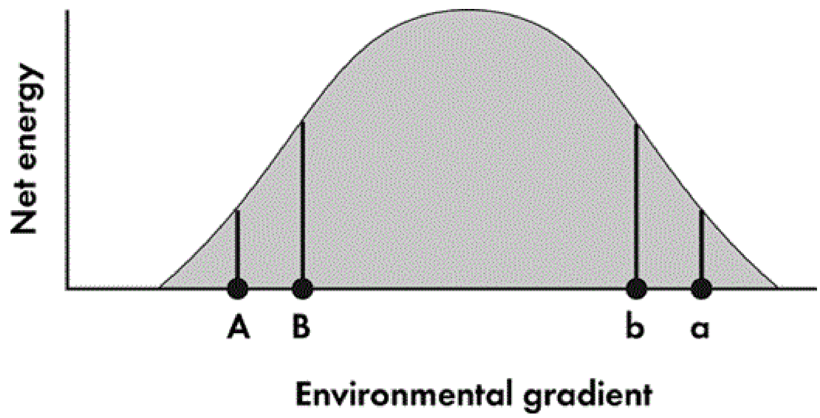
Figure 2.5



The joint effects of assimilation and respiration rates determine whether particular regions of ecological space (here associated with temperature) are occupied by particular species. The exact form and location of rate curves are species-specific and determine the net energy balance (represented by the area under the bell-shaped curve) available for allocation to growth and reproductions.

Modified from Hall et al. (1992a).

Figure 2.6



The net energetic profit based on the difference between assimilation and respiration is a Gaussian or bell-shaped curve, with the presence of sink and source populations predicated on considerations of energy allocation. Positions along the environmental gradient between points B and b provide sufficient energetic rewards so that populations can produce an excess of individuals (positive growth) and may colonize other areas. Positions along the environmental gradient between points A and B or points a and b do not allow for a population increase, even though individuals can persist there indefinitely. Consequently, populations at these locations in the environmental gradient must be maintained in the long term by immigration from source areas. At positions along the environmental gradient <A or >a, individuals cannot survive indefinitely; thus, a species is represented in those regions by only transient individuals.

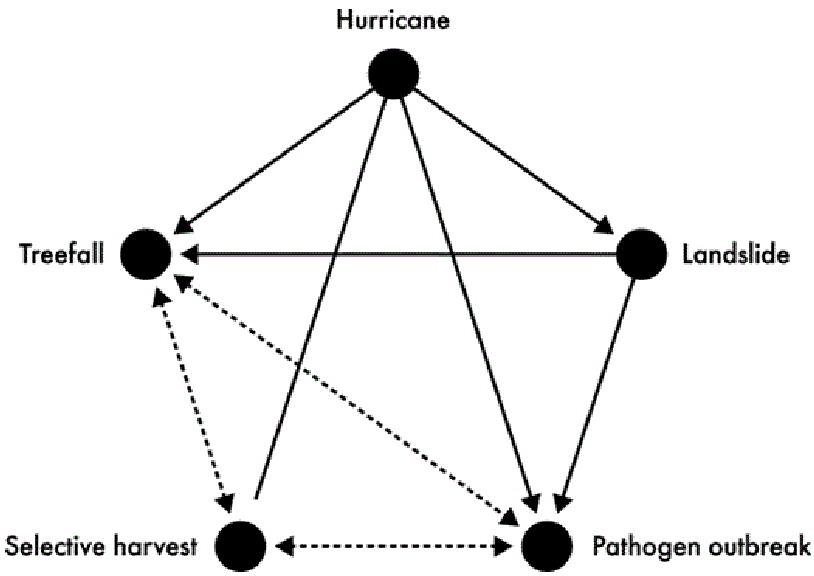
Modified from Hall et al. (1992a).

Disturbance and Biotic Response

Disturbance is one of the most important factors that elicit changes in the structural or functional aspects of ecosystems. Structural elements include community attributes such as species richness, species diversity, guild diversity, species composition, rarity, and species dominance. Functional elements are related to ecosystem processes such as decomposition and production and include primary productivity, secondary productivity, decomposition rates, mineralization rates, and nutrient fluxes. The sequence of changes in these characteristics that follow disturbance can be visualized as a vector or trajectory of response.

p. 54 Disturbance is caused by an agent or entity (e.g., the winds of a hurricane, the heat of a fire) that initiates changes in the spatiotemporal characteristics of the ecological system of interest, often detected as changes in the amount or distribution of biomass. Most ecological systems are subject to a number of disturbance agents. The combination of agents at a particular place represents the disturbance regime. Any particular disturbance event might alter the frequency, extent, or intensity of other disturbances (figure 2-7). Such interactions can be additive, synergistic, or antagonistic and are important considerations when attempting to understand disturbance and response in ecological systems (Walker and Willig 1999; Willig and Walker 1999).

Figure 2.7



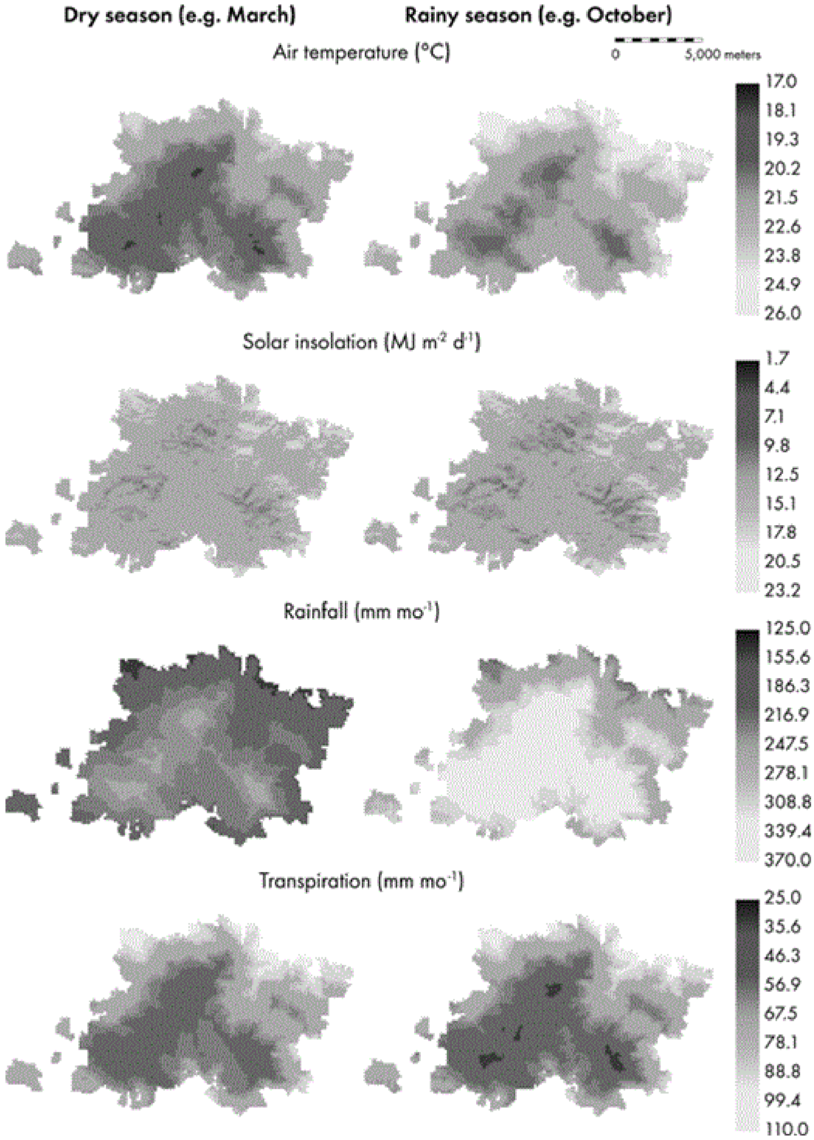
Representation of aspects of the disturbance regime for the Luquillo Mountains as embodied by the interactions between disturbance elements (e.g., hurricanes, landslides, treefalls, selective harvest, pathogen outbreak). For simplicity of exposition, only a few of all possible elements are illustrated. Arrows represent the influence of one element of a disturbance regime on another (e.g., the occurrence of a hurricane increases the likelihood of subsequent disturbance from landslides). Solid lines indicate strong influences, whereas dashed lines indicate weak influences. Double-headed arrows represent reciprocal causality or effects.

Modified from Willig and Walker (1999).

p. 55 Because the Luquillo Mountains are situated on an island in the Caribbean with a long history of human settlement and are in the path of the Atlantic Trade Winds, they have a complex disturbance regime. The regime (or a portion of it) may be represented as a number of interacting agents including hurricanes, landslides, treefalls, selective harvest, and pathogen outbreaks (figure 2-7). The occurrence of one agent of disturbance (e.g., a hurricane) might enhance the likelihood of subsequent disturbances (e.g., landslides). Moreover, some agents of disturbance might have reciprocal effects: treefalls enhance the likelihood of pathogen outbreaks, and pathogens enhance the likelihood of treefalls (Goheen and Hansen 1993; Webb 1999). At any point in time, the disturbance regime might enhance or reduce the spatial heterogeneity in local climatic or abiotic characteristics, thereby affecting the abundance and distribution of species across the landscape.

Heterogeneity or variability in the environmental characteristics to which organisms respond can arise in a variety of ways, including as a result of topography, disturbance, and succession. All of these sources of variation interact within a landscape, and in turn they are affected by their spatial context. In the Luquillo Mountains, topographic variation generates gradients in important climatic drivers such as solar insolation, temperature, and precipitation (figure 2-8) and produces environmental heterogeneity of abiotic factors (Cox et al. 2002). At broad spatial extents, we evaluate how elevational variation in key environmental
p. 56 drivers produces gradients that induce variation in populations ↳ and communities, as well as in associated biogeochemical processes. At narrower spatial extents, we describe how environmental variation associated with the local topographic position—ridge, slope, upland valley, and riparian valley (i.e., the catena)—translates into population-, community-, and ecosystem-level variability.

Figure 2.8

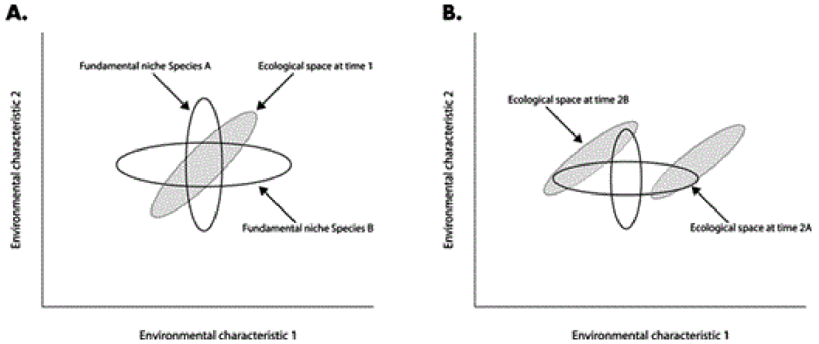


Spatial variation in temperature, insolation, precipitation, and transpiration in the Luquillo Mountains based on the spatially explicit model TOPOCLIM (Wooster 1989). Slope, aspect, and elevation are used as input data for the model. Historical climate data are used to parameterize model equations that estimate climatic variables. Simulated air temperature (°C), solar insolation (MJ m^{-2} day^{-1}), rainfall (mm/month), and transpiration (mm/month) are shown for dry and rainy seasons (Wang et al. 2002). Values increase from violet to red in the color spectrum.

The response of organisms to environmental factors defines their niches and facilitates the prediction of species distributions, provided that key environmental factors have a consistent association with geographic space over time. Modeling algorithms (e.g., GARP) (Peterson 2001) can be used to define key factors associated with species occurrences. When combined with spatially explicit environmental data, these algorithms predict the fundamental niches of organisms. Differences between predicted and actual distributions might point to biotic interactions that affect realized niches or to dispersal limitations. However, these models often are based on average conditions that do not reflect temporal extremes, and as a result they might predict overly broad distributions. Consequently, such models might fail to capture the full temporal variability in the spatial distribution of organisms.

Because of their particular niche characteristics, species are predisposed to exist under environmental conditions associated with particular geographic areas. However, points in geographical space do not maintain a constant relationship with ecological space because of disturbances and biotic responses, including succession. Thus, species can persist in a particular area only if they can survive and reproduce under the environmental conditions that occur over long time scales relative to the life of an organism. Because the relationship between geographic space and ecological space is dynamic, the relationship between the physical template and the distribution and abundance of animal, plant, and microbial species cannot be understood without reference to the disturbance regime. As the mapping of ecological space to geographical space changes, species co-occurrences might be affected, with consequent cascading effects on competitive, predatory, or mutualistic relationships (figure 2-9; see also chapter 6). The biota's response to the dynamic relationship between geographic and ecological space is reflected in successional changes that have their origins in disturbance.

Figure 2.9



In order for a species to persist at a geographic location, it must be able to survive the full range of environmental conditions and resources that occur there over time. Alternatively, the species' behavior (e.g., emigration or migration) can result in the avoidance of unfavorable environmental or resource conditions. Moreover, variations in the ecological attributes of geographic space over time affect species interactions, niche breadth, and co-occurrence at a smaller spatial scale. (A) At a particular point in geographic space, the ranges of values that exist for each of a number of environmental characteristics (e.g., temperature, rainfall) define the ecological space at that point. A species can occur at this geographic point if its fundamental niche overlaps with the corresponding ecological space. Species with fundamental niches that overlap within the existing ecological space (gray shading) can co-occur. (B) As the result of a disturbance, the values of environmental characteristics might change, redefining the ecological space at time 2. If ecological space shifts to position 2A, only one species can persist under the new conditions; if ecological space shifts to position 2B, both species can persist, but they cannot co-occur. In systems in which disturbance creates shifts in ecological space that are frequent compared to species' generation times, broad fundamental niches would be favored (Waide 1996).

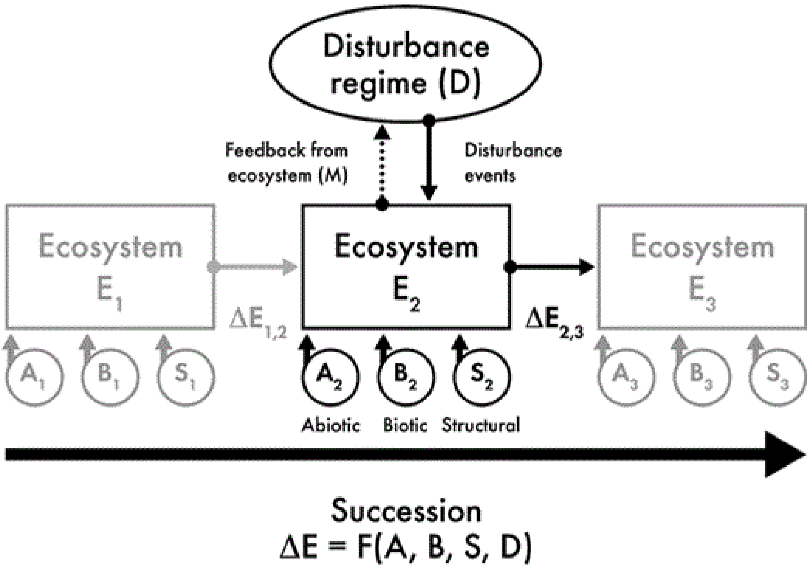
Long-term responses to a disturbance are determined by the postdisturbance environment, which includes the character and heterogeneity of the abiotic environment, the composition of the surviving organisms, and the structural legacies of the disturbance event. However, the characteristics of the postdisturbance environment also are influenced by preceding disturbances, so that at any one time the biota generally is responding to multiple historical disturbances. It is this integrated response that determines the trajectory of the community composition, structure, and function (i.e., successional dynamics) over time after any particular disturbance event. Knowledge of the natural variability (Landres et al. 1999) of an ecosystem is critical to an understanding of responses to a specific disturbance, including those involved in human-managed ecosystems (chapter 7). Consequently, the interplay between disturbance and biotic response is
p. 57 best understood within the context of succession. ↳

p. 58 ↳

Succession

Disturbance initiates succession, influences subsequent trajectories in abiotic and biotic characteristics, and moderates successional rates, endpoints, and durations. We follow a basic conceptual model (Willig and Walker 1999) when attempting to understand how disturbance and succession interact to produce a spatially and temporally dynamic tapestry in the Luquillo Mountains (figure 2-10). Regions of geographic space might be subject to a disturbance, such as a hurricane. A hurricane alters abiotic conditions such as temperature or moisture, as well as the distribution of biomass or necromass and the composition or abundance of species (see Walker et al. 1991, 1996). In essence, the abiotic and biotic conditions of a point in geographic space quickly are altered as a result of the initial disturbance. In the Luquillo Mountains, hurricanes kill and uproot trees (Walker 1991), causing gaps in the forest canopy (Brokaw and Grear 1991). Gaps in the canopy result in higher temperatures and lower humidity throughout a cylindrical area from the top of the canopy to the forest floor (Fernández and Fetcher 1991). Biomass from affected vegetation becomes necromass and is redistributed to the forest floor (Lodge et al. 1991), altering the quality, quantity,
p. 59 and dispersion of resources and ↳ substrates. These conditions subsequently influence the abundance and distribution of microbial, plant, and animal species (Walker et al. 1991). The spatial and temporal scales on which organisms integrate or perceive environmental variability in part determine the severity of a disturbance event, as well as subsequent trajectories of change.

Figure 2.10



Conceptual model linking disturbance and succession as the mechanistic basis for the temporal and spatial complexion of the ecological tapestry of the Luquillo Mountains. Abiotic, biotic, and structural environments (A, B, and S, respectively) interact with one another and the disturbance regime (D) to determine changes in the state of an ecosystem (E). At the same time, the state of an ecosystem can influence the disturbance regime (feedback M). Subscripts indicate the location of the system in time.

Modified from Willig and Walker (1999).

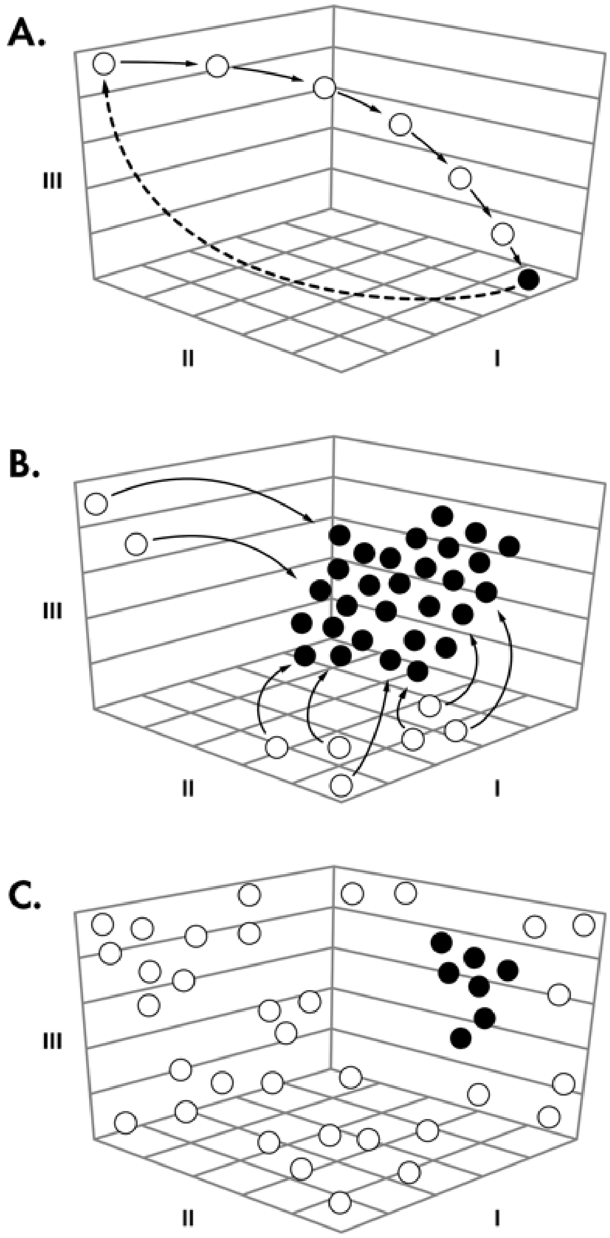
Residuals and Legacies

Disturbance directly alters the abiotic and biotic characteristics of geographic space. We distinguish between the immediate manifestations of a disturbance (residuals [Clements 1916]) and the subsequent dynamic nature of the ecosystem as a result of the existence of these residuals (legacies [Vogt et al. 1997]). Residuals can be abiotic (e.g., mineral soil exposed after a landslide, redistribution of rocks and sediment in a stream after a hurricane) or biotic (e.g., coarse woody debris deposited on the forest floor after a hurricane, community composition after selective harvesting; see chapter 4). The relative importance of abiotic and biotic residuals depends on the disturbance's type, frequency, intensity, and extent (see chapter
p. 60 5). For example, the response to a landslide that exposes mineral soil will be strongly ↳

p. 61 ↳
influenced by abiotic residuals, whereas the response to a pathogen outbreak will be strongly influenced by biotic residuals. Moreover, the composition and configuration of the landscape in which a disturbance is situated can affect the importance of biotic and abiotic residuals, because geographic proximity can determine the likelihood of dispersal into an area by native or introduced species.

Residuals influence ecosystem response in many ways (figure 2-11) (Clements 1916; Franklin et al. 2000). Alterations in geomorphology resulting from intense rainfall change hydrologic patterns, as well as soil water and nutrient availability, modifying multiple environmental gradients in geographic space. Organisms that survive a disturbance provide a springboard for succession, and the composition and distribution of the postdisturbance community can have strong effects on the ecosystem that develops under the new abiotic conditions. Organisms that fail to survive a disturbance might alter ecosystem structures and processes (e.g., hydrology) or provide long-term sources of energy and nutrients (Vitousek and Denslow 1986; Zimmerman et al. 1995). For example, a tree blown over and killed by a hurricane (a residual) creates a legacy in the nutrient composition of the soil. Thus, a disturbance event can have strong effects on the abiotic and biotic environments and might even alter the geomorphic template of an ecosystem. The effects of intense disturbances might be apparent in the ecosystem even after subsequent disturbance events. Legacies of previous disturbance events, some of them dating back hundreds of years, contribute to the present-day structure of the Luquillo Mountains (Scatena 1989; García-Montiel and Scatena 1994; Aide et al. 1996; also see chapters 4 and 5).

Figure 2.11



Ecological space may be envisioned as a multidimensional hypervolume that reflects the critical abiotic, biotic, and structural components of a system. Multivariate data reduction methods can be used to reduce these multiple dimensions to a few components (i.e., I, II, and III) that represent the salient features of variation among sites in ecological space. (A) Changes in the ecological characteristics of a site over time facilitate the quantification of the direction and magnitude of successional change. Successional trajectories (solid arrows) are envisioned as the temporally linked ecological conditions of a site (circles) over time in response to some initial disturbance (dashed arrow). In this particular instance, the characteristics of the site return to the predisturbance state in six time increments. (B) Prior to Hurricane Hugo, the tabonuco forest in the vicinity of El Verde Field Station comprised a number of sites, most of which shared similar ecological conditions (solid circles). As a result of numerous minor disturbances (e.g., treefalls), some sites (six open circles in the lower right of the panel) were slightly displaced from the ecological conditions of the “matrix.” More intense disturbances, such as landslides, altered the ecological characteristics of sites to a greater degree (open circles in the upper left of the panel). Secondary succession (arrows) occurred as these sites changed over time and converged on the characteristics of the original matrix. (C) As a result of Hurricane Hugo, the ecological configuration of sites in the Luquillo Mountains was altered. Only a few sites (solid circles), generally those protected on the leeward sides of ridges, remained within the range of conditions previously characteristic of the original matrix. Most sites (open circles) were variously displaced in ecological space as a consequence of the hurricane.

Modified from Willig and Walker (1999).

p. 62

Legacies of Natural Disturbances

Residuals from natural disturbances can include characteristics that arise from changes in geomorphology, the modification of environmental conditions and resources, the distribution of surviving organisms and propagules, or alterations in the structural heterogeneity (Franklin et al. 2000). Both abiotic and biotic residuals influence subsequent responses to disturbance, and that influence can manifest as persistent legacies in the forest structure, composition, or function. Spores, seeds, and seedlings that survive a disturbance can initiate succession with minimal delay. However, thick layers of litter might change the rates of germination of surviving seeds (Guzmán-Grajales and Walker 1991), leading to changes in plant species composition that might persist for decades. Modified environmental gradients in geographic space influence rates of productivity and decomposition. Structural residuals can provide critical habitat for other species and moderate change in the microclimate. Living and dead structural elements can persist long after a disturbance and affect the trajectory and rate of succession through legacy effects on soil nutrients and forest structure. Because recurrent natural disturbances, even when infrequent on ecological time scales, occur within the evolutionary experience of organisms in the Luquillo Mountains, the persistence of biotic residuals can increase the resilience of ecosystems after disturbances. However, anthropogenic disturbances, although they sometimes share characteristics with natural disturbances, can have quite different effects on populations, communities, and ecosystems.

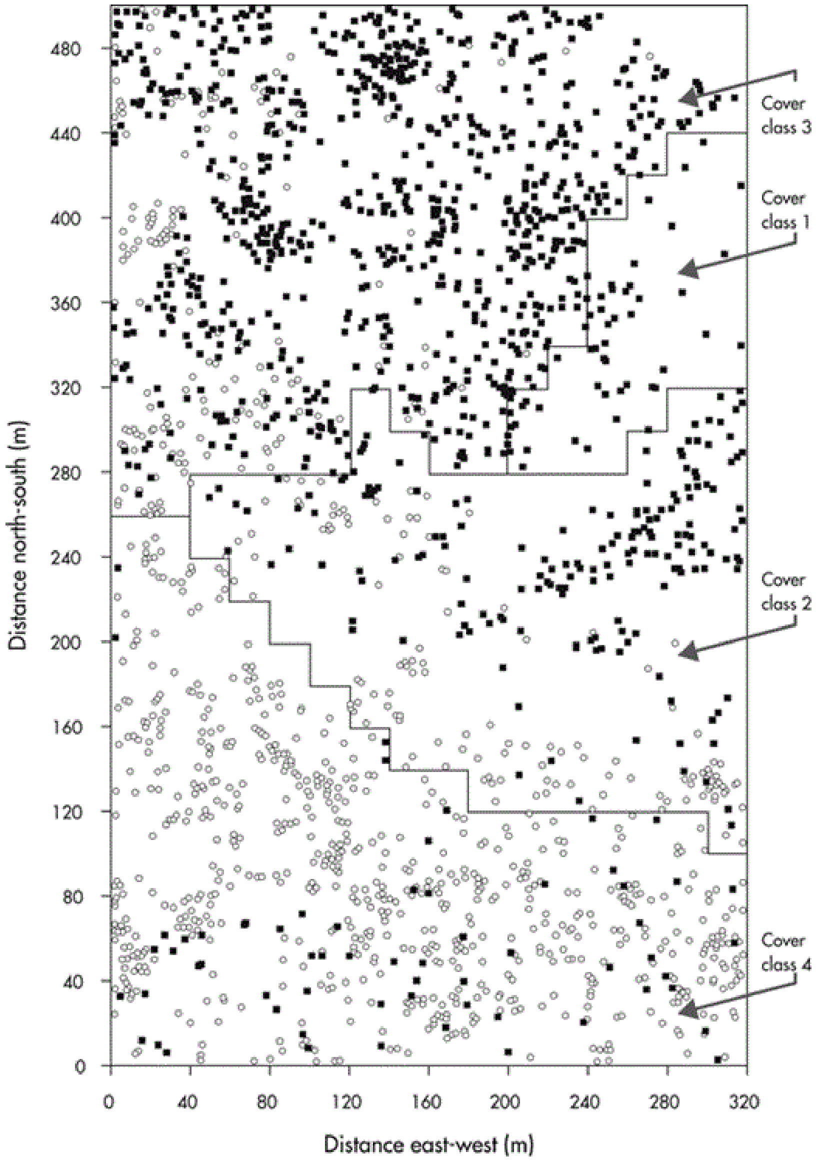
Legacies of Anthropogenic Disturbance

The intensities of anthropogenic disturbances differ greatly, from the removal of selected plant parts to the mass harvest of entire populations or communities. In the most intense anthropogenic disturbances, such as deforestation or agriculture, a severe effect is associated with the small quantity of biotic residuals (including structure) that remain in the postdisturbance environment. Anthropogenic disturbances often remove large quantities of the biomass of an ecosystem and leave behind an environment that is greatly altered, nutrient-poor, and often highly homogeneous. Moreover, repeated disturbances that are imposed by design (as in annual tilling and biocide application) forestall natural successional responses (Franklin et al. 2000). Anthropogenic disturbances generally have severe effects on both abiotic and biotic components of the ecosystem, often decoupling the covariation of these components in space and time, and thus moving the ecosystem's characteristics farther from those of the original system in ecological space than would a natural disturbance. The resilience of an ecosystem after anthropogenic disturbance might be low because of severe modifications to the environment that include the absence of biological residuals.

In many instances, the abiotic environment resulting from anthropogenic disturbance constitutes conditions that are beyond the natural variability (Landres et al. 1999) of the system and thus outside the evolutionary experience of native organisms. In these circumstances, the parameters defining the fundamental niches of many native species might not overlap with the ecological space created by a disturbance, and succession might be arrested or co-opted by introduced or immigrating ↳ p. 63 species that are better adapted to the novel combinations of environmental characteristics. The trajectory of response in these cases might be unique and result in new local combinations of species. Nonetheless, intervention by humans (e.g., the establishment and cultivation of selected tree species) can enhance ecosystem resilience. One of the goals of human intervention in this case is to modify the abiotic environment to conditions that occur within the range that is acceptable to native species (Landres et al. 1999). If the abiotic environment returns to predisturbance conditions, biological processes create positive feedbacks that enhance the rate of succession. In some instances, anthropogenic disturbance has created novel ecosystems (sensu Chapin and Starfield 1997) that cannot be restored to conditions within their historical range of environmental variability (Veblen 2003) and which need to be managed using innovative approaches. In the words of Seastedt et al. (2008:548), "In managing novel ecosystems, the point is not to think outside the box, but to recognize that the box itself has moved."

An example of the long-term effect of anthropogenic disturbance comes from the Luquillo Forest Dynamics Plot on the eastern slopes of the Luquillo Mountains. In the past, parts of this 16 ha plot were subjected to different intensities of use, resulting in four distinct categories of canopy cover in 1936 (figure 2-12). The ordination of data from tree surveys conducted in 1989 produced groupings that corresponded closely to the degree of historical anthropogenic disturbance, with secondary relationships to soil type and topography (Thompson et al. 2002). Natural disturbances (hurricanes) and forest development in the intervening period failed to mask the existence of anthropogenic disturbance or the relative severity of disturbance in different parts of the plot. Moreover, the community composition of other organisms (e.g., snails) and functional diversity (e.g., bacteria) showed differences among these same cover classes (Willig et al. 1996, 1998, 2007).

Figure 2.12



Previous land use and distribution of dominant species in the Luquillo Forest Dynamics Plot (after Willig et al. [1996] and Thompson et al. [2002]). Cover classes reflect land uses before 1936, derived from aerial photography. Cover classes 1 through 3 were clear-cut or heavily logged and then used for agriculture or silviculture, whereas cover class 4 was selectively logged. In 1936, canopy cover in classes 1 through 4 was 10 to 20 percent, 20 to 50 percent, 50 to 80 percent, and 80 to 100 percent, respectively. *Dacyodes excelsa* (open circles), a tree of mature forest, dominates the southern half of the plot, whereas *Casearia arborea* (solid squares), a secondary forest species, is more common in the northern section.

Many human activities that modify ecosystems are usefully viewed from the perspective of regimes of disturbance, rather than as isolated disturbance events (see chapter 4). Indeed, the repeated and systematic application of treatments (i.e., multiple disturbance elements) to prevent recovery might be the salient feature that distinguishes anthropogenic disturbances from natural disturbances. For example, roads in the Luquillo Mountains are initially constructed by clearing corridors of vegetation, bulldozing the land to a convenient configuration, and paving those cleared surfaces with asphalt. The maintenance of roads represents a human-directed disturbance regime designed to sustain ecological conditions at a desirable ecological state and retard succession. Vegetation is cut along the periphery of roads, debris from landslides and landslips is removed, and surfaces are repaired when substrate erosion degrades road surfaces. Similarly, agriculture in the Luquillo Mountains was a human-directed disturbance regime that involved deforestation, plowing, and planting crops. The application of fertilizers and biocides (e.g., fungicides, herbicides, insecticides, and rodenticides), weeding, and replanting are all activities of a human-initiated regime of disturbance that has a profound effect on the ecological state of the system. Conservation, restoration, and reclamation efforts are aspects of human management (see chapter 7) that can be profitably viewed as directed disturbance regimes that attempt to achieve a particular composition and
p. 64 functionality in the targeted ecosystems. ↳

Disturbance and the Relationship between Biodiversity and Ecosystem Processes

An environment enriched by the effects of disturbance provides many opportunities to understand the interaction between pattern and process. Disturbance affects both species–area (Grime 1973; Sousa 1984) and species–time (White et al. 2006) relationships and thus influences the diversity and identity of species (the biotic environment) that imbue an ecosystem with structure and functionality. Indeed, in order to predict ecosystem function, it is critical that one understand the interactions among aspects of diversity, species identity, and disturbance (see chapter 6) from a long-term perspective. Disturbance-driven changes in biodiversity influence the abiotic environment through their impact on resource availability and microclimate. Disturbance modifies the community composition, and interactions among new combinations of species alter the effect of species on ecosystem processes (Chapin et al. 2002). Changes in biodiversity feed back to modify the disturbance regime directly through the behavior of species in the community and indirectly through changes in the structural environment. The cumulative effect of all of these factors determines the resistance and resilience of ecosystem processes.

As patch-generating phenomena, disturbances alter spatial heterogeneity at a variety of scales and consequently have the potential to affect beta diversity as well as gamma diversity. Indeed, of the 17 general models posited to represent the relationship between species diversity and productivity (Scheiner and Willig 2005), two directly involve disturbance and five others indirectly involve disturbance to the extent that it creates patches associated with distinctive levels of critical resources (see box 2-1).

Box 2.1. Models representing the relationship between species diversity and productivity that involve disturbance directly and indirectly.

Directly involve disturbance

- Disturbance and competition (Huston 1979; Huston and Smith 1987)
- Hump-back model (Grime 1973, 1979)

Indirectly involve disturbance

- Available habitat (Denslow 1980; Rosenzweig and Abramsky 1993)
- Resource competition and resource heterogeneity (Tilman 1982, 1988; Abrams 1988)
- Intertaxon competition (Rosenzweig and Abramsky 1993; Tilman and Pacala 1993)
- Adaptive tradeoffs (Vander Meulen et al. 2001)

Moreover, empirical studies clearly document that not all aspects of diversity (e.g., richness, evenness, diversity, dominance, rarity) are correlated spatially (Wilsey and Potvin 2000; Stevens and Willig 2002; Chalcraft et al. 2004; Wilsey et al. 2005). As a result, the way in which disturbance affects the relation between productivity and biodiversity depends on the particular metric used to characterize biodiversity, as well as the spatial scale at which it is measured in nature (see chapter 8).

Summary and Implications

The ecological tapestry is a vibrant metaphor that captures important aspects of the spatiotemporally dynamic ecosystems of the Luquillo Mountains. Our conceptual approach considers historical factors, as well as contemporary geology, topography, and abiotic conditions, to create spatial variability in ecological space that favors some taxa more than others. This ultimately determines the abundance and distribution of species in the Luquillo Mountains. In addition, interspecific interactions (competition, predation, and mutualism) and heterogeneity arising from a complex disturbance regime (e.g., hurricanes, tropical storms, landslides, treefalls, droughts) that includes anthropogenic elements (e.g., forestry, agriculture, urbanization) combine to add further complexity, variability, and heterogeneity to the warp and weft of the p. 66 ↳ fabric composing the Luquillo tapestry. Finally, the various species of the Luquillo Mountains interact with matter and energy to form dynamic ecosystems, with tight coupling between aquatic and terrestrial systems. A number of important implications or insights can be derived from the application of our conceptual framework to the ecosystems of the Luquillo Mountains.

- Understanding present-day functionality requires knowledge of present-day, historical, and ancient processes. These different processes transpire at characteristic rates and interact to produce dynamism in the system.
- Geology, topography, regional climate, and disturbance produce heterogeneity or variation in the abiotic environment.
- The distribution of the biota is influenced by variability created at multiple spatial scales by multiple processes.
- The abundance and distribution of species affect biogeochemical processes and the capacity of the biota to moderate the environment after disturbance events and thus affect successional trajectories.
- The presence, abundance, and behavior of a species are linked intimately to the energetic costs and benefits associated with living in a particular geographic position, provided that key environmental factors have a consistent association with geographic space over time.
- The response to a disturbance is determined by the immediate postdisturbance environment, which includes the character and heterogeneity of the abiotic environment, the composition of the surviving organisms, and the structural legacies of the disturbance event. The integrated response of the biota to these circumstances determines the trajectory of change in the p. 67 ↳ community composition, structure, and biogeochemical processing (i.e., successional dynamics).

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