CHAPTER 4

Causes of Landscape Pattern

When we view a landscape, we look at its composition and spatial configuration: the elements present and how these elements are arranged. In an agricultural landscape, we may observe forests occurring along streams and on steep ridges, whereas croplands and pastures occupy upland areas of gentler slope. In a fire-dominated boreal forest landscape, we may observe large contiguous areas of old forest, young forest, and early successional vegetation. In a deciduous forest, we may observe small gaps in an otherwise continuous canopy of trees, and we may detect transitions between forest communities dominated by different species of trees. In a coastal landscape, we may observe long narrow bands of similar vegetation as one moves from the land–water margin further inland. In landscapes of small extent (e.g., 100 m by 100 m), we may observe complex patterns of vegetated and unvegetated surfaces. How do all these different patterns develop? How do they change through time?

Today's landscapes result from many causes, including variability in abiotic conditions such as climate, topography, and soils; biotic interactions that generate spatial patterning even under homogeneous environmental conditions; past and present patterns of human settlement and land use; and the dynamics of natural disturbance and succession. Broad-scale variability in the abiotic environment sets the constraints within which biotic interactions and disturbances act. In this chapter, we discuss a variety of ways in which patterns develop on landscapes and provide a longer temporal context for understanding present-day patterns.

Much of what we as humans observe as landscape pattern is actually the spatial distribution of dominant vegetation types: for example, forest versus grasslands versus desert. The dominant vegetation establishes the resource base for the rest of the ecosystem. The pattern in the dominant vegetation, therefore, affects the spatial patterning of all components of the system. The patterning of the dominant vegetation may be defined by *ecotones*, the spatial divisions between vegetation types used to identify *patches* of similar vegetation or land cover. The ecotone forms the demarcation line that divides the dominant vegetation types and structures the basic spatial pattern on the landscape. In general, conditions of steep environmental gradients or recent disturbance lead to sharper boundaries between communities.

Levin (1976a) identified three general categories of causes of spatial pattern. The first category, *local uniqueness*, deals with unique features of a point in space, such as abiotic variability or unique land uses imposed by society. In addition to unique constraints at a local point, there are also the vagaries of colonization. In a sort of founder's effect, the seeds of a long-lived plant can become established and determine unique local features for decades. Chance alone may determine which of several different long-lived species arrives first at a site and becomes established. Finally, local uniqueness may depend on the existence of multiple stable states that may result from competition. That is, competition among interacting populations at a particular site may result in different relative abundances of these populations.

Levin's second category, *phase difference*, deals with spatial pattern resulting from disturbances (also see Chapter 7). The ecosystem responds to a local disturbance by going through succession. When viewed at any point in time, the landscape will have a number of disturbance sites of different age and in different stages of succession, that is, different phases. The individual sites will be in different phases of recovery, and the result will be a patchy pattern of vegetation.

Levin's third category, *dispersal*, prevents the landscape from becoming uniformly covered with a single, dominant population. The mechanism is a simple "fugitive" strategy (Platt and Weis, 1985). Prairie plants found in small patches of disturbed ground provide an example of this strategy. By producing many seeds that disperse far and wide, a fugitive species can establish itself whenever an opportunity arises, such as when ground squirrels or badgers have dug holes and displaced the prior vegetation. The fugitive species reach adulthood and produce seeds their first year, and plants from the surrounding undisturbed prairie spread slowly over the disturbed area. Given spatial heterogeneity of the landscape, frequent small disturbances, and limited dispersal ability of the dominant species, a fugitive species can maintain itself at isolated places throughout the landscape. Finally, interacting populations with differential dispersal abilities can also impose a quasi-periodic pattern on the landscape.

The following sections introduce a variety of factors that contribute to the patterns observed in landscapes, including abiotic factors, biotic interactions, human land-use patterns, and disturbance and succession. Climate, physiography, and soils establish the template for biotic interactions characteristic of each landscape. Because these abiotic factors are spatially and temporally variable, spatial patterning in soil formation and vegetation growth naturally occurs. Other processes, including disturbance and recovery from disturbance, as well as variability in human land use, may amplify this heterogeneity over a broad range of spatial and temporal scales.

ABIOTIC CAUSES OF LANDSCAPE PATTERN

Landscape patterns result, in part, from variability in climate and landform. *Climate* refers to the composite, long-term, or generally prevailing weather of a region (Bailey, 1996), and climate acts as a strong control on biogeographic patterns through the distribution of energy and water. Climate effects are modified by *landform*, the characteristic geomorphic features of the landscape, which result from geologic processes producing patterns of physical relief and soil development. Together, climate and landform establish the template on which the soils and biota of a region develop.

All landscapes have a history; understanding landscape pattern and process requires an understanding of landscape history. *Paleoecology* is the study of individuals, populations, and communities of plants and animals that lived in the past and their interactions with and dynamic responses to changing environments. This field offers a wealth of insight into the long-term development of today's landscapes. Although we do not attempt to review this rich field, we draw on paleoecological studies to discuss the role of climate in the spatial structuring of the biota and the role of prehistoric humans in influencing landscapes.

Climate

General climatic patterns will be familiar to all ecologists from introductory classes in biology or geography. At the broadest scale, climate varies with latitude, which influences both temperature and the distribution of moisture, and with continental position. Because of differential heating of land and water, coastal regions at a given latitude differ from inland regions. The distributions of biomes on Earth result from these broad-scale climate patterns. However, the effects of both latitude and continental position are then modified locally by topography, leading to finer-scale heterogeneity in climate patterns (Bailey, 1996). Temperatures generally decrease with increasing elevation, and north- and south-facing slopes experience different levels of solar radiation and hence different temperatures and evaporation rates.

Long-term Climate Change

The distribution of plant and animal communities, and indeed of entire biomes, has varied tremendously with past changes in climate, even in the absence of human activities. The spatial distribution of life forms today as a function of latitude and longitude look very different compared to those of 5000 or 10,000 years (yr) before present (BP). Furthermore, present assemblages of plants and animals represent only a portion of the ecosystems that have existed during Earth's history.

Climatic changes on Earth during the past 500,000 yr have been dramatic (Figure 4.1). Each glacial–interglacial cycle is about 100,000 yr in duration, with 90,000 yr of gradual climatic cooling, followed by rapid warming and 10,000 yr of interglacial warmth. The peak of the last glacial period, or ice age, was about 18,000 yr BP and ended approximately 10,000 yr BP. These long climate cycles may be produced by cyclic changes in solar irradiance resulting from long-term and complex variation in Earth's orbital pattern (the Milankovitch cycles) as Earth wobbles on its rotational axis (Crowley and Kim, 1994). This orbital eccentricity results in approximately 3.5% variation in the total amount of solar radiation received by Earth and changes its latitudinal distribution.

Looking more closely at the most recent climate cycle, we can examine changes in mean global temperature for the past 150,000 yr. Mean global temperature is the only reliable expression of global surface air temperature because climatologists want to remove the spatial variability in climate to detect trends in the entire global climate system; thus, small changes in mean global temperature may reflect very large fluctuations in temperature at many locations on Earth. During the past 150,000 yr, there was a 5°C shift in average global temperature between the glacial and interglacial periods (Figure 4.2). Peak warming, about 1°to 2℃ warmer than today, occurred between 9000 and 4000 yr ago. This seemingly small increase led to a 70-km shift eastward in the prairie–forest boundary in the upper Midwest compared to its present location. Since the end of the last ice age, mean global temperature has fluctuated by little more than 1℃; indeed, the Little Ice Age, which lasted for >500 yr, was a 1℃ fluctuation. If past patterns continue, the Milankovitch cycle indicates a decrease in global temperatures with the onset of another glaciation during the next 25,000 yr. Alternatively, a major climatic warming of at least 2℃ is proposed as a superinterglacial that will last for at least 1000 yr because of the anticipated build up of carbon dioxide (CO_2) and other greenhouse gases that trap infrared radiation within the atmosphere and warm Earth.

Earth's biota obviously must respond to these large fluctuations in climate. In general, organisms may respond in three ways (Cronin and Schneider, 1990), which contribute to long-term changes in their distribution: (1) they may evolve and speciate; (2) they may migrate long distances, each according to its limits of tolerance and movement capability; or (3) they may become extinct. Considerable work has been done to describe and understand the vegetation changes that accompanied past changes in climate. For example, range limits of tree species in eastern North America changed dramatically during the past 13,000 yr (Figure

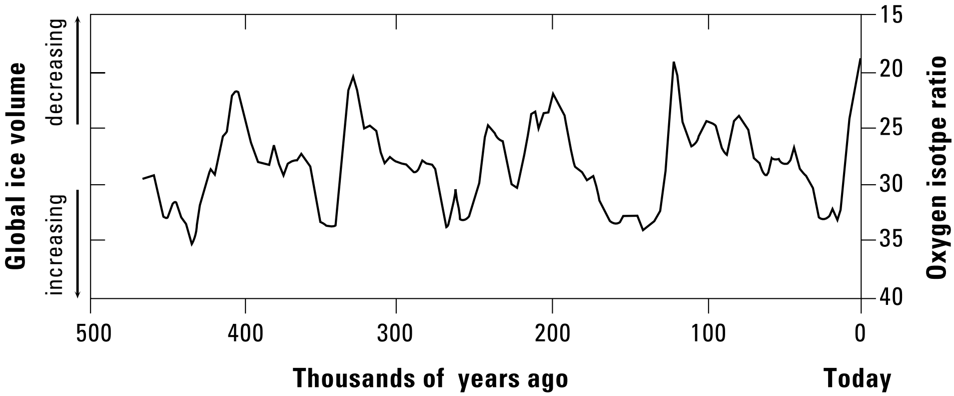

Figure 4.1.

Record of climatic changes over the past 500,000 years as measured by oxygen isotope ratios from cores of deep-sea sediments obtained from the Indian Ocean. Note the cycles of rapid warming followed by gradual cooling.

Adapted from Delcourt and Delcourt, 1991, based on Imbrie and Imbrie, 1979.

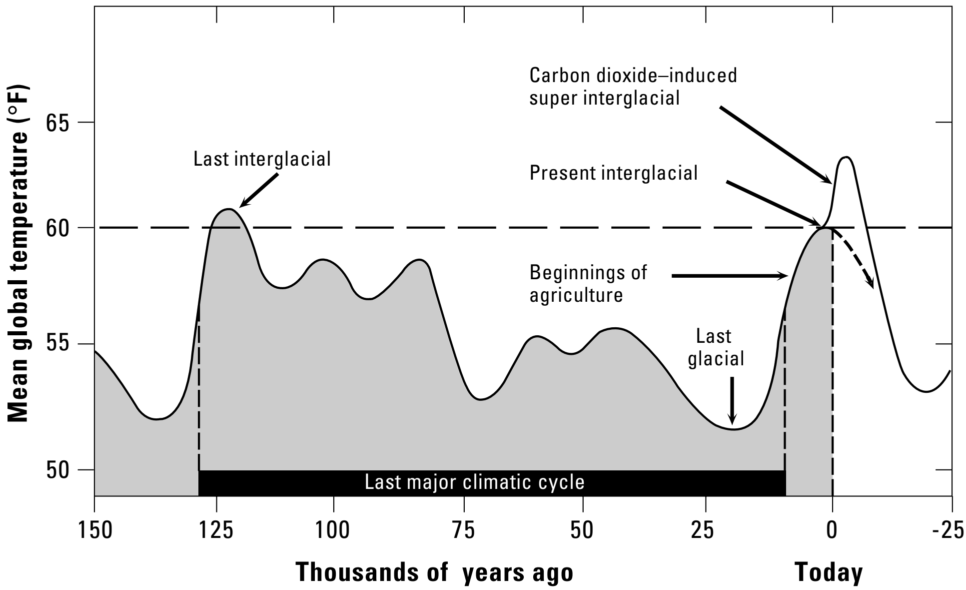

FIGURE 4.2.

Global climate changes over the past 150,000 years and projected for the next 25,000 years. A future cooling trend is projected based on the Milankovitch cycles, but this may be delayed by a warming period induced by elevated concentrations of carbon dioxide and other greenhouse gases in the atmosphere.

ADAPTED FROM DELCOURT AND DELCOURT, 1991, BASED ON IMBRIE AND IMBRIE, 1979.

4.3) (Davis, 1983). Not only have species varied in their ranges, but also the local abundances, and thus relative dominance, of taxa have changed. The range of oak (*Quercus*) in eastern North America has expanded northward during the past 20,000 yr, and the population centers where oak dominated also varied spatially (Delcourt and Delcourt, 1987).

Several points important for providing a context for interpreting patterns on today's landscapes emerge from the studies of vegetation response to climate. First, the glacial–interglacial cycles trigger the disassembly of communities, followed by reassembly that is unpredictable in terms of either species composition or abundance. Compared to present-day communities, the past communities at many sites feature mixtures of species that are absent or very rare on the modern landscape (e.g., Barnosky et al., 1987). Second, the characterization of past plant communities suggests that the displacement of entire vegetation zones or communities was the exception rather than the rule. That is, species responded individualistically to climatic change, each according to its limits of tolerance, dispersal capability, and interactions with the surrounding biota. Third, disturbance regimes (see Chapter 7) have been very sensitive to past changes in climate. For example, the fire regime in northwestern Minnesota, USA, shifted from a 44-yr fire cycle during the warm, dry 15th and 16th centuries to an 88-yr fire cycle after the onset of cooler, moister conditions after AD 1700 and throughout the Little Ice Age (Clark, 1990). In summary, it is important for the landscape ecologist to recognize the dynamic responses of the biota to variability in climate in space and time.

The implications of potential climate change for the distribution of Earth's biota and the patterns observed across landscapes are profound. Current climate exerts a very strong effect on landscape patterns (see Bailey, 1996, for an excellent treatment of this), and the most conspicuous effect of climate change may be shifts in landscape pattern (Neilson, 1995). Teams of mathematical modelers have pro-

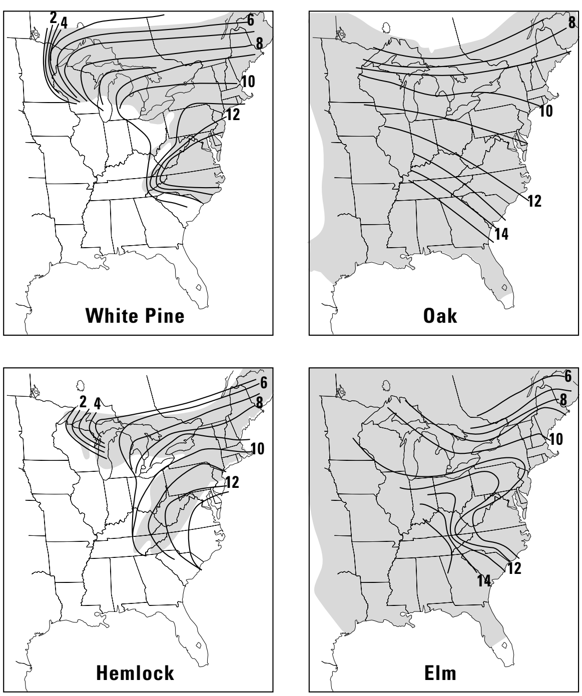

FIGURE 4.3.
Changes in northern and western range limits for four eastern North America tree taxa during the late Quaternary based on pollen records. Numbers indicate the time (in thousands of years before the present) at which pollen from each species was recorded at a given site. Shading indicates current geographic range.

ADAPTED FROM DAVIS, 1983.

BOX 4.1
LONG-TERM VEGETATION CHANGES AT GRAYS LAKE, IDAHO, USA

Many examples could be used to illustrate vegetational changes during the Pleistocene and Holocene. Beiswenger's (1991) study of the Grays Lake Basin in southeastern Idaho, USA, offers one fine case study. Grays Lake sits within the central Rocky Mountains at relatively low elevation (1950 m) and is ideal for studying late-Quaternary vegetation dynamics because it was not glaciated. The current vegetation includes marshes dominated by *Scirpus americanus*, sagebrush (*Artemisia*) steppe, coniferous forests (including *Pseudotsuga menziessii, Pinus contorta, P. flexilis, Picea engelmannii*, and *Abies lasiocarpa*), and aspen (*Populus tremuloides*) forest. Fossil pollen were identified and dated from sediment cores obtained from the lake at the snow–ice surface; the cores ranged in length from 14 to 21 m. Results demonstrate a dominance of *Artemisia* ~70,000 to 30,000 yr before present (BP) prior to the last major glacial advance in the Rocky Mountains. This indicates an arid climate in which trees were limited to the adjacent mountains. *Pinus* pollen then dominates between ~30,000 and 11,500 yr BP, and the increase in pine pollen indicated that a forest occupied the basin during the full glacial period. At the transition from the late-glacial to Holocene ~11,500 to 10,000 yr BP, there is an increase in pollen from both *Picea* and *Artemisia* along with a tenfold increase in total pollen influx, suggesting a vegetation response to increased moisture accompanying climatic warming. Initial climatic change produced cool, moist conditions suitable for *Picea*, which had been limited by a cold and dry glacial climate. However, this transitional period of increased moisture reversed before 10,000 yr BP, and the percentages of *Picea* and *Pinus* pollen both decline near the end of the period. The conifers moved to higher elevations, while *Artemisia* and other species (e.g., Compositae) became more abundant at lower elevations. As the Holocene began, the percentage of pollen from steppe plants increased, with a peak in Gramineae pollen ~8500 yr BP. Warm, dry conditions occurred from ~10,000 to at least 7100 BP, with a xeric maximum suggested ~8200 yr BP. Around 7300 to 2000 yr BP, *Pinus, Artemisia,* and *Juniperus* pollen all increased, reflecting moderate cooling, increased precipitation, or both. The most recent 2000 yr were characterized by increases in *Pinus, Picea, Abies, Pseudotsuga,* and *Populus* pollen percentages and declines in *Juniperus, Artemisia*, Compositae, and Chenopodiaceae pollen. Further cooling and/or increased precipitation has continued since ~2000 yr ago.

The Grays Lake study reveals a strong relationship between vegetation and climate in the Central Rocky Mountains over the past 70,000 yr (Beiswenger, 1991). The data indicated that the vegetation around Grays Lake has shifted from a cold, dry, *Artemisia* steppe to a conifer woodland during the last glacial period. Rapid expansion of spruce and sagebrush followed with the cool, moist conditions produced by climatic warming. A dry steppe developed next with the rising temperatures and increased aridity of the early Holocene, but conifer forest established with a subsequent cooling. This work demonstrates the wide range of vegetation types that occupied a particular landscape through time and emphasizes that the landscapes that we observe today are by no means static. Landscape ecologists must strive to understand the history of the landscapes that they study.

duced maps of how the dominant ecotones will move across the United States in response to temperature and moisture shifts caused by a doubling of atmospheric CO_2 (VEMAP, 1995). Bartlein et al. (1997) projected the potential distributions of selected tree taxa in the region of Yellowstone National Park, Wyoming, USA. They used a coarse-resolution climate model that incorporated a doubling of atmospheric CO_2 and interpolated the projections onto a 5-min grid of topographically adjusted climate data. Simulated vegetational changes included elevational and directional range adjustments. That is, taxa could move up or down elevational gradients or latitudinally. The ranges of high-elevation species (e.g., *Pinus albicaulis*) diminished under the future climate scenario, and some species were

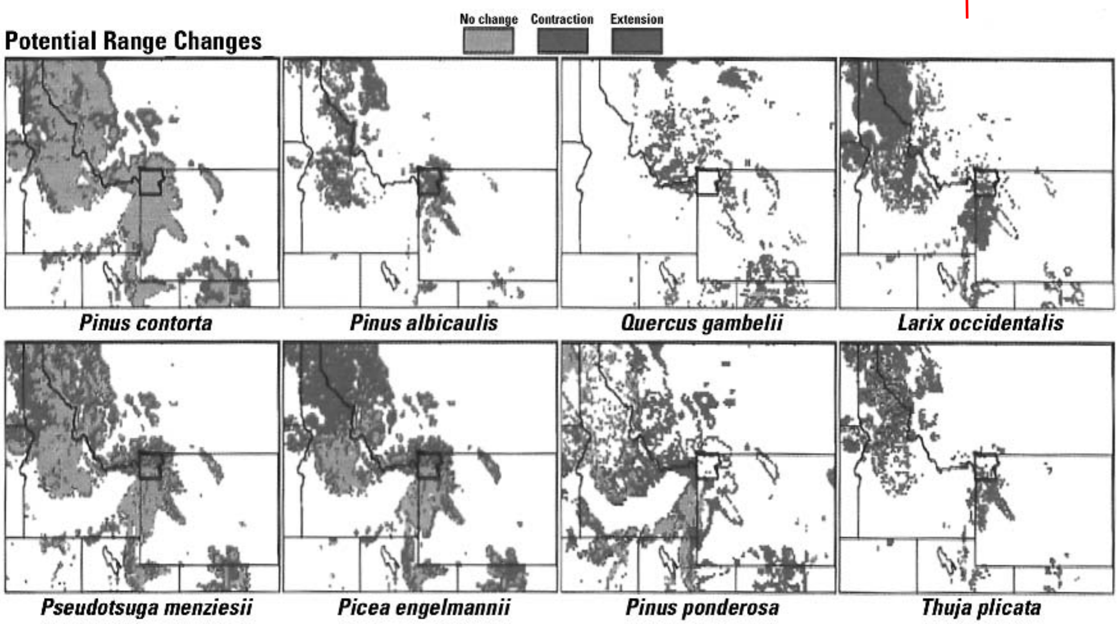

FIGURE 4.4.

Potential range changes of selected tree taxa in the Yellowstone National Park region of the Rocky Mountains under projections of a $2 \times CO_2$ climate. Green shading indicates grid points where the taxon occurs under both the current and $2 \times CO_2$ scenario. Red shading indicates grid points where the taxon occurs under current climate, but does not occur under the $2 \times CO_2$ climate. Blue shading indicates grid points where the taxon does not occur under current climate, but does occur under the $2 \times CO_2$ climate. (Refer to the CD-ROM for a four-color reproduction of this figure.)

REPRODUCED FROM BARTLEIN ET AL., 1997.

extirpated locally (Figure 4.4). Projected mild, wet winters also produced new areas of suitable habitat for other taxa (e.g., *Pinus ponderosa, Larix occidentalis*, and *Quercus gambelii*) (Figure 4.4). Of particular note was that the new communities had no analogue in the present-day vegetation, because low-elevation montane species currently in the region were mixed with species that might colonize from the northern and central Rocky Mountains and the Pacific Northwest. In addition, the potential range adjustments projected for different species equaled or exceeded the changes seen in the paleoecological record during previous warming intervals (Bartlein et al., 1997).

Landform

Landforms range from nearly flat plains to rolling, irregular plains, to hills, to low mountains, to high mountains (Bailey, 1996) and are identified on the basis of three major characteristics: (1) relative amount of gently sloping (<8%) land, (2) local relief, and (3) generalized profile, that is, where and how much of the gently sloping land is located in valley bottoms or in uplands (Bailey, 1996). Landforms may be described further by considering the topographic sequence of variation, or *soil catena*, of soils and associated vegetation types within each landform. For example, a mountainous landform may have a toposequence that includes ridgetops, steep slopes, shallow slopes, toe slopes, and protected coves. If different areas are composed of similar landforms with similar geology, then soil catenas and vegetation types may also be expected to be similar.

Four general effects of landform on ecosystem patterns and processes (Figure 4.5) were categorized by Swanson et al. (1988).

1. The elevation, aspect, parent materials, and slope of landforms affect air and ground temperature and the quantities of moisture, nutrients, and other materials available at sites within a landscape. For example, south-facing slopes receive more solar radiation than northward slopes, resulting in warmer, drier conditions. These topographic patterns are strongly related to the distribution of vegetation across a landscape (e.g., Whittaker, 1956).
2. Landforms affect the flow of many quantities, including organisms, propagules, energy, and matter through a landscape. The funneling of winds, for example, may lead to dispersal pathways for wind-blown seeds. The position of lakes relative to groundwater-flow pathways may strongly influence the chemical and biological characteristics of these lakes (Kratz et al., 1991; also see Chapter 9).

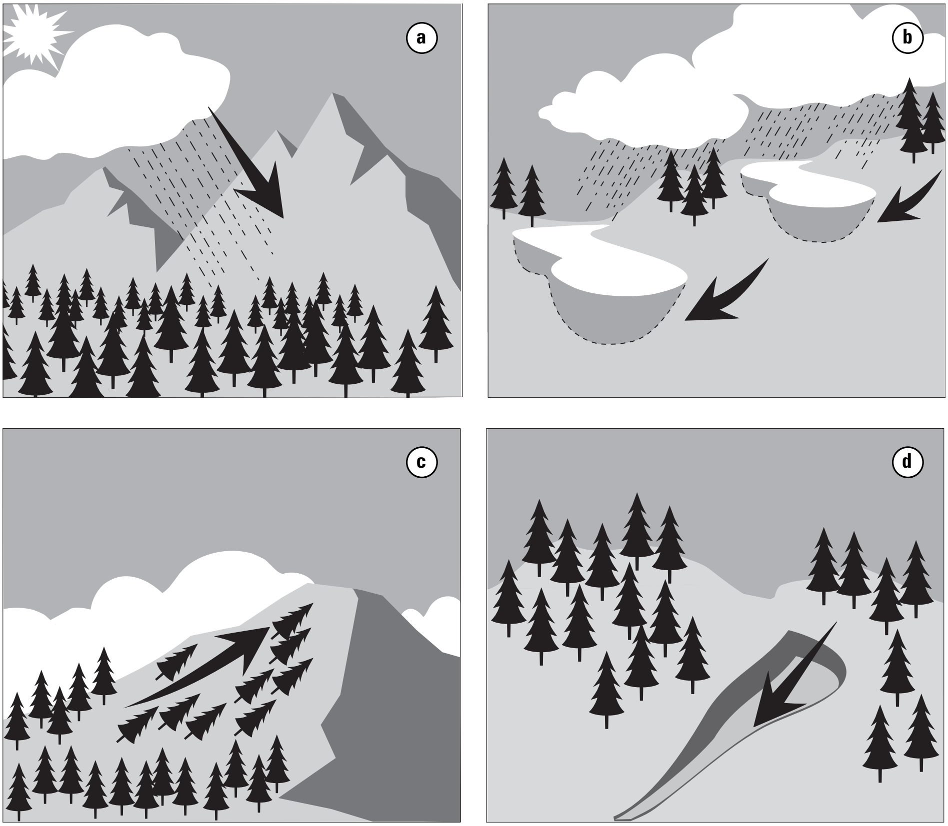

Figure 4.5.

Examples of four classes of landform effects on ecosystem patterns and processes. (a) Topographic influences on rain and radiation (arrow) shadows. (b) Topographic control of water input to lakes. Lakes high in the drainage system receive a greater proportion of water input by direct precipitation than lakes lower in the landscape, where groundwater (arrows) predominates; also see Chapter 9. (c) Landform-constrained disturbance by wind (arrow) may be more common in upper-slope locations; also see Chapter 7. (d) The axes of steep concave landforms are most susceptible to disturbance by small landslides (arrow).

Modified from Swanson et al., 1988.

3. Landforms affect the frequency and spatial pattern of natural disturbances such as fire, wind, or grazing. Across a New England landscape, susceptibility to damage from hurricanes varied with landscape position, with greater damage observed in more exposed topographic positions (Foster and Boose, 1992; Boose et al., 1994). In Labrador, fire and topography jointly influenced vegetation patterns (Foster and King, 1986) with nearly all patches of birch (*Betula*) forest occurring on steep slopes or ridges with high moisture (Figure 4.6). Lightning would ignite fires on ridge tops covered by spruce–fir (*Picea–Abies*) forest, sweep down the ridges, and stop at existing birch stands or wetter areas in the valley bottoms. These newly burned areas along the slopes provided opportunities for birch to colonize.

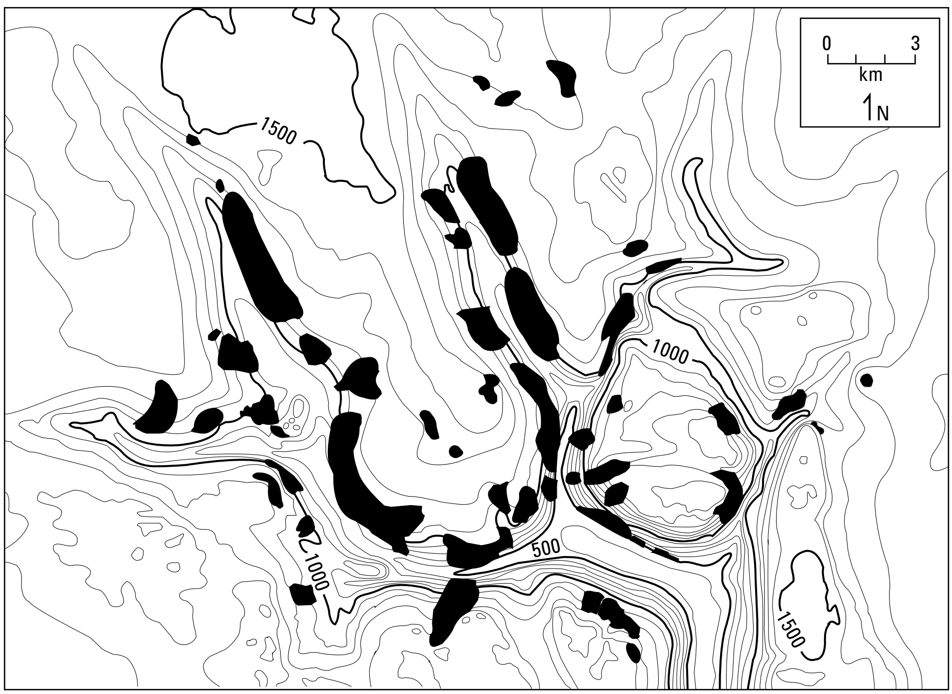

FIGURE 4.6.
Distribution of *Betula papyrifera* forests (black) on the hillslopes and canyon walls of the St. Augustin River Valley, southeast Labrador.

ADAPTED FROM FOSTER AND KING, 1986.

4. Landforms constrain the spatial pattern and rate or frequency of geomorphic processes, the mechanical transport of organic and inorganic material, that alter biotic characteristics and processes. Portions of a landscape may be more or less susceptible to landslides or to shifts in river channels. Taken together, landforms significantly contribute to the development and maintenance of spatial heterogeneity across a landscape through their multiple effects on soils, vegetation, and animals (Swanson et al., 1988). Even in areas of relatively little topographic relief, such as the glacial landforms of the upper Midwest of the United States, landform explains a great deal of the variability in successional pathways (Host et al., 1987) and biomass (Host et al., 1988) across the landscape.

BIOTIC INTERACTIONS

Interactions among organisms, such as competition and predation, may lead to spatial structuring even in a completely homogeneous space. Theoretical population ecology focuses much attention on these dynamics (Ives et al., 1998), with an emphasis on how interactions within and among populations can generate spatial patterns and how these patterns influence the outcome of interactions. The product of these theoretical approaches often is a map of species distributions.

Competition between two species in a landscape without any abiotic variation theoretically could result in homogeneous spatial distribution (i.e., one species remaining) through competitive exclusion (Gause, 1934). The best competitor would win out and establish itself throughout the landscape, resulting in a homogeneous distributional pattern. However, there are important exceptions to competitive exclusion.

Groups of competing organisms may interact in complex ways so that final distributions take on one of many alternative stable states. These *multiple stable states* (Sutherland, 1974) may often occur when several different species can potentially occupy and dominate a site. Which species actually occurs on a specific site is determined by very small stochastic changes in the initial conditions. Once in one of these states, the community may remain dominant in spite of minor disturbances. However, a major disruption may result in a new configuration that is different, but also stable. This type of shifting, stochastic pattern may be observed near ecotones between major community types. For example, small, stable stands of trees may extend out into grassland, and small stable patches of grasses may intrude into the forest. Along this ecotonal edge, both communities are stable, and there are very small differences in the competitive advantage of one community over the other. Chance plays a role in which community is established, and once established this community can maintain itself until a major disruption occurs.

Competition between vegetation types can also form ecotones, resulting in a sharp line between vegetation, even when differences in environmental conditions on either side of the ecotone are small. Along a north–south transect, for example, temperature and moisture may change gradually and continuously, with no sharp discontinuities. Conditions to the south may favor one species and conditions to the north, another. Somewhere along the transect, conditions will be suitable for the growth of both species. Competition for space may form a sharp ecotone between them, rather than a gradation or intermingling.

A different sort of pattern emerges from *reaction–diffusion models* of interacting populations (Okubo, 1975). In these models, the growing and competing populations are also dispersing across a uniform environment. In many cases (Levin, 1978), the expected uniform distribution is destabilized by the action of diffusion, and the system spontaneously assumes a patchy, periodic spatial distribution. For example, in *predator–prey models*, a patchy distribution results if the diffusion coefficient of the predator is sufficiently larger than the prey. A fixed spatial pattern with peaks and troughs in the density of both predators and prey can result. This mechanism of *diffusive instability* has been suggested as the cause of patchy distribution in plankton (Kierstead and Slobodkin, 1953; Steele, 1974a; Edelstein-Keshet, 1986; Murray, 1989). We might suspect this type of mechanism whenever a periodic or quasi-periodic pattern is detected on the landscape.

Pattern also results from the activities of a *keystone species*. Paine (1974, 1976) studied the interactions between the mussel *Mytilus californianus* and its starfish predator, *Pisaster ochraceous*, in the intertidal zone. The mussel is a superior competitor, but predation by the starfish keeps the mussel population in check. Higher up on the shoreline, the starfish has difficulty reaching the mussels. The mussels completely dominate the rock surfaces and eventually grow too large for the starfish to handle. Farther down the shoreline, the starfish consumes all young mussels. The result is a very distinct striped pattern on the rocks, mussel above, but not below this line. When Paine (1974) experimentally removed the starfish, the mussels moved down the surface of the rock, outcompeting and eliminating 23 other species of invertebrates. The starfish is clearly the keystone predator that creates and maintains the spatial pattern. Holling (1992) believes that keystone species and processes are a common cause of pattern, stating that "All ecosystems are controlled and organized by a small number of key plant, animal, and abiotic processes that structure the landscape at different scales."

Influence of Dominant Organisms

In many respects, it is the dominant organisms that define spatial pattern on the landscape. It is, for example, the patches of trees or natural vegetation that define the pattern on most natural terrestrial landscapes. Within the context of the abiotic template, the dominants alter the abiotic conditions and provide resource base and substrate for the other populations in the ecosystem. In these cases, the rest of the ecosystem is constrained to operate within the spatial pattern of the dominants. The interactions of the plants with the soil, climate, and topography produce the underlying spatial context. This is not only true in terrestrial ecosystems; for example, coral is a dominant organism along tropical shorelines. The coral forms the substrate and resource base for the entire food web, and its spatial distribution dictates the spatial pattern for the rest of the ecosystem.

A common example of a dominant consumer that may produce and maintain spatial pattern is a lethal pest. Insects such as the spruce budworm (*Choristoneura fumiferana*) and the balsam wooly adelgid (*Adeiges picea*) act very much like other disturbances in causing patches to revert to earlier successional stages. The bark beetle provides a simple example (Rykiel et al., 1988). Lightning strikes and kills a single tree and permits the beetle to invade. Once established, the beetle can attack adjacent trees and spread from this original point of attack. Eventually, a large patch is opened and reverts to early successional stages.

The beaver (*Castor canadensis*) provides a fascinating example of landscape pattern resulting from the activities of a dominant organism. The beaver uses sticks and mud to dam a second- to fifth-order stream, impounding water behind the dam (Johnston and Naiman, 1990a). Aerial photography (Johnston and Naiman, 1990b) shows that as much as 13% of the landscape can be altered in this way. The animals also affect the riparian vegetation and saturate the soils, forming wetlands (Naiman et al., 1986). When the dam breaks down and the pond is abandoned, a characteristic beaver meadow remains as a distinct spatial feature on the landscape (Remillard et al., 1987).

A similar story can be told of the American bison (*Bison bison*). At one time there were 75 million bison in North America (Roe, 1951). Huge herds migrated regularly and determined plant composition along these linear routes, both by preferential grazing and by recycling nutrients in dung. The animals also used dust baths to control skin parasites and formed characteristic circular patches on the landscape. In general, large mammals will act as a mechanism in pattern formation (Botkin et al., 1981). More generally, large mammals often directly alter vegetation and rates of nutrient recycling (Dyer et al., 1986). A moose, for example, consumes five to six metric tons of food a year (Pastor et al., 1988), increasing nutrient recycling and altering patterns of productivity. By selectively browsing hardwoods (Pastor et al., 1993), moose also directly affect species composition at landscape scales. An effect of excluding elephants from their native habitat is a change in the pattern of vegetation (Harton and Smart, 1984).

HUMAN LAND USE

Patterns of land use can alter both the rate and direction of natural processes, and land-use patterns interact with the abiotic template to create the environment in which organisms must live, reproduce, and disperse. *Land use* refers to the way in which and the purposes for which humans employ the land and its resources (Meyer, 1995). For example, humans may use land for food production, housing, industry, or recreation (Nir, 1983). A related term, *land cover*, refers to the habitat or vegetation type present, such as forest, agriculture, and grassland. Although they are related, it is important to note the distinction between these terms: an area of forest cover may be put to a variety of uses, including low-density housing, logging, or recreation. We use *land-use change* to encompass all the ways in which human uses of the land have varied through time. The ways in which humans use the land are important contributors to landscape pattern and process.

Prehistoric Influences

Prehistoric humans had a major role in influencing landscapes, and their past effects contribute to present-day landscape patterns. Using the pollen record, indications of human activities can be traced back thousands of years, and discrete episodes of human disturbance can be correlated with archeological data. Consider, for example, the historical expansion of human influences in Europe (Delcourt and Delcourt, 1991). In the early Holocene, there was broad-based foraging throughout the Mediterranean region. The switch from a nomadic to a more sedentary way of life was just beginning ~10,000 BP, and by ~8000 BP permanent settlements were established in Greece. These settlements included cultivation of crops and maintenance of livestock, and food production became more labor intensive. Cereal cultivation caused a major shift in patterns of land use because the permanent fields needed weeding and required nutrient replenishment, both of which were activities requiring considerable human labor. By about 6500 BP, farming expanded north of Greece as winters became warmer and precipitation increased. Development of more efficient technologies also contributed to the continued expansion of agriculture in Europe. Use of the *ard*, a tool that used the angle between the trunk and roots of a tree to break through the soil and that was pulled by an oxen, became prevalent ~5000 BP. Further human expansion became based on the maintenance of work animals, because the oxen-drawn *plow* that could both furrow and turn over the soil was developed and used by ~3000 BP. More efficient bronze sickles also replaced wooden sickles.

What were the effects of this expansion of human activities in Europe on native vegetation? The impact of the axe and spade on ecosystems began to transform natural landscapes into cultural ones through plowing, burning, and trampling. The ard, because it did not overturn the soil, left perennial roots intact. The plow, however, removed perennials from the soil and encouraged establishment of annual plants. The process of deforestation and conversion of land to pasture or crop cultivation changed the landscape from a natural to a cultural mosaic (Delcourt, 1987). This also occurred in North America, although early settlements of Native Americans were more restricted to floodplains; uplands were used much later than in Europe (Delcourt, 1987). However, Native Americans in North America profoundly influenced the landscape by establishing settlements, practicing agriculture, hunting, and using fire to induce vegetation changes (Denevan, 1992).

The influences of prehistoric humans on landscapes were characterized by Delcourt (1987) into five main types.

1. Humans changed the relative abundances of plants, especially the dominance structure in forest communities. In the pollen record from Crawford Lake, Ontario, land clearance and maize cultivation by the Iroquois is documented by pollen sequences spanning the 14th to 17th centuries. During this time, the dominance of tree species in the surrounding forest changed from late-successional species such as beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) to forest of oak (primarily *Quercus rubra*) and white pine (*Pinus strobus*).
2. Humans extended or truncated the distributional ranges of plant species (woody and herbaceous). In Europe, for example, the range of olives (*Olea europaea*) after 3000 yr BP was extended through cultivation from the Mediterranean coast only to throughout southern Europe. Truncation of the

range of a native tree species by prehistoric humans has been documented for bald cyprus (*Taxodium distichum*) in the central Mississippi and lower Illinois valleys in eastern North America. Charcoal evidence suggests a preference for cyprus wood during the period from 2000 yr BP to AD 1450, with the species becoming locally extinct as human populations increased (Delcourt, 1987).

3. Opportunities were created for the invasion of weedy species into disturbed areas. In many places, weedy species assemblages associated with cultivated fields increase in abundance in the pollen record, and these increases are correlated with archeological evidence of human occupation (Delcourt, 1987).
4. The nutrient status of soils was altered through both depletion and fertilization.
5. The landscape mosaic was altered, especially the distribution of forest and nonforest. This last change is also easiest to detect in the paleoecological record by examining ratios of tree to herbaceous pollen.

A key point from this brief discussion of the long-term development of the cultural landscape is that the landscapes we may perceive to be natural today probably have a history of human influence that dates back a long time. Of course, there is variability in the degree to which humans influenced different ecosystems on different continents. However, humans have long been a presence in many landscapes, and their role in creating landscape pattern should not be discounted.

Historic and Present-Day Effects

Both worldwide and in the United States, land-cover patterns today are altered principally by direct human use: by agriculture, raising of livestock, forest harvesting, and construction (Meyer, 1995). Human society relies on natural habitats for a variety of services, including productivity, recycling of nutrients, breakdown of wastes, and maintenance of clean air, water, and soil. In North America, land-use changes have been particularly profound since Europeans settled the continent three centuries ago. Landscapes have become mosaics of natural and human-influenced patches, and once-continuous natural habitats are becoming increasingly fragmented (e.g., Burgess and Sharpe, 1981; Harris, 1984).

Land-use changes in the United States serve as a handy example. At the time of European settlement, forest covered about half the present lower 48 states. Most of the forestland was in the moister east and northwest regions, and it had already been altered by Native American land-use practices (Williams, 1989). Clearing of forests for fuel, timber, and other wood products and to open the land for crops led to a widespread loss of forest cover that lasted through the early 1900s. So extensive was this loss that by 1920 the area of virgin forest remaining in the conterminous United States was but a tiny fraction of that present in 1620 (Figure 4.7). Some originally cleared areas, for example, New England, the Southeast, and the upper Midwest, have become reforested due to lack of cultivation. In other regions, clearing for agriculture has been more permanent (e.g., the lower Midwest), or harvest of primary forest has continued until recent times (e.g., Pacific Northwest).

Developed land in the United States has expanded as the population has grown in number, with most of the population now living in cities, towns, and suburbs

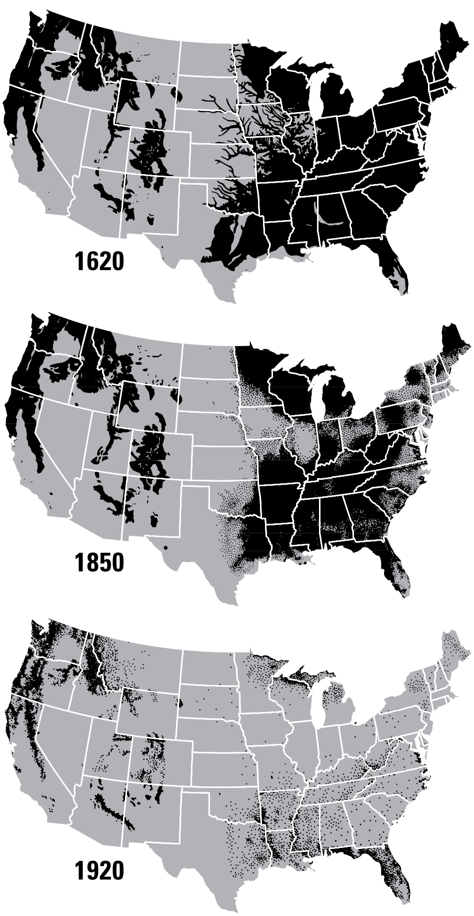

Figure 4.7.
Approximate area of virgin old-growth forest in the contiguous United States in 1620, 1850, and 1920. Note that this does not depict total forest area, because many forests, especially in the eastern United States, have regrown following clearing and the abandonment of agriculture.

Adapted from Meyer, 1995.

rather than on farms. Americans spread out more across the land as transportation technologies improved, especially as the automobile became the primary mode of transportation. Present-day patterns of settlement take up more land per person than in the past, and homes and subdivisions are more dispersed across the landscape. A frontier of rapid and sometimes chaotic land-use change surrounds urban areas (Meyer, 1995). Trends in developed land are unique because they run in only one direction; that is, developed land expands and does not revert to other categories. Thus, the distribution of developed land across the United States will leave a long-lasting footprint on the landscape (Turner et al., 1998a). The most remarkable aspect of the landscape of the United States since European settlement is its continual change. Effects of these vast changes are long lasting and crucial to our understanding of the present-day plants and animals that inhabit our landscapes (Foster, 1992; Dale et al., 2000).

DISTURBANCE AND SUCCESSION

Disturbance and the subsequent development of vegetation are key contributors to pattern on the landscape. By *disturbance*, we mean any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource availability, substrate, or the physical environment (White and Pickett, 1985). Examples include fires, volcanic eruptions, floods, and storms. Disturbances are often described by a variety of attributes, including their spatial distribution, frequency, spatial extent, and magnitude. The spread of disturbance and spatial patterns of recovery have received considerable attention in landscape ecology, and we devote a chapter to exploring these dynamics (see Chapter 7). Here, we simply recognize disturbance as an important agent of pattern creation at a variety of spatial and temporal scales.

SUMMARY

Today's landscapes result from many causes, including variability in abiotic conditions such as climate, topography, and soils; biotic interactions that generate spatial patterning even under homogeneous conditions; past and present patterns of human settlement and land use; and the dynamics of natural disturbance and succession. Three general causes of spatial pattern were identified by Levin (1976a): (1) local uniqueness, that is, the unique features of a point in space, such as abiotic variability or unique land uses imposed by society; (2) phase differences, or variation in spatial pattern resulting from disturbances; and (3) dispersal, which prevents landscapes from becoming uniformly covered with a single, dominant population.

Landscape patterns result, in part, from variability in climate and landform; these broad-scale abiotic drivers constrain other causes of landscape change. Climate refers to the composite, long-term, or generally prevailing weather of a region (Bailey, 1996). Climate effects are modified by landform, which includes both geology and topography, or physical relief. The distribution of plant and animal communities and indeed of entire biomes has varied tremendously with past changes in climate, even in the absence of human activities. Not only have species varied in their ranges, but also the local abundances and thus the relative dominance of taxa have changed. Landforms are important influences on landscape pattern because they influence moisture, nutrients, and materials at sites within a landscape; they affect flows of many quantities; they may influence the disturbance regime; and they constrain the pattern and rate of geomorphic processes. It is important for the landscape ecologist to understand the influence of climate and landform on the biota and to recognize the dynamic responses of the biota to variability in climate in space and time.

Interactions among organisms, such as competition and predation, may lead to spatial structure, even in the absence of abiotic variation. Keystone species or dominant organisms may define spatial pattern on a landscape. Disturbance and succession (see Chapter 7) are key contributors to landscape pattern. Humans are also a strong driver of landscape patterns, because land-use patterns interact with the abiotic template to create the environment in which organisms must live, reproduce, and disperse. Nearly all landscapes, even those that we perceive as natural today, probably have a history of human influence that dates back a long time. Many landscapes today have become mosaics of natural and human-influenced patches, and once-continuous natural habitats have become increasingly fragmented. Effects of past land use are increasingly recognized as important determinants of the present-day biota that inhabit our landscapes.

The understanding of what causes landscape pattern and pattern change with time is often translated into models used to project future landscape scenarios (Baker, 1989b). These models simulate changes in the abundance and spatial arrangement of elements on the landscape, such as vegetation or cover classes. Developing predictive models of landscape pattern and how such patterns vary through time is an active, rapidly changing field.

~ DISCUSSION QUESTIONS

1. For a landscape of your choice, define its spatial extent and describe the dominant factors causing landscape pattern in each of the following categories: abiotic factors, biotic interactions, human land use, and disturbance and succession. Repeat this exercise after reducing the extent of the landscape to 10% of its original size. Does the importance of the factors shift when the scale is changed? Why or why not?
2. Consider the variety of factors that create landscape pattern. How would you rank their relative importance? Do you think this ranking has changed through time? Explain your answers.
3. How do abiotic factors provide the template for the development of landscape pattern?
4. Why is it important to understand the history of a landscape? What types of effects of events from the past may remain in present-day landscape patterns?

~ RECOMMENDED READINGS

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