Landform Effects on Ecosystem Patterns and Processes

Geomorphic features of the earth's surface regulate the distribution of organisms and processes

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Understanding the form, behavior, and historical context of landscapes is crucial to understanding ecosystems on several temporal and spatial scales. Landforms, such as floodplains and alluvial fans, and geomorphic processes, such as stream erosion and deposition, are important parts of the setting in which ecosystems develop and material and energy flows take place. Over the long term, geomorphic processes create landforms; over a shorter term, landforms are boundary conditions controlling the spatial arrangement and rates of geomorphic processes.

Ecosystems respond to both landforms and geomorphic processes. The history of geomorphic processes may be expressed directly in the composition and structure of vegetation, where geomorphic events and vegetation develop together. Geomorphic processes operating before the establishment of existing vegetation, or those subtly coexisting with the vegetation, may have their greatest influence on vegetation through controlling patterns of soil properties across a landscape, as in toposequences (Hack and Goodlett 1960).

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Landform effects provide temporal and spatial perspectives for examining soil, vegetation, and aquatic ecosystems and for interpreting ecosystem processes

Fascinating interactions among geomorphic processes, landforms, and biota occur on various temporal and spatial scales. On a fine spatial scale, for example, parts of individual plants may retard soil erosion or may be damaged by earth movement. On a much greater scale, the geographic distribution and height of landmasses broadly control distributions of plants and animals through influences on environmental gradients of temperature and moisture and on corridors of migration during environmental change. Rigorous examination of interactions among geomorphology, ecosystems, and landscapes at the spatial scales of hectares to thousands of square kilometers is required for further understanding of landscape ecology (Risser et al. 1984) and ecosystem structure and function.

In this article, we identify and explore four classes of effects of landforms on ecosystems, providing examples from a range of ecosystem types. The static and dynamic physical characteristics of landscapes highlighted in the identification of these classes are important considerations when analyzing individual ecosystems and making comparisons among ecosystems. We will not consider here other classes of geomorphology-ecosystem interactions, such as effects of fauna and flora on rates of geomorphic processes.

This article is based on ongoing efforts to compare ecosystems among the 15 diverse sites studied in the Long-Term Ecological Research (LTER) program (Callahan 1984). These sites include an old-growth conifer forest in the Cascade Range of Oregon, Rocky Mountain alpine tundra in Colorado, lakes in forest land of Wisconsin, and shortgrass steppe in Colorado. Within this diversity we find valuable generalities.

Landscapes, landforms, and geomorphic processes

A discussion of effects of landforms on ecosystems is hindered by a lack of concise, widely accepted definitions of key terms and concepts. Naveh (1982) traces some of the history of usage and perception of *landscape*, a particularly crucial but poorly defined term. From roots in the Bible, secular literature, and art emphasizing a highly idealized view of nature, *landscape* has gained increasing use in fields such as physical geography, ecology, and landscape architecture. *Landscape* commonly refers to the form of the land surface and associated ecosystems at scales of hectares to many square kilometers. *Landform* is usually used at a finer scale and more specifically, such as a landform carved out by a landslide or created by sediment deposition forming a gravel bar. Landscapes are composed of landforms and ecological units, such as *patches* (Forman and Godron 1986).

By *geomorphic processes* we refer to mechanical transport of organic and inorganic material. In addition to surface erosion and mass movement, geomorphic processes include transport of material in solution in surface and subsurface water and biogenic soil movement by animals and root throw. A drawback of the term *geomorphic process* is the implication that the process is necessarily shaping landforms. Frequently, however, geomorphic process refers to transfer of material or disturbance of biota without regard to development of landforms or the time scale in which that occurs. We use the term in this general sense.

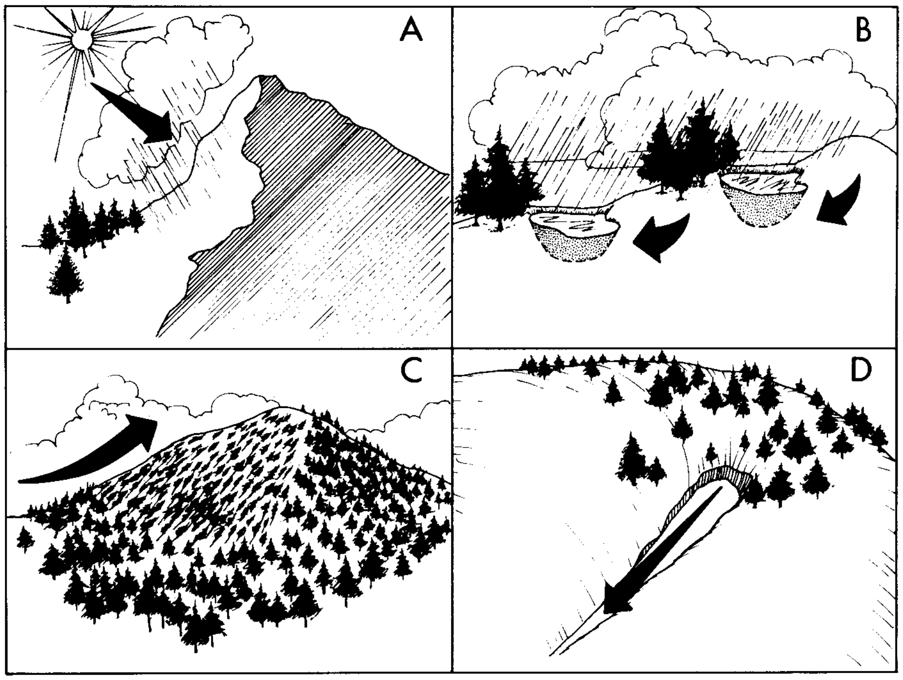

Figure 1. Examples of the four classes of landform influence on ecosystem patterns and processes. **a.** Class 1. Topographic influences on rain and radiation (arrow) shadows. **b.** Class 2. Topographic control of water input to lakes. Lakes high in the drainage system may receive a higher proportion of water input by direct precipitation than lakes lower in the landscape where groundwater input (arrow) predominates. **c.** Class 3. Landform-constrained disturbance by wind (arrow) may be more common in upper-slope locations. **d.** Class 4. The axes of steep concave landforms are most susceptible to disturbance by small-scale landslides (arrow).

Effects of landforms on ecosystems

We consider four classes of landform effects on ecosystem patterns and processes (Figure 1):

- Class 1: Landforms—by their elevation, aspect (direction in which land surface faces), parent materials, and steepness of slope—influence air and ground temperature and the quantities of moisture, nutrients, and other materials (e.g., pollutants) available at sites within a landscape.
- Class 2: Landforms affect the flow of organisms, propagules (e.g., seeds and sproutable root fragments), energy, and material (water, dissolved material, and organic and inorganic particulate matter) through a landscape.
- Class 3: Landforms may influence the frequency and spatial pattern of nongeomorphically induced disturbance by agents such as fire, wind, and grazing.
- Class 4: Landforms constrain the spatial pattern and rate or frequency of geomorphic processes that alter biotic features and processes.

In classes 1–3, we consider landforms to be unchanging boundaries that influence other environmental and biotic factors. Ecosystems are considered static in class 1, but dynamic in classes 2 and 3. In class 4, we regard both landforms and ecosystems as dynamic.

These four classes are valuable as a framework for discussion rather than as a rigorous classification scheme. In the following discussion, we give examples of each class, address the aggregated effects landforms have in determining the patterns of natural landscapes, and consider implications for landscape ecology. Some effects of landforms on ecosystems at the spatial scale of interest for this discussion do not fall neatly into one of these four classes.

Landforms and environmental gradients. Elevation and aspect are environmental gradients that have been widely recognized in mapping and in gradient analysis of patterns of vegetation across landscapes ranging from a few hectares to thousands of square kilometers (Billings 1973, Hack and Goodlett 1960, Kessell 1979, Whittaker and Niering 1965). Implicit in the relations between patterns of vegetation and landforms are the influences of elevation and aspect on solar energy and water regimes at patches within complex ecosystems. As moist air masses flow over hills and mountains, higher precipitation commonly falls at higher elevations (orographic effects), but such simple patterns may be confounded by the effects of rain and shadow, fog and cloud belts, and timing of snow accumulation and melt. Neither the simple nor the complex effects of landforms on environmental gradients, however, can commonly be separated from the effects of landforms on movement of materials and energy.

Landforms and movement of material, organisms, propagules, and energy. Landforms regulate movement of material, organisms, propagules, and energy across a landscape by defining gravitational gradients, influencing flow paths of wind, and forming barriers and corridors for movement. The role of landforms in controlling movement of material is implicit in studies of nutrient cycling and sediment routing within drainage basins, along transects crossing topographic features, and in other landform settings involving flow paths. The flow paths of material and energy movement across a landscape may vary greatly depending on factors operating at several scales. Water follows gravitational gradients. Dominant wind direction or paths of animal migration, on the other hand, may produce other patterns of material flux, controlled by landforms at broader scales.

To analyze transport through and temporary storage of soil and sediment in landscapes, scientists commonly use natural landform units to compartmentalize a landscape (Dietrich and Dunne 1978, Swanson et al. 1982). Such landform units are additionally characterized by their predominant process of transfer or dynamics of storage, because landforms strongly control the location and rate of processes that move both soil and sediment. For example, steep, concave hillslopes are landform units that are the predominant site of small, rapid landslides (Dietrich and Dunne 1978).

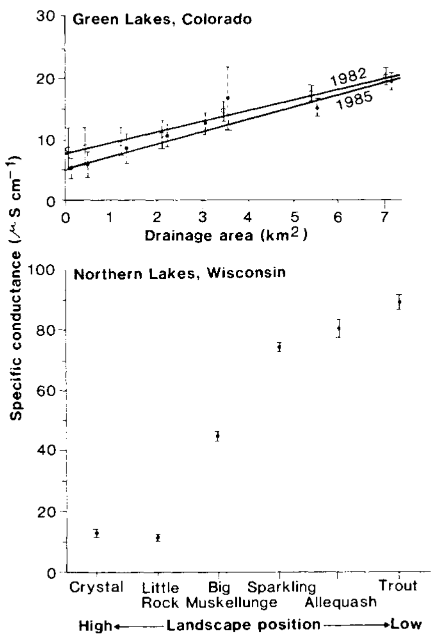

Figure 2. Specific conductance in the Green Lakes, Colorado, and Northern Lakes, Wisconsin, study sites. The Green Lakes record shows conductance (K) increasing with drainage area (1982: K = 8.1 + 1.8 area [km^2] [r = 0.996]; 1985: K = 5.7 + 2.0 area [km^2] [r = 0.992]). Values for Wisconsin lakes during spring and fall mixes 1982–1985 demonstrate higher conductances with lower landscape position. Specific conductance was measured at 25° C. Values shown ± 1 standard deviation.

Landforms also influence the temporal and spatial patterns of fluxes of material carried across landscapes by surface water. In lakes at LTER sites in the Colorado alpine (Caine 1984) and in the forest land of Wisconsin (Magnuson et al. 1984), characteristics of water quality vary with a lake's position in the landscape. At both sites, specific conductance—a general measure of solute concentration and acid neutralizing capacity—is greater in lakes lower in the landscape, reflecting the proportionate increase of surface or groundwater contributed to lakes lower in a flow system (Figure 2). More of the water entering such lakes has passed through the vegetation and soil, entraining products of rock weathering and decomposition and therefore giving higher solute concentrations. Lakes high in the flow system, in contrast, receive a higher proportion of water by precipitation, which falls directly into the lakes or which drains rapidly from adjacent steep, rocky slopes.

Not only can landforms influence mean values of certain lake parameters, but also their seasonal or annual variability. In the lakes of the Colorado alpine, where spring snowmelt causes large seasonal pulses in water flow, seasonal variation in specific conductance decreases as a function of drainage area. This change reflects the buffering effects of larger lakes lower in the landscape. Smaller lakes at higher elevations appear to be affected more by snowmelt and exhibit a larger seasonal amplitude in specific conductance.

In contrast, specific conductance in the Wisconsin lakes exhibits small variation, on the order of analytical uncertainty, because of a much less pronounced effect of snowmelt and the relatively conservative behavior of most of the important cations and anions. Although seasonal variation in specific conductance is low in the Wisconsin lakes, annual variation in supply of limiting nutrients can be significant and can vary with a lake's position in the landscape.

Concentrations of silica, for example, are several orders of magnitude greater in groundwater than in precipitation; biological productivity of lakes high in the flow system can become seasonally limited by silica, whereas lakes low in the flow system are likely to be limited by light or atmospherically supplied nutrients. In Crystal Lake, a lake high in the Wisconsin landscape, groundwater accounts for less than 8% of the water budget, yet it accounts for 50% of the annual silica budget, the rest coming from regeneration from bottom sediments (Hurley et al. 1985). Small variations in the amount of groundwater entering the lake—caused, for example, by differences in snowfall or timing of snowmelt—can lead to major differences in the spring algal blooms in the lake. In contrast, lakes lower in the flow system are not limited by silica, so small fluctuations in the groundwater supply will not affect algal dynamics in those lakes.

Landforms may also delimit the ranges of some vertebrates (Forman and Godron 1986). Gullies, streams, and cliffs may form physical barriers to movement, or they may act as convenient, but passable, features to mark the boundaries between home ranges of neighboring animals. Cliff faces and associated talus slopes form habitats at several scales for a community of small mammals and birds in semiarid landscapes (Maser et al. 1979).

The distribution of size and abundance of cavities in outcrops of bedrock and in accumulations of boulders control the distribution of rodents. Raptors use the air space above, riding convective wind currents induced by the heating of cliff and talus surfaces. These birds prey on rodent populations occupying fine-scale landform features below.

The grazing behavior of large animals may exhibit profound effects of landforms (Schimel et al. 1986, Senft et al. 1985). In semiarid grasslands, cattle preferentially graze lowland swales, presumably because the influence of landforms on spatial patterns of soil moisture and nutrients results in better forage. This response of animals to landforms may lead to redistribution of nutrients on the landscape (Schwartz and Ellis 1981, Senft et al. 1985).

Landforms and nongeomorphically induced disturbances. The roles of landforms in controlling patterns of ecosystem disturbance across landscapes are not clearly understood except in a few obvious cases, such as inundation by floodwaters in channels and on floodplains. Effects of landforms on frequency and intensity of disturbance by fire, snow, and wind, for example, are recognized in anecdotes, but generally only qualitatively (e.g., Swanson 1981).

Landforms can protect certain areas from disturbance by providing firebreaks and shelter from physical damage by disturbances such as wind. In studies of the forests of Mount Rainier National Park, Hemstrom (1982) notes the importance of major ridges and valley bottoms in constraining the spread of wildfire. Consequently, boundaries between stands of differing structure and age are more likely to occur at these topographic positions than at others.

Landforms may also increase frequency of disturbance by channeling fire, wind, and other nongeomorphic agents of disturbance into an area. Topography, even subtle ridges and depressions, controls patterns of snow accumulation in alpine settings and the plains of Colorado and determines the locations of snow sources and sinks during periods of snow redistribution by wind. Persistent snow accumulation may suppress vegetation, creating a site of bare soil that is a source of sediment associated with a source of water—the snowbank. Landforms thereby trigger a chain of events beginning with redistribution of water in the form of snow (a class 2 effect) that leads to localized disturbances of vegetation by shortening the growing season and the period of possible establishment (a class 3 effect). Disturbance of the immediate site and adjacent areas by surface erosion and sediment transport (a class 4 effect) may follow.

Interactions among landform, geomorphic process, and ecosystem. The distinction between landform effects of classes 3 and 4 is the emphasis on physical dynamics of the landscape in class 4. For both classes, landforms constrain the movement of agents that disturb the ecosystem—fire, surface and subsurface water, wind, and animals. In class 3, agents of disturbance operate through vegetation, which may lead to secondary disturbance by acceleration of geomorphic processes, such as increased surface erosion after wildfire. In class 4, geomorphic processes are the primary disturbances.

Two dramatic examples of geomorphic disturbances are landslides and lateral shifts of river channels. Portions of the landscape subject to these disturbances are characterized by distinctive processes and frequencies of change, and in each case landforms constrain the frequency and magnitude of change.

River channels. The geomorphic dynamics of valley floors differ substantially between mountain and lowland areas because of contrasts in the degree of landform control. Using age analysis of floodplain forests, Everitt (1968) determined that, during the preceding 100-year period, persistent lateral migration of a reach of the meandering Little Missouri River (slope = 0.00085) in North Dakota eroded and reconstructed floodplain surfaces in an area of valley floor averaging 5.9 channel widths (0.54 km^2 per km of valley length). Over the same period, the steep (slope = 0.042), straight channel of French Pete Creek in the Oregon Cascade Range reset an area of only 1.0 channel width (0.015 km^2 per km of valley length) (Grant 1986). North Boulder Creek in the Colorado Front Range has a similar gradient (0.030) and quasimeandering form, but it accomplished even less reworking of its valley floor (less than 0.0005 km^2 per km of valley length) over a thousand years or more (Furbish 1985). The steep channel, coarse bed and bank sediment, and bedrock outcrops limit lateral channel change in both the Oregon and Colorado mountain streams.

These mountain and lowland fluvial environments also have contrasting regimes of chronic disturbance by overbank sedimentation. Vertical growth of floodplains beside the Little Missouri River continues by overbank deposition for more than a century after establishment of initial vegetation on a freshly deposited floodplain surface (Everitt 1968). In the boulder-dominated channels of French Pete and North Boulder Creeks, lateral and vertical channel changes appear to have occurred much more catastrophically when infrequent, major floods move the coarse bed material. Chronic, overbank deposition appears to be limited in part by a paucity of fine sediment, particularly in North Boulder Creek where upstream lakes trap sediment. Consequently, the composition of floodplain vegetation along mountain streams may be less restricted to species that are best adapted to frequent, minor deposition of fine-grained sediment.

These physical dynamics of fluvial environments can make a substantial imprint on ecosystem patterns by controlling the distribution of substrates on which plant and animal communities develop. Pastor et al. (1982) provide examples of how geomorphic features, operating through soil moisture and chemistry, influence patterns of vegetation composition and productivity.

Landslides. In many steep landscapes, small landslides are believed to occur repeatedly from depressions on bedrock, variously termed bedrock hollows, swales, zero-order basins, and headwalls (Dietrich and Dorn 1984, Dietrich and Dunne 1978). These hollows slowly collect soil from the surrounding hillslopes by surface erosion, root throw, soil creep, and other processes over periods of centuries and millenia. Eventually a landslide removes all or a portion of the stored soil from the hollow. Such a landslide commonly occurs during periods of heavy rainfall or rapid snowmelt. The potential for a landslide may increase as soil depth in hollows exceeds the rooting depth of woody plants growing in and around hollows, thereby limiting the effectiveness of soil mass anchoring by roots passing vertically and horizontally into stable substrates. Potential for occurrence of a landslide also increases when the contribution of roots to soil strength is minimized by decomposition after mortality caused by wildfire, logging, or other disturbance of vegetation.

Landform units prone to landslides may experience dramatic change on ecologically relevant time scales. From one geologic terrane to another, the frequency of a landslide reoccurring at a particular site can range from a few decades (Shimokawa 1984) to 10,000 years or more (Dietrich and Dorn 1984, Kelsey 1982). At sites with a high frequency of landslides, landslides can truncate the succession of vegetation. Where landslides occur less frequently, soil development and climate change may alter both the potential for landslides and the character of vegetation developed on the site between landslides. Gradual filling of landslide scars with soil from adjacent slopes (Shimokawa 1984) may be viewed as a form of chronic disturbance of vegetation at the same time that it is contributing to soil and landform recovery, much like siltation on sites of overbank deposition on floodplains.

Catastrophic events are more important in the geomorphic disturbance regimes of some landform units than in others. Bedrock hollows subject to periodic landslides, for example, operate on a pulse-reset basis. Other landform units, such as floodplains of meandering rivers, experience progressive resetting by frequent, small, discrete increments of change. In yet other landform units, the soil, geomorphic processes, and landform are believed to have coevolved gradually through time, resulting in conditions of a steady-state dynamic equilibrium along a topographic sequence, as inferred for some soil catenas.

Complex landscapes

Patterns of biota across natural landscapes typically reflect interactions among most or all of the four classes of landform effects on biota, soil, and geomorphic disturbances. These interactions are commonly so complex and entwined in the history of a site (embodied in its soils and other system components with long memory) that individual landform effects may be impossible to identify.

The usefulness and appropriateness of examining each of the classes of landform effects we have discussed depends on the objectives of a study and the characteristics of the ecosystems and landscapes involved. In the most dynamic systems, geomorphic and ecological changes occur on similar time scales. The potential importance of class 4 interactions, for example, depends in part on the rate of geomorphic change relative to the rate of development of soil and biological features of interest.

In the Cascade Range of the Pacific Northwest, trees are long lived and changes in landform by fluvial processes and various types of mass movements are frequent, so the spatial distribution of age classes of vegetation on geomorphically active portions of the landscape reflect some of the history of geomorphic disturbances. Other systems, such as much of the alpine environment of the southern Rocky Mountains and the lake district of northern Wisconsin, may be so stable geomorphically that it is reasonable to consider the landscape as a static physical template for ecosystem development, even on the time scale of many millenia. In many of these areas, however, there is abundant evidence that the landscape was much more dynamic in the past. In the southern Rockies this was especially true during and immediately after glacial stages, the "paraglacial" conditions of Church and Ryder (1972).

The complex interactions among landforms and spatial patterns of ecosystem characteristics are exemplified by vegetation in the steep, high-relief landscape of Mount Rainier National Park (see cover). Long, smooth slopes with more than a 1000-meter range in elevation result in distinctive zones of vegetation habitat types by altitude, clearly visible from the opposite valley wall (Hemstrom 1982, Hemstrom and Franklin 1982). This pattern develops in response to temperature and moisture gradients (a class 1 effect). Superimposed on this pattern is one of higher productivity in valley bottoms, where moisture and nutrients are least limiting as a result of downslope movement (a class 2 effect). Hemstrom (1982) documents two class 3 effects. Landform features, especially major ridges and valley bottoms, serve as barriers to the passage of fire, a major disturbance in the forest around Mount Rainier. Snow avalanches repeatedly move down bedrock-defined paths, cutting distinctive swaths through forest vegetation. The floors of several valleys draining Mount Rainier also experienced severe disturbance by mudflows triggered high on the volcano (a class 4 effect) (Figure 3).

An even more complex set of landform effects on ecosystems are found in studies of soil catenas in the shortgrass steppe of Colorado. The Colorado State University LTER program has analyzed catenas, the connected series of soil and plant associations extending down a topographic sequence of sites from ridge to valley bottom (Jenny 1980). Schimel et al. (1985) observed that, going down the catena, organic carbon, nitrogen, and phosphorous and soil depth increase. These and similar patterns in other soil constituents both result in and are the result of higher productivity in lower slope positions.

In the subtle topography of the shortgrass steppe near Fort Collins, Colorado, the effects of aspect and relative elevation on the input of moisture and solar energy to sites (class 1 effects) are not pronounced, but landform effects on movement of fluvial and aeolian material have a variety of influences on landscape patterns. Higher biomass production in lower slope positions occurs in response to more fertile soils and higher moisture availability as a result of subsurface water flow from upslope (a class 2 effect). Furthermore, surface and subsurface flow transport fine soil particles and organic matter to lower slope positions (a class 2 effect). Aeolian deposits also occur in lower slope positions (Schimel et al. 1985). Topographic effects on alluvial and aeolian deposits, combined with faster pedogenesis in the more moist toeslopes, result in higher concentrations of silt and clay in toeslope locations and, therefore, greater moisture-holding capability.

This description of a catena is consistent with conventional wisdom, as described by Jenny (1980), and it is valid for sites in the Colorado shortgrass steppe, where toposequences are strongly developed. Field studies, however, reveal that conventional catena concepts are not sufficient to explain soil and vegetation patterns in much of this area. The pervasive effects of wind redistribution of soil and snow impose other landform-controlled patterns on ecosystem properties that are not explained by toposequence landform elements.

The importance of interactions between wind and landform is indicated by soil stratigraphic studies, which include observation of buried soils (Doehring et al. 1984, Schimel et al. 1985). Erosion and deposition events forming buried soil must have constituted geomorphic disturbances of vegetation (a class 4 effect). Furthermore, snow drifting to the lee side of hills creates localized sites with augmented water supply, which can lead to substantial differences in vegetative production (Woodmansee and Adamsen 1983). These, and perhaps other, processes have resulted in a surprisingly uniform A-horizon (the upper soil layer) given the highly variable properties of the B-horizon (the underlying soil layer). Because the water-holding capacity of the A-horizon (1.5–2.0 cm) exceeds most single rainfalls and snowmelts, the water resource is relatively uniformly distributed over the landscape. Consequently, the composition of the vegetation also tends to be rather constant spatially.

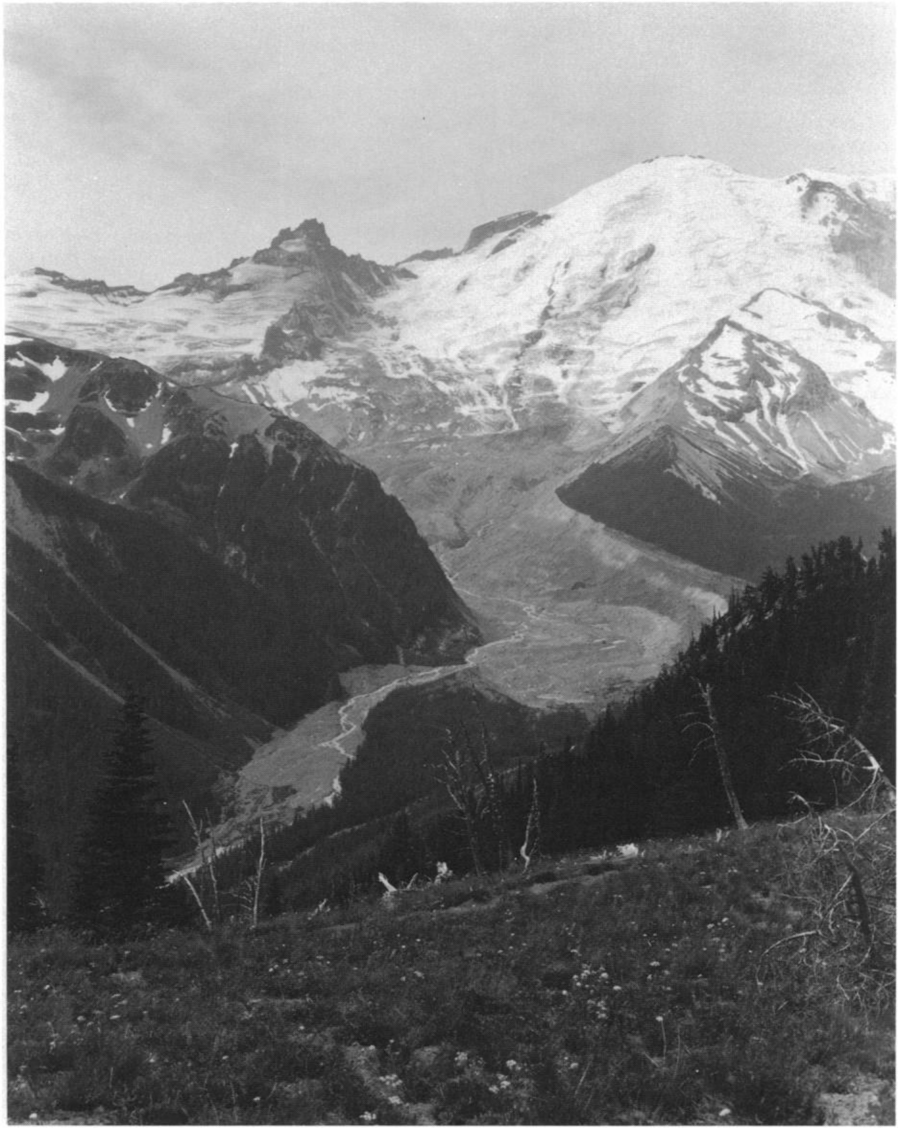

Figure 3. The valley of White River draining the flanks of Mt. Rainier contains numerous examples of landform influences on vegetation and disturbance patterns.

Conclusions

The effects of landforms on ecosystem development and change have several important implications for the developing field of landscape ecology (Forman and Godron 1986, Naveh 1982, Risser et al. 1984). Landscape ecology as defined by Risser considers "the development and dynamics of spatial heterogeneity, spatial and temporal interactions and exchanges across heterogeneous landscapes, influences of spatial heterogeneity on biotic and abiotic processes, and management of spatial heterogeneity." In this article we have identified various ways in which patterns of ecosystem structure, composition, and function are controlled by landforms and geomorphic processes. Knowledge of these geomorphic underpinnings of ecosystems is essential to interpreting ecosystems in the context of their landscapes.

The influence of landforms on patterns of soil, vegetation, animals, and aquatic ecosystems across a landscape contribute to developing and maintaining a patchwork ecosystem. This influence occurs through the effects of landforms on environmental gradients (class 1 and 2 effects) and regulation by landform of the patterns and frequency of the disturbance (class 3 and 4 effects). To date, the full spectrum of landform effects has received little attention in the literature of landscape ecology.

Several points emerge:

- In general, patterns of landscape and landforms are easier to observe than ecosystem processes, so an understanding of how landforms affect processes yields some power in predicting ecosystem behavior. The effects of landscape position and soil factors on lake processes, for example, imply that lakes high in the landscape will be more sensitive to acid deposition than lower lakes (Eilers et al. 1983). Therefore, position within a drainage basin is an important factor in designing sampling programs for many aspects of lake water chemistry and biology.
- Patterns of soils and vegetation studied in the shortgrass steppe of Colorado indicate that landform-ecosystem interactions may take multiple forms and that patterns imposed by one set of interactions may be overridden by another set. Careful field studies to explore multiple working hypotheses are essential to elucidating the full range of important interactions.
- The interactions of landform effects on ecosystem development during periods without major disturbance and on movement of disturbances

across a landscape may influence strongly the persistence and geometry of the landscape mosaic defined by patches of vegetation, soils, or other ecosystem components. To our knowledge, these important interactions have not been examined quantitatively.

These concepts of landform effects on ecosystems provide broad temporal and spatial perspectives for designing sampling of soil, vegetation, and aquatic ecosystems and for interpreting community and ecosystem processes in dynamic landscape.

Acknowledgments

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