

## AN INTRODUCTION TO TERRESTRIAL DISTURBANCES

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### WHY STUDY DISTURBANCE?

Dramatic, large-scale natural disturbances (e.g., volcanic eruptions, fires, hurricanes, floods) are important to understand because they destroy property, cause human injury, and disrupt emotional lives. Human interference with natural disturbances (e.g., fire suppression) may actually make them more destructive (e.g., larger, hotter fires: Bond and van Wilgen, 1996). Disturbances are also important to all living organisms because they have beneficial effects such as nutrient recycling, resetting of successional pathways, and maintenance of species diversity (Luken, 1990). The exponential increase in human population density guarantees that more people are affected by natural disturbances every year. It is clear that one needs to continue efforts to predict and avoid disturbances, minimize damage, and maximize the ability of human society to restore degraded systems.

Some anthropogenic disturbances are well publicized (e.g., spills of oil or toxic waste, bomb explosions). Yet the more gradual disturbances that do not receive as much attention, such as urbanization, excavation of minerals, soil erosion as a result of agriculture, or logging of forests, may have far greater consequences. In fact, anthropogenic disturbances are ubiquitous and all ecosystems of the world are disturbed at least partially by human activities. Both natural and anthropogenic disturbances clearly impact the entire earth. Understanding how to live with or mitigate natural disturbances, and moderate the consequences of human actions, is imperative (Thomas, 1956; Botkin et al., 1989).

The consequences of increased human population represent the ultimate disturbance. Humans currently consume or utilize 40% of the earth's primary production (Vitousek et al., 1986). The human population

is now  $5.8 \times 10^9$  and is projected to reach  $10\text{--}12 \times 10^9$  by the year 2040. What are the consequences of such growth? What is the carrying capacity of the earth (Cohen, 1995)? Can human intelligence and technology prevent or even postpone a global collapse? Estimates of the ecological footprint (a concept that calculates how much arable land is needed to sustain a given level of energy consumption per member of a human population; Wackernagel and Rees, 1996) of those countries with the highest standards of living already are 15 times greater in area than the geographical space they occupy. Clearly, the world does not have the resources to sustain the entire human population at a standard of living similar to that in the more affluent nations of the world. Giampietro (Chapter 32, this volume) explores ways in which wise resource management and curtailment of resource abuse can improve the future prospects of humans and the biosphere.

### PERSPECTIVES ON DISTURBANCE

Disturbances have been the subject of many myths and legends. Gods have been associated with disturbances such as volcanoes (Ixtocewatl and Pococatepetl in Mexico; Vulcan in ancient Rome; Pele in Hawaii), windstorms (Luquillo in Puerto Rico; Hurakan in Mayan culture), floods (Janaina in Brazil; Poseidon in ancient Greece), and fire (Loki in Norse mythology; Prometheus in ancient Greece). The biblical Noah dealt with a flood, and Moses' enemies were subjected to a herbivore (locust) outbreak.

Disturbances have directly altered human history. Volcanoes have destroyed cities (e.g., Pompeii in Italy; St. Pierre in Martinique) and altered world climates (Karakatau in Indonesia) (Sheets and Grayson, 1979;

Simkin and Fiske, 1983). Hurricanes have repeatedly damaged buildings and biota (e.g., Hurricane Hugo in the Caribbean and the eastern United States: Bénito-Espinal and Bénito-Espinal, 1991; Finkl and Pilkey, 1991; Walker et al., 1991, 1996). Fertile soils along river floodplains (e.g., the Nile, Tigris, or Euphrates) have nurtured civilizations, but often at the cost of extensive losses of lives and property (Officer and Page, 1993). Famous fires have altered the histories of cities such as Chicago, Rome and San Francisco, and the vegetation of entire continents (Komarek, 1983). Biotic disturbances are perhaps most damaging. The Black Death killed one-third of all people in medieval Europe, and many Native Americans died from diseases such as smallpox and malaria introduced by Europeans (cf. Crosby, 1986; Officer and Page, 1993).

Cultural and environmental concerns traditionally have been shaped by the interplay between resource availability and the local disturbance regime. Degradation of land caused by erosion and deforestation was noted by Greek and Roman writers, and Confucianism in China addressed environmental concerns (Barrow, 1991). Humans typically have responded to natural disturbances by management (use of fire by many native cultures), exploitation (use of early-successional plants for food), or avoidance (minimal use of deserts, lava fields, and glacial valleys). Attitudes toward natural resources can evolve from exploitation to conservation when human population densities reach local carrying capacities. However, the demise of some societies [e.g., the Maya in Central America, the Hohokam in Arizona (U.S.A.), and the Assyrians in Mesopotamia] has been attributed in part to the collapse of the local resource base from over-exploitation (Thomas, 1956). The remarkable ability of humans to accommodate to naturally or anthropogenically caused environmental change (or to migrate out of disturbed areas - as with the Dust Bowl in Oklahoma, U.S.A.: Worster, 1979) suggests that most disturbances modify but do not destroy cultures. Most landscapes are now the product of a long history of human land use (e.g., the Mediterranean basin: Rundel, Chapter 10, this volume).

For the last 100-200 years, Western cultures have been systematically recording observations about various natural disturbances (e.g., volcanoes: Whittaker et al., 1989; glaciers: Chapin et al., 1994) and anthropogenic disturbances (e.g., changes in levels of atmospheric carbon dioxide: Vitousek, 1994) and ecosystem responses to disturbance (e.g., succession:

Clements, 1928). Such long-term observations allow an examination of disturbance on various time scales with the partitioning of short-term fluctuations from longer-term cycles (Magnuson, 1990). They also facilitate the distinction of human impacts from natural fluctuations. Recognition of the role of humans in global warming or acid rain, and the growing impacts of mining, agriculture, and urbanization have increased environmental awareness in recent decades. This awareness has fostered the growth of environmental politics (e.g., the Green Parties in Europe), entrepreneurship (e.g., the purchase of natural areas by private agencies such as the Nature Conservancy operating from the United States), and cooperation at the local level (restoration activities), the regional level (credits to companies that reduce pollution), and the global level (relief of national debt in exchange for establishment of nature reserves). Interactions of culture and disturbance are further discussed in this volume by Ghersa and Leon (Chapter 20), Barrow (Chapter 28), Hobbs (Chapter 29), Eckert and Carroll (Chapter 30) and Giampietro (Chapter 32).

#### DEFINITIONS OF DISTURBANCE

As the literature on disturbance ecology has proliferated in the last two decades, so too has the lexicon. Nonetheless, maturation of the science requires a precise use of terminology along with straightforward clarification when terms are used in different ways. At the same time, terms should be sufficiently general so that they are useful to an appreciable segment of the practitioners in the discipline. On occasion, growth of a discipline can be stymied significantly by vague or ill-defined terminology, in part because synthesis requires incisive understanding and in part because confusion over terminology can lead to division among practitioners who disagree about definitions. Such semantic differences can give the impression of disagreement over substantive or conceptual issues, lead to heated or senseless debate, and delay the maturation of a scientific discipline.

We do not attempt to resolve such semantic and conceptual differences here. Indeed, authors contributing to this volume were given broad latitude in the use of terms so as to engender individual creativity. Nonetheless, we follow White and Pickett (1985) and provide an introduction to widely accepted meanings of selected terms in the lexicon of disturbance ecology,

so that the general reader will have an appreciation of the scope of the discipline, and specialists will be motivated to provide more detailed definitions or alternate terminology as appropriate (see Pickett et al., Chapter 31, this volume).

A disturbance is a relatively discrete event in time and space that alters the structure of populations, communities, and ecosystems. It can do so by altering the density, the biomass, or the spatial distribution of the biota, by affecting the availability and distribution of resources and substrate, or by otherwise altering the physical environment. It often results in the creation of patches and the modification of spatial heterogeneity. Disturbance is a relative term that requires explicit delineation of the system of concern, including the spatial and temporal scale of the components of interest.

The cause of a disturbance may be thought of as the agent or entity initiating the changes in the structure of the ecological system of interest. For example, high-speed winds are agents of disturbance for hurricanes. If the cause originates outside the system of interest, as is the situation for hurricanes, the disturbance is considered to be exogenous, whereas if the cause of the disturbance originates inside the system of interest, as when a tree-fall results from natural senescence, the disturbance is considered to be endogenous. Clearly, definition of the system of interest is integral to such considerations, and a clear distinction is not always possible. The likelihood of an exogenous disturbance may be affected by the state of the system of interest and characteristics of endogenous disturbances may be affected by characteristics of previous exogenous disturbances. Indeed, the dichotomy between purely endogenous and exogenous disturbances might more appropriately be considered as a continuum of intermediate possibilities.

Disturbances are most often characterized by the central tendency, variability, and distribution of three attributes: frequency, extent, and magnitude. *Frequency* measures the number of events per unit of time or the probability that an event will occur. *Extent* is the actual physical area affected by a disturbance. It can be estimated from the area of a single event (e.g., a tree-fall), or from the sum of the areas affected by equivalent events over a particular time period (e.g., gap area created by all tree-falls in a year). Extent is often reported as the proportion of an entire landscape in which a particular disturbance occurred

in a given time period. *Magnitude* includes two inter-related attributes: intensity and severity. *Intensity* is the physical force of an event (e.g., wind-speed for hurricanes), whereas the impact on or consequences to the system of interest is the *severity* (e.g., the biomass of trees that were killed by passage of a hurricane). Intensity and severity are usually correlated, and the terms often are used interchangeably, at least in part, because the physical forces of many disturbances, especially those generated by the biota (e.g., tree-falls, rodent mounds, insect outbreaks) are difficult to quantify. Clearly, severity reflects the response of the biota to the disturbance and may not be fully documented until a considerable time has elapsed since the disturbance event impinged on the system of interest.

Most systems are simultaneously subjected to a number of disturbances (e.g., hurricanes, landslides, tree-falls, herbivory, droughts, and human activities all affect the structure and function of Caribbean forests). The sum of all disturbances at a particular place and time is termed the disturbance regime. The different disturbance events enhance or diminish the frequency, extent, or magnitude of other disturbances. Such interactions are considered synergisms, and are important considerations to address in understanding disturbance and recovery in ecological systems.

## TYPES OF DISTURBANCE

Because virtually every habitat experiences some level of disturbance, no book can easily cover the entire topic. This book focuses on disturbances that physically impact the ground. It does not address atmospheric or aquatic disturbances. Primarily natural disturbances (Chapters 2–13) can be categorized by the four classical elements: earth, air, water, and fire (Table 1.1). Disturbances linked to the earth are independent of all causal factors other than tectonic forces (del Moral and Grishin, Chapter 5, this volume). Disturbances involving air, water, and fire are primarily driven by an interplay of climatic, topographic, and soil factors. In addition, biotic variables influence fire and are represented by both non-human disturbances (e.g., herbivory) and human disturbances (Table 1.1).

Disturbances often trigger other disturbances, so that there is an interlacing web of disturbance interactions (for a detailed example, see Fig. 33.2 below). For instance, volcanoes can trigger earthquakes, earthquakes

Table 1.1  
Examples of some of the major types of disturbance of the earth<sup>1</sup>

Element	Primary disturbance <sup>2</sup>
Earth (tectonic)	earthquake (1)
	erosion (>50)
	volcano (1)
Air	hurricane (15)
	tornado (<1)
	tree-fall (nd)
Water	drought (30)
	flood (15)
	glacier (10)
Fire	fire (>50)
Biota non-human	herbivory (nd)
	invasion (nd)
	other animal activity <sup>3</sup> (nd)
Biota human	agriculture (45)
	forestry (10)
	mineral extraction (1)
	military activity <sup>4</sup> (1 40)
	transportation <sup>5</sup> (5)
	urban (3)

<sup>1</sup> Data from many sources; nd = no data available.

<sup>2</sup> Approximate percent of earth's terrestrial surface regularly affected by each disturbance is in parentheses.

<sup>3</sup> Includes building, excavating, waste products, movement, death, diseases, parasites.

<sup>4</sup> U.S.A., 1%; Vietnam, 40%.

<sup>5</sup> Includes motorized and non-motorized transportation.

or hurricanes can trigger landslides, hurricanes or landslides can induce flooding, and flooding can cause landslides. These interactions may augment, diminish, or neutralize the interacting disturbances. Anthropogenic disturbances are, of course, always interacting with natural disturbances (e.g., road-building can trigger a landslide). A hierarchical view of disturbance types (cf. O'Neill et al., 1986; Pickett et al., 1987) may be most useful in examining disturbance interactions, and in making spatial and temporal scales explicit for each disturbance under consideration.

When the common types of disturbance of the world (from Table 1.1) are compared by frequency, extent, and severity using a subjective ranking procedure (1, least; 5, most), several patterns emerge (Fig. 1.1). Primarily anthropogenic disturbances are usually greater in extent (mean score=3.2) than

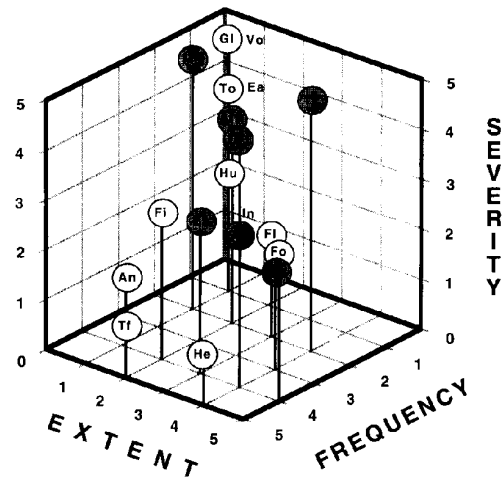


Fig. 1.1. The frequency, spatial extent, and severity of 19 types of disturbance throughout the world based on their subjectively ranked scores from 1 (least) to 5 (most). Intensity and severity scores were highly correlated and thus are represented on a single axis. Disturbances are: AG, agriculture; AN, animal activities; DR, drought; EA, earthquakes; ER, erosion; FI, fire; FL, flooding; FO, forestry; GL, glaciers; HE, herbivory; HU, hurricanes; IN, invasions; MI, mining; ML, military; TF, tree falls; TO, tornadoes; TR, transportation; UR, urban; VO, volcanoes. Anthropogenic disturbances are shaded. Uncircled letters occupy the same location as adjacent circles (VO, GL; EA, TO; IN, AG).

natural disturbances (mean score=2.1), presumably because of the cosmopolitan distribution of humans. Anthropogenic disturbances are also slightly more severe (mean score=3.8) than natural disturbances (mean score=3.0), but similar in frequency (mean scores 3.1 and 2.8, respectively). Of the five most severe disturbance types (score=5), natural disturbances (glaciers and volcanoes) were less extensive and frequent than anthropogenic disturbances (mining, transportation, urban development). Transportation was rated uniquely high in both extent and severity. Other outliers were herbivory, tree-falls, and animal activities, all of which received very low scores for severity, but high scores for frequency. Most important, perhaps, is the broad range of extent, severity, and frequency among the disturbance types, particularly those representing natural disturbances.

At relatively large spatial scales ( $\sim 10^4$ – $10^{10}$  m<sup>2</sup>) and long temporal scales ( $\sim 10^2$ – $10^4$  yr), many areas of the earth are dominated by only one or a few major disturbance types. Inside the front cover of this book, we have mapped areas where disturbances related to

earth, air, water, and fire predominate on terrestrial surfaces of the earth. Volcanoes and earthquakes result from plate tectonics (earth element) and predominate around the rim of the Pacific Ocean and in central Asia. Hurricanes (air element) develop in the tropics, but occasionally reach latitudes  $>45^{\circ}$  N or S. Tornadoes reach further inland than hurricanes. Less severe windstorms are nearly ubiquitous at smaller spatial scales and were not included in the map. Floods or ice (excess of the water element) are important disturbances along river corridors and in boreal and polar regions. Drought (deficiency of the water element) is primarily a factor in mid-latitude, hot deserts, but also in northeastern Brazil (Mares et al., 1985). Droughts and floods are dictated largely by ocean currents, global wind patterns, and regional topography, although human activities often influence both droughts (e.g., desertification) and flooding (river channelization). Fire is the most ubiquitous type of terrestrial disturbance after human urban and agricultural activities (Bond and van Wilgen, 1996). It is important in tundra, coniferous forests, temperate grasslands and shrublands, and tropical grasslands and savannas, although only the most flammable biomes (coniferous forests and Mediterranean-climate shrublands) are shown.

Biotic disturbances can be considered a fifth category of disturbance. Non-human biotic disturbances include plant and animal invasions, herbivory, and other animal activities (e.g., excavating, building, movement, waste products, disease, and parasitism). These activities are too ubiquitous and small in scale to map globally. In contrast, anthropogenic disturbances, equally ubiquitous but occurring at larger spatial scales,

can more readily be mapped globally (Fig. 1.2). There is a strong similarity between the distributions of human population (Fig. 1.2A) and common human disturbances (Figs. 1.2B, 1.2C, 1.2D). Current anthropogenic disturbances reflect human land-use patterns that are a consequence of historical settlements based primarily on the presence of soils suitable for agriculture (Fig. 1.2B), and appropriate waterways or land routes for transportation. More recent urbanization reflects primarily transportation centers (Fig. 1.2C) that have excellent access to power sources or to agricultural products (cf. Cronon, 1991). Many humans (45%) now live in or near cities, and this trend is accelerating. Nevertheless, some human activities such as mineral extraction (Fig. 1.2D) and military installations may actually promote low human population densities, but still represent severe disturbance (e.g., northern Alaska, northern Venezuela, eastern Saudi Arabia). Inside the back cover of this book, we have mapped all human influences together, using four hemeroby classes (see Sukopp and Starfinger, Chapter 16, this volume) representing degrees of human influence: (1) minimal: mountains, tundra, undeveloped forest; (2) moderate: low human population densities, some agriculture; (3) major: moderate human population densities, intense agriculture (e.g., deep plowing, clear-cutting, biocides); and (4) maximal: high urban population densities, sealed or poisoned land surfaces. This measure of combined influences of humans emphasizes that most damage occurs where population densities are high. Agriculture and resource extraction, although often locally severe, do not alter the environment as much as pavement and urban buildings.

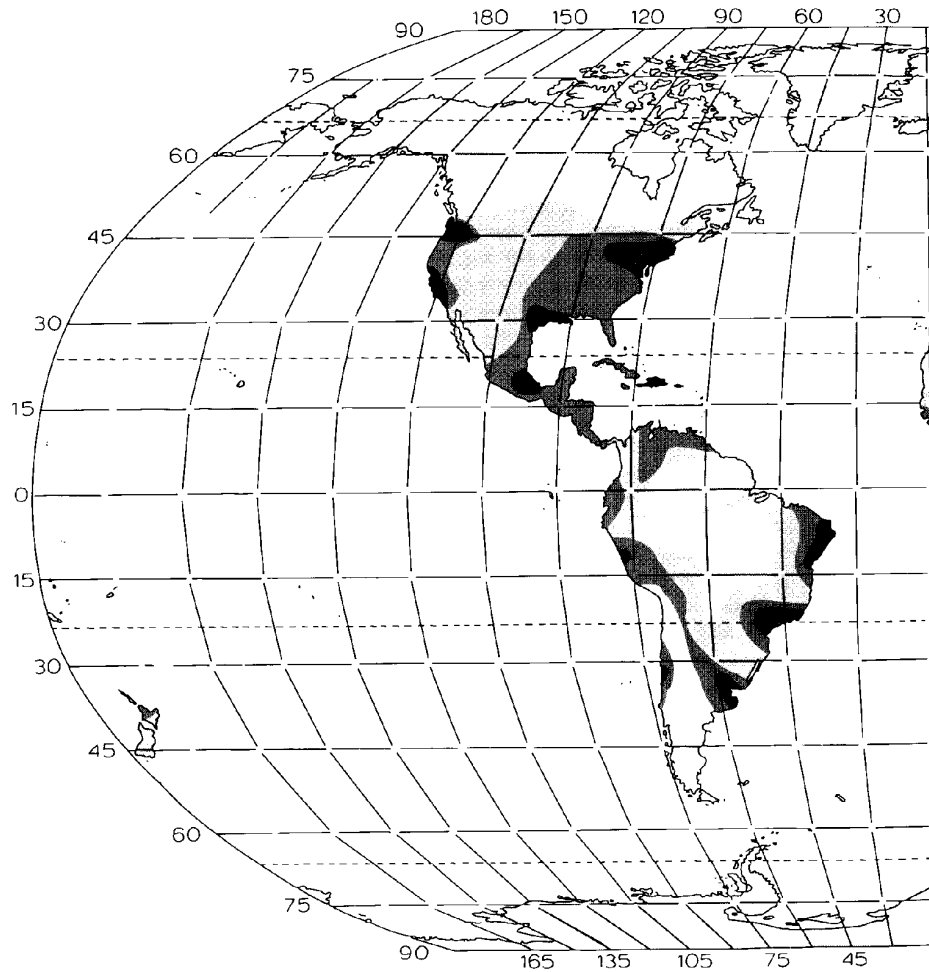


Fig. 1.2A. Global distribution of four aspects of anthropogenic disturbance. A. Human population distribution. Grey levels indicate different population densities:  $0-20 \text{ km}^{-2}$ ;  $20-100 \text{ km}^{-2}$ ;  $100-400 \text{ km}^{-2}$ ;  $400 \text{ km}^{-2}$ . Various sources were used, including: Oxford World Atlas (1973) and The Times Atlas of the World (1990, 1995).

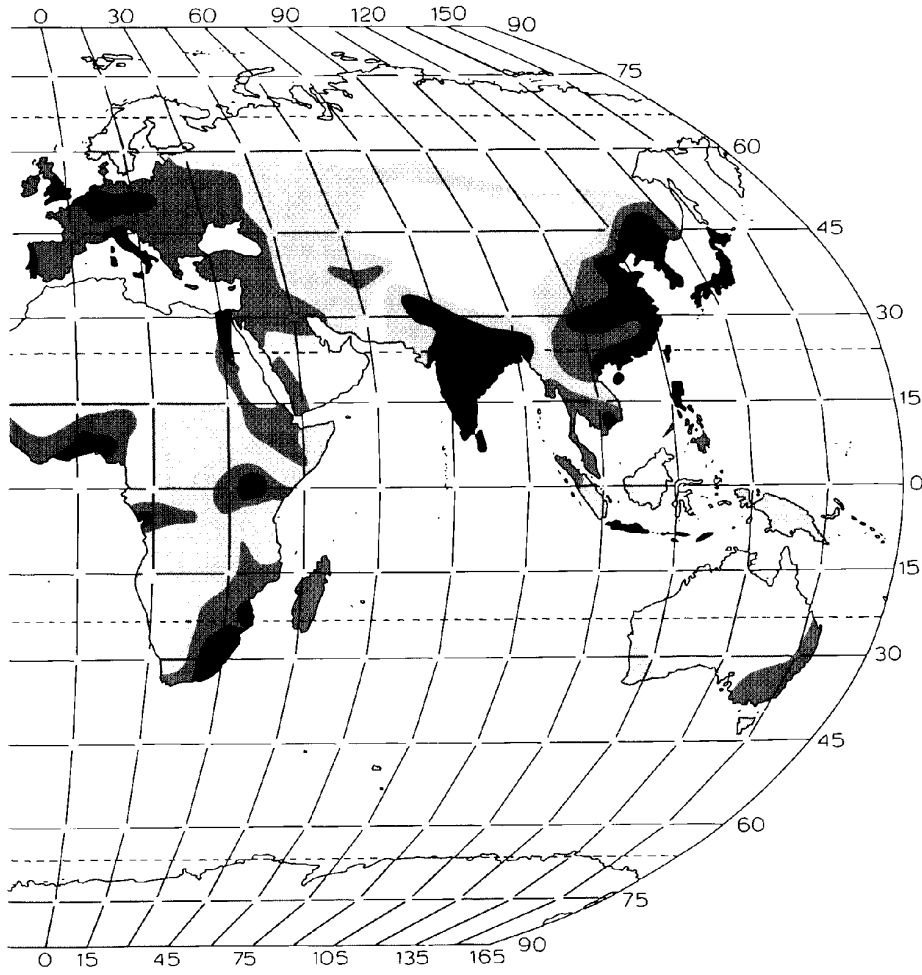


Fig. 1.2A (continued).

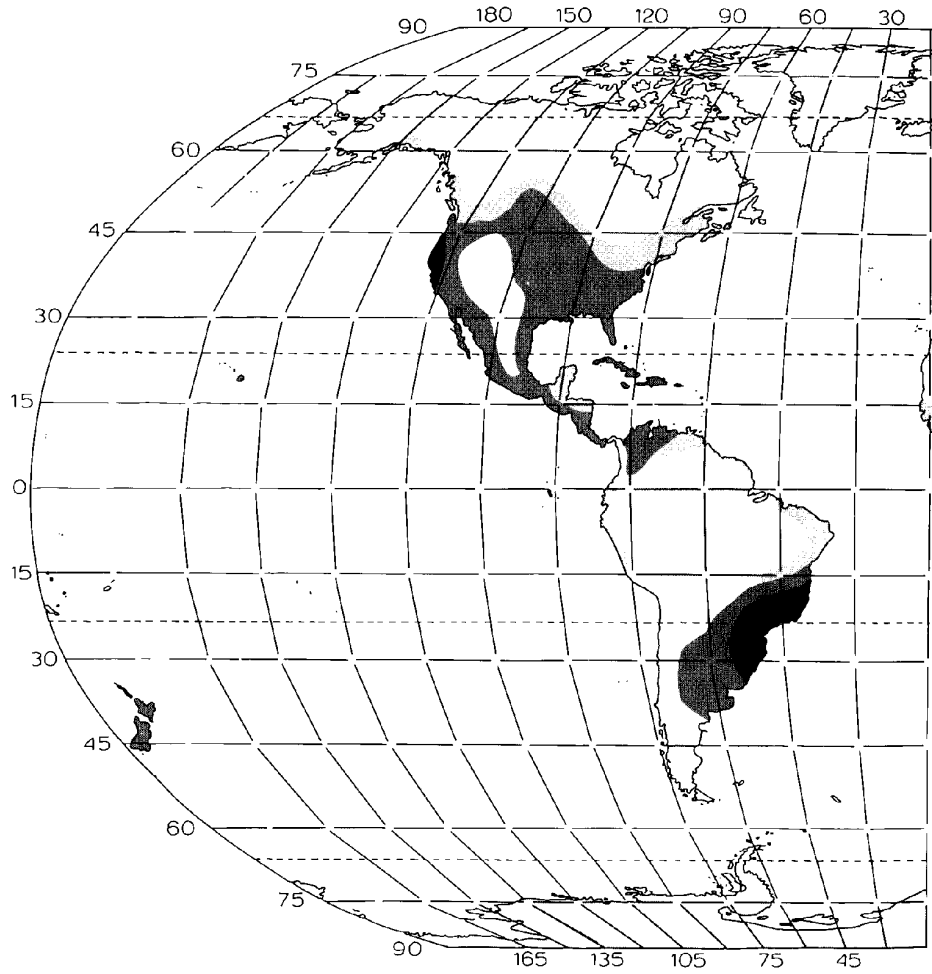


Fig. 1.2B. Agriculture excluding forestry. Grey levels indicate relative intensity: sparse; low; moderate; high.



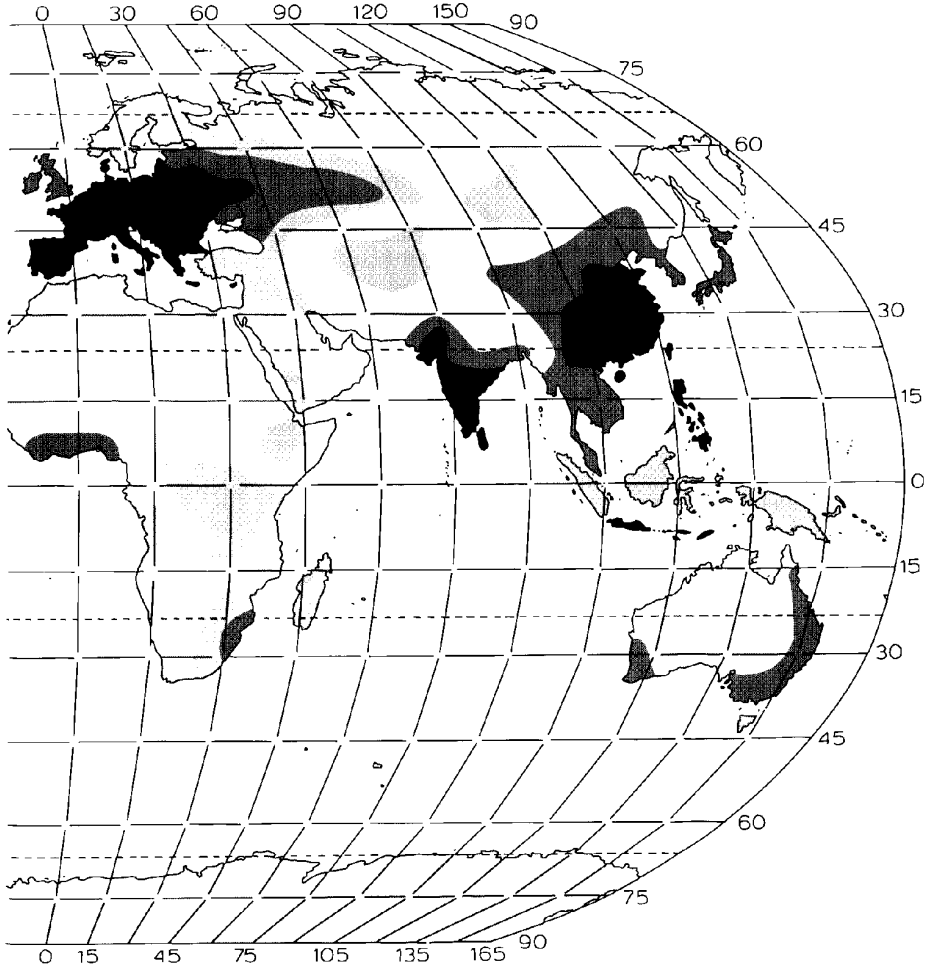


Fig. 1.2B (continued).

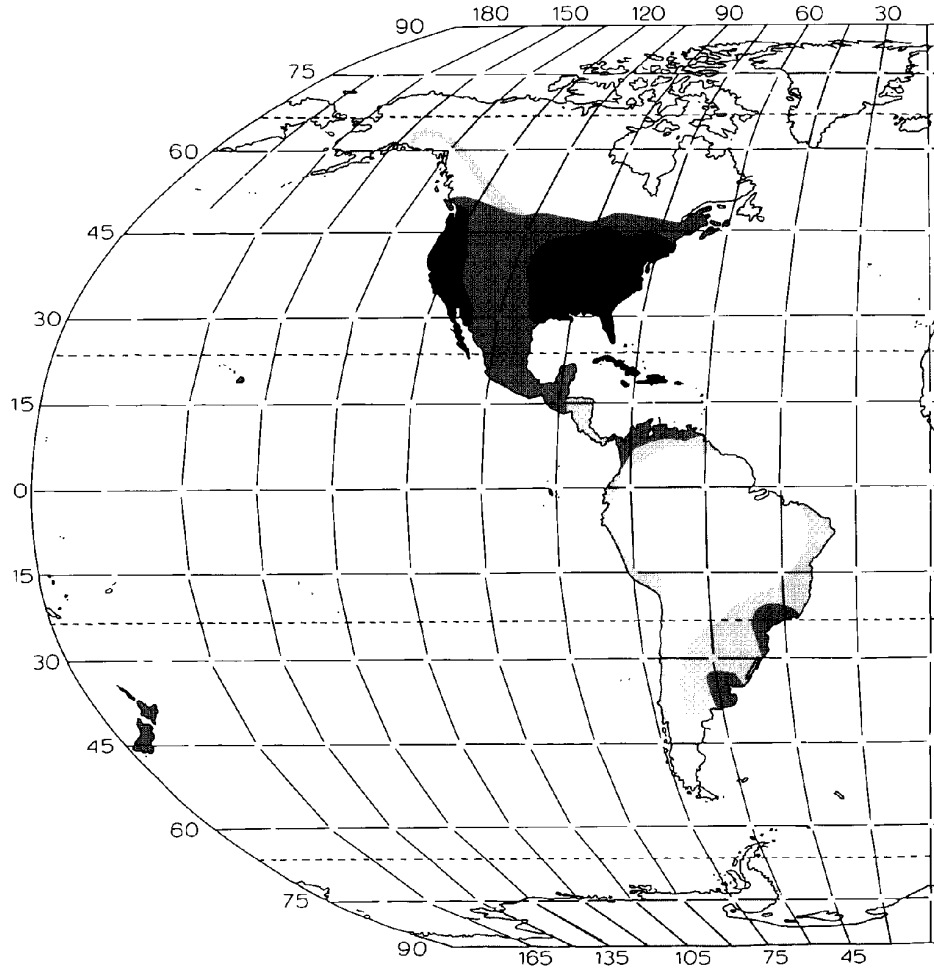


Fig. 1.20 . Surface transportation (roads and railroads). Grey levels indicate relative intensity: sparse; low; moderate; high.

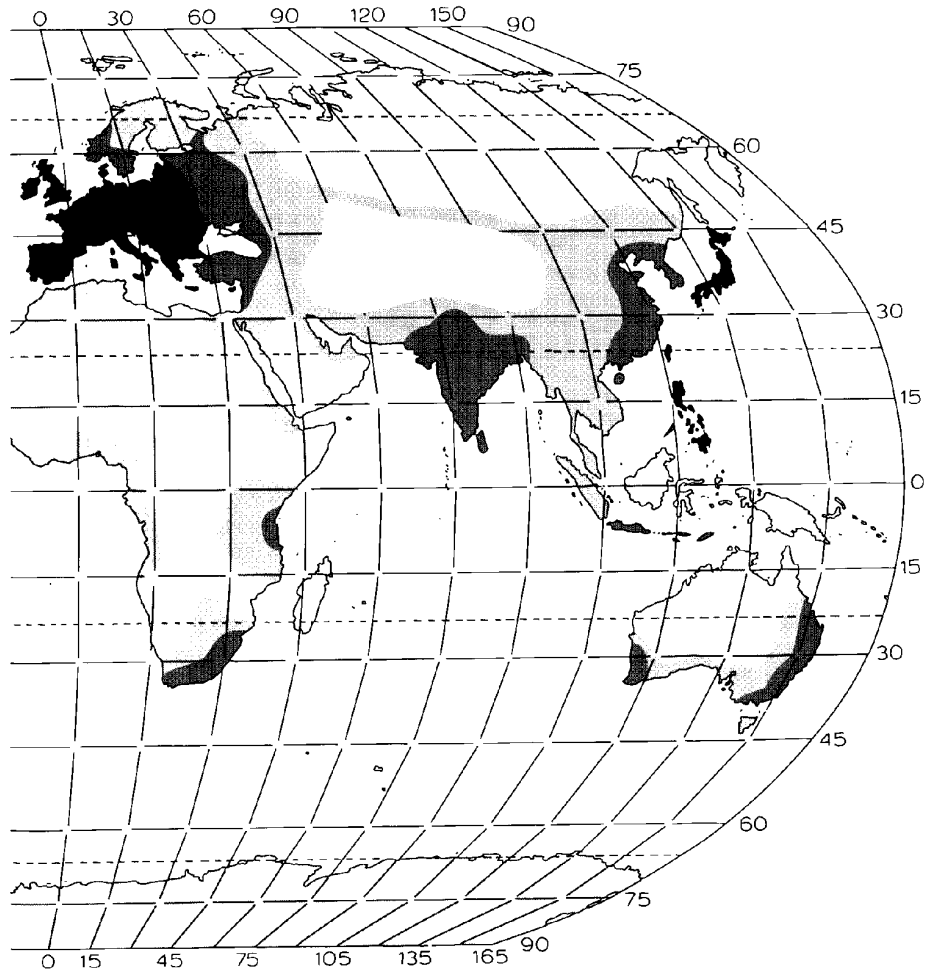


Fig. 1.2C (continued).

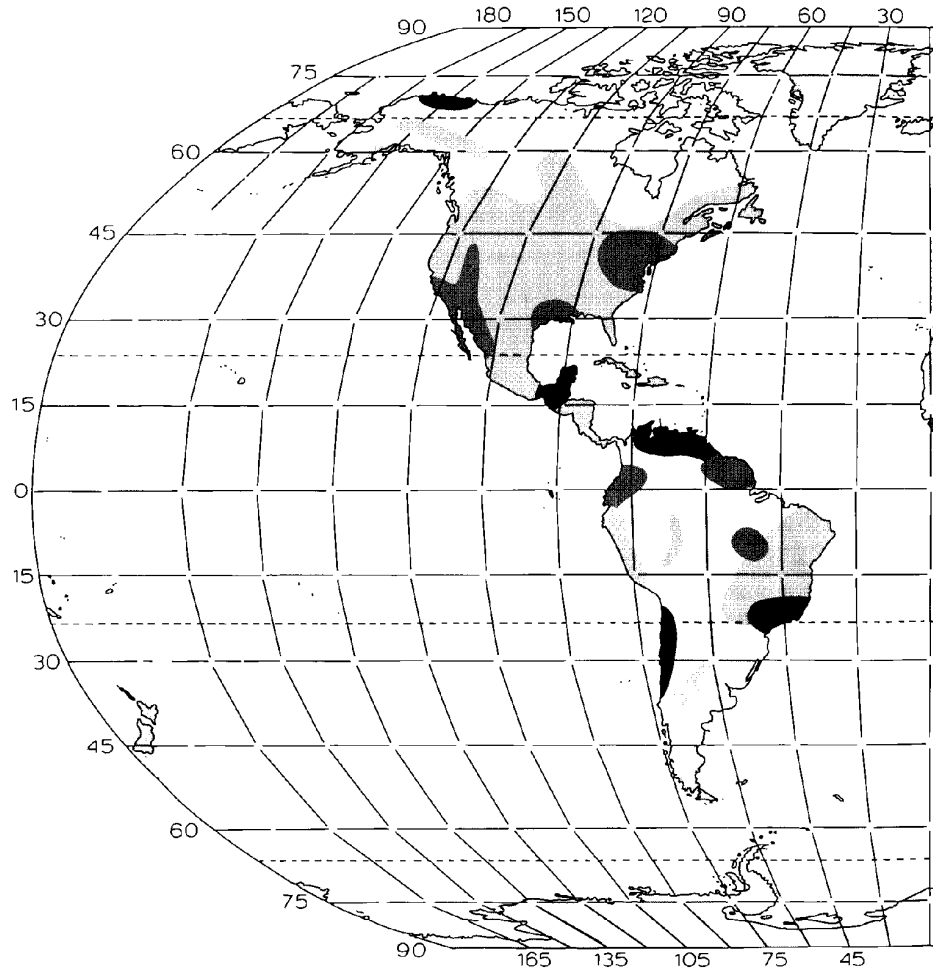


Fig. 1.2D. Mineral resource extraction (including oil, gas and coal). Grey levels indicate relative intensity: sparse; low; moderate; high.

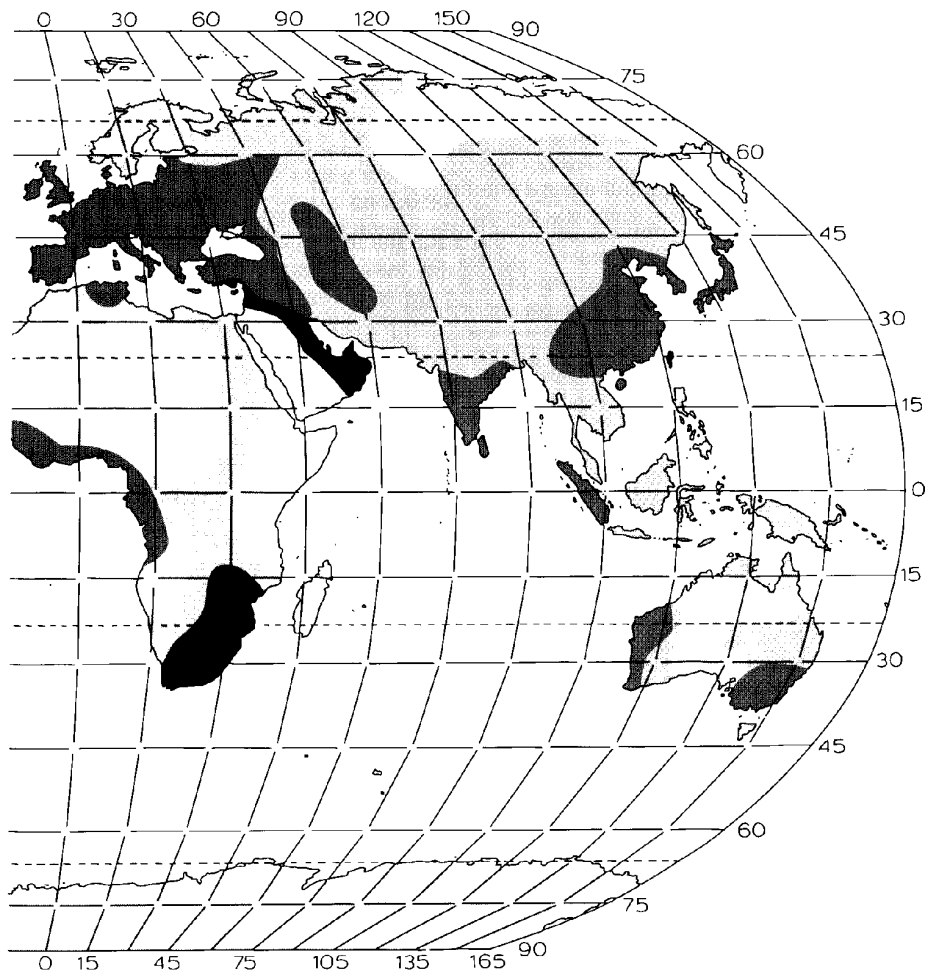


Fig. 1.2D (continued)

Table 1.2  
Distribution of topics discussed in each chapter. Parentheses indicate minor topics

Chapter	Element <sup>1</sup>	Geographic region <sup>2</sup>	Ecoregion <sup>3</sup>	Trophic level <sup>4</sup>	Theme <sup>5</sup>
2	1,2,3	1,2,(3),(4),5,6	1,5	1,(2),3	1,3,(4),7,8
3	1,2,3,4,5	2,3,4,5,6,7,8	1,2,4,6	1,2,(3)	2,(4),5,6,7,9,12
4	1,2,3,5	(1),3,(5),6,7	(2),5,8	1,(2),3	1,5,6,10
5	1,(2),3	3,4,(5),6,8	4,5	1,2,3	1,2,3,8,10,12
6	2,4,5	3,5,6	5	1,2	2,3,4,7,(10)
7	2,5	3,4,5,6,7,8	5,6	1,2,3	1,2,3,(4),5,8,10,13
8	2,(4)	1,3,4,6,7,8	5,6	1	1,2,3,5,6,8,14
9	5	4,6	5	1,2	1,2,3,5,6,9,11
10	4,5	1,4,5,6,7	1,2,4,5,8	1	1,10,12
11	4,5	1,6,7	(1),2,3,(5)	1,2,(3)	1,5,6,7,9,14
12	2,3,4,5	1,3,4,5,6,7	1	1,2,(3)	1,2,3,(4),14
13	(2),3,4,5	3,6,8	6	1,2	1,2,3,4,5,6,(7),9,10,(14)
14	1,5	1,(3),4,5,6,(7)	1,2,3,5	1	1,3,5,6,13
15	5	4,5,6	1,2,4,5,6	1,2	1,10,13
16	5	(3),5,6	5,7	1,2	(2),3,(5),10,12
17	(1),(2),(3),4,5	1,4,5,6,8	1,2,3,4,5,6,8	1,2	1,3,4,5,(10),12
18	1,2,4,5	4,5,6	5,8	1,2	2,3,5,6,(10)
19	1,2,3,4,5	1,3,4,6,7,8	5	1,2	1,2,3,9,10,12,13
20	5	7	2,8	1,(3)	2,3,4,5,7,(8),10,12,14
21	1,3,5	6	(6),8	1,2	1,5
22	1,4,5	5,6	1,4,5	1,2,3	3,5,13,14
23	5	1,5,6	2,4,5	1,2,3	1,3,4,5,(6)
24	1,4,5	1,4,5,6	2,4,5	1,2	1,5,6
25	1,2,3,5	1,2,3,4,5,6,8	5	1,2,3	1,3,4,5,6
26	5	(4),6	2,5,(6),8	1	2,3,4,5,6
27	2,4,5	4,6,8	2,4,5,8	1,2,3	1,2,3,4,5,6,10,14
28	4,5	4,5,6,7	(2),(4),(5)	2	1,(2),5,7,9,13,14
29	5	4,6,7	2,4,5,(6),8	1,2,3	1,5,7,9,11,12,13,14
30	5	1,3,6,7,8	(1),2,5,6,8	1,2,3	3,7,9,10,13,14
31	1,2,3,4,5	6,7	5	2	2,(3),7,(13),14
32	5	1,3,4,5,6	8	1,2	5,6,8,14

<sup>1</sup> Element: 1, earth; 2, air; 3, water; 4, fire; 5, biota.

<sup>2</sup> Geographic region: 1, Africa; 2, Antarctica; 3, Asia; 4, Australasia (Australia, New Zealand, Micronesia); 5, Europe; 6, North America; 7, South America; 8, Islands.

<sup>3</sup> Ecoregion: 1, desert; 2, grassland; 3, savanna; 4, shrubland; 5, forest; 6, wetland; 7, urban; 8, agroecosystem.

<sup>4</sup> Trophic level: 1, producer; 2, consumer; 3, decomposer.

<sup>5</sup> Theme: 1, interactions; 2, spatial heterogeneity; 3, succession; 4, competition; 5, nutrient cycling; 6, productivity; 7, stability and resilience; 8, predictability; 9, thresholds; 10, biodiversity; 11, functional redundancy; 12, invasive species; 13, restoration and management; 14, modeling.

## DISTURBANCE THEMES

The chapters in this volume approach the topic of disturbance from many perspectives (Table 1.2). Each chapter addresses how at least one of the four basic elements or ethers (earth, air, water, fire) and the biota may be an agent of disturbance, and a few chapters address all of them. The most frequently covered type of disturbance is biotic (particularly human). The most frequently described geographical region is North America, but all regions of the world are discussed (more than simply a reference or brief mention) in the following rank order:

North America » Australasia = Europe > Africa = Asia – South America > islands » Antarctica.

This representation probably reflects both author bias and available literature, although all regions except Antarctica are discussed in at least ten chapters. Ecological regions were discussed in the order:

forests » grasslands > shrublands = agroecosystems > deserts = wetlands » savannas > urban areas,

again suggesting the distribution of available literature (and humans), and despite the global importance of urbanization. Most chapters address effects of disturbance on primary producers and consumers, but a substantial fraction also consider decomposers.

Fourteen themes emerge in the following order:

nutrient cycling > interactions = succession » spatial heterogeneity > productivity = biodiversity > competition = modeling > stability and resilience > thresholds = invasive species = restoration and management > predictability » functional redundancy.

This order suggests that disturbances often interact and that there are intimate links between disturbance and nutrient cycling, succession, spatial heterogeneity, productivity, and biodiversity. In the last chapter of the volume, we examine the lessons learned from earlier chapters in this volume about the relationships between disturbance and these important themes.

Ecologists have made great strides in understanding the role of disturbance in shaping natural systems. Successional responses and competitive interactions among species have generated particularly large numbers of papers. Other responses to disturbance (notably below-ground processes) have received very little attention. Land managers have developed a broad base of knowledge about practical issues relating to intentional human disturbances such as agriculture. However, neither ecologists nor land managers have developed a

robust set of predictions about the consequences of disturbances. Much more integration of management and theory is needed in order to address the environmental challenges which humans face. Especially important to understand are the consequences of irregular natural disturbances such as hurricanes or volcanoes, the recent and overwhelming human impacts such as erosion or clear-cutting, and the interactions among them. This global compendium of examples of disturbed ground offers a sampling of the types of data that are available and some preliminary generalizations and conceptual models. We hope this book will stimulate more long-term monitoring of disturbed ground, experiments that address the mechanisms behind biotic responses to disturbance, and studies that compare responses within and among various types of disturbances (and ideally across gradients of disturbance severity). Such types of data are needed to provide the basis for predictions about disturbance.

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