

Landscape heterogeneity determines the regional consequences of processes occurring in individual ecosystems. In this chapter, we describe the major causes and consequences of landscape heterogeneity.

aid in understanding and quantifying landscape interactions. We then discuss sources of spatial heterogeneity within and among ecosystems and the consequences of that heterogeneity for interactions among ecosystems on a landscape.

Introduction

Spatial heterogeneity within and among ecosystems affects the functioning of individual ecosystems and entire regions. In previous chapters, we emphasized the controls over ecosystem processes in relatively homogenous units or **patches** of an ecosystem. The spatial pattern of ecosystems in a region, however, also influences ecosystem processes. Riparian ecosystems between upland agricultural systems and streams, for example, may filter nitrate and other pollutants that would otherwise enter streams. At a finer scale, nutrient cycling and organic matter accumulation in arid ecosystems occurs more rapidly beneath than between shrubs. The fragmentation of ecosystems into smaller units separated by other patch types influences the abundance and diversity of animals. All of the processes and mechanisms that operate in ecosystems (see Chaps. 4–11) have important spatial dimensions. In this chapter, we first discuss the concepts and characteristics of landscapes that

A Focal Issue

Human land-use change has fragmented landscapes throughout the world, often shifting the balance so that managed patches become the widespread matrix in which small fragments of less managed lands persist (Fig. 13.1). The increase in ratio of edge to area of these fragments alters physical environment throughout the patch, and the loss of connectivity among patches reduces their capacity to support many species. As global demand for food increases, how do we manage landscapes to meet these needs and to sustain the functioning of natural patches in the landscape? What are sustainable proportions of lands of differing management intensity? What happens if that proportion is exceeded? What configuration of natural and managed patches best meets the needs of nature and society? Careful attention to landscape configuration and dynamics can reduce the regional impacts of human actions in an increasingly human-dominated planet.



Fig. 13.1 Shifting agriculture in the uplands of Yunan Province of China. The pressure of rising population has reduced the time that lands remain forested and increased the proportion of agricultural

lands on the landscape. Photograph by Desmanthus4food (http://upload.wikimedia.org/wikipedia/commons/ba/Swidden_agriculture_in_Yunnan_Province_uplands.JPG)

Concepts of Landscape Heterogeneity

Spatial patterns control ecological processes at all scales. Landscapes are mosaics of patches that differ in ecologically important properties. **Landscape ecology** addresses the causes and consequences of spatial heterogeneity (Urban et al. 1987, Forman 1995, Turner et al. 2001, Cadenasso et al. 2007). This field focuses on both the interactions among patches on the landscape and the behavior and functioning of the landscape as a whole. Landscape processes can be studied at any scale, ranging from the mosaic of gopher mounds in a square meter of grassland to biomes that are patchily distributed across the globe (Fig. 13.2). Landscape processes are often studied at scales of watersheds or regions.

Some landscape patches are **biogeochemical hot spots** with high process rates, causing them to be more important than their areal extent would

suggest. Beaver ponds, for example, are biogeochemical hot spots for methane emissions in boreal landscapes (Roulet et al. 1997); recently cleared pastures in the central Amazon Basin are hot spots for nitrous oxide emissions (Matson et al. 1987); and cities are hotspots for carbon emissions. Hot spots are defined with respect to a particular process and occur at all spatial scales, from the rhizosphere surrounding a root to urine patches in a grazed pasture, to wetlands in a watershed, to tropical forests on the globe. The environmental controls over biogeochemical hotspots often differ radically from controls in the surrounding **matrix**, that is, the predominant patch type in the landscape. Only by studying processes in hot spots can we understand these processes and extrapolate their consequences to larger scales. Landscape ecology therefore plays an essential role in understanding the Earth System because of the importance of estimating fluxes (and their controls) of energy and materials at regional and global scales.

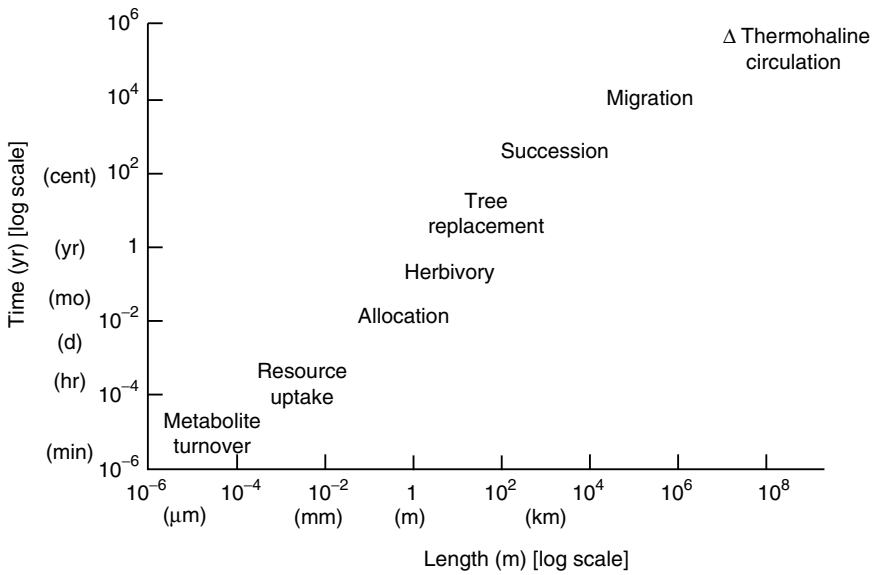


Fig. 13.2 Temporal and spatial scales at which selected ecosystem processes occur. The study of any ecosystem process requires understanding at least one level below

(to provide mechanistic understanding) and one level above (to provide context with respect to patterns of temporal and spatial variability)

The size, shape, and spatial distribution of patches in the landscape govern interactions among patches. Patch size influences habitat heterogeneity. Large forest fragments in an agricultural landscape, for example, contain greater habitat heterogeneity and support more species and bird pairs than do small patches (Freemark and Merriam 1986, Wiens 1996). Patch size also influences the spread of propagules and disturbance from one patch to another (see Chap. 12). **Patch shape** influences the effective size of patches by determining the average distance from each point in the patch to an edge. Patch size and shape together determine the ratio of edge to area of the patch. The edge-to-area ratio of lakes, for example, is critical in determining the relative importance of pelagic and lake-margin production in supplying energy to aquatic food webs.

The **configuration**, that is, the spatial arrangement of patches in a landscape, influences landscape properties because it determines which patches interact and the spatial extent of their interactions. Riparian areas are important because they are an interface between terrestrial and aquatic ecosystems. Their linear configuration and location make them much more important than their small areal extent would suggest.

Configuration, together with patch size and shape, influence the **connectivity** among patches. The population dynamics of many organisms depend on movement between patches, which is strongly influenced by their connectivity (Turner et al. 2001). Birds and small animals in an agricultural landscape, for example, use fencerows to travel among patches of suitable habitat. In a patchy environment, local populations may go extinct, and the dynamics of **metapopulations**, that is, populations that consist of partially isolated subpopulations, depend on relative rates of local extinctions in patches and colonization from adjacent patches (Hanski 1999). Species conservation plans often encourage the use of corridors to facilitate movement among suitable habitat patches (Fahrig and Merriam 1985, Chetkiewicz et al. 2006, Saura and Pascual-Hortal 2007), although the effectiveness of corridors is debated (Rosenberg et al. 1997, Turner et al. 2001). Connectivity may be particularly critical at times of climatic change. Isolated nature reserves, for example, may contain species that cannot adapt or migrate in response to rapid environmental change. The effectiveness of corridors among patches depends on the size and mobility of organisms and the nature of disturbances that

move among patches (Wu and Loucks 1995). A fencerow, for example, may be a corridor for voles, a barrier for cattle, but invisible to birds. A high connectivity among patches is not always beneficial. The high connectivity of extensive cornfields of the Midwestern U.S., for example, might allow pests to decimate large regions in response to climate change.

Ecological **boundaries** are critical to the interactions among neighboring landscape elements (Gosz 1991). Animals like deer, for example, are edge specialists that forage in one patch type and seek protection from predation in another. The size of the patch and its edge-to-area ratio determine the total habitat available to edge specialists. Edges often experience a different physical environment than do the interiors of patches. Forest boundaries adjacent to clearcuts, for example, experience more wind and solar radiation and are drier than are patch interiors (Chen et al. 1995). In tropical rainforests, the trees within 400 m of an edge experience more frequent blowdowns than do trees farther from an edge (Laurance and Bierregaard 1997). These differences in physical environment affect rates of disturbance and nutrient cycling, which translate into variations in recruitment, productivity, and competitive balance among species. The depths to which these edge effects penetrate differ among processes and ecosystems. Wind effects, for example, may penetrate more deeply from an edge than would availability of mycorrhizal propagules.

The abruptness of boundaries (that is, edge contrast) influences their role in the landscape (McCoy et al. 1986). Relatively broad gradients often occur at the boundaries between biomes, where there is a gradual shift in some controlling variable such as precipitation or temperature. Sharper boundaries tend to occur where steep gradients in physical variables control the distribution of organisms and ecosystem processes (e.g., between a stream and its riparian zone) or where an ecologically important functional type (e.g., trees) reaches its climatic limit. Physically determined boundaries can be stable under climate change whereas climatically determined boundaries can fluctuate or move directionally

(Peters et al. 2009). Climatically determined boundaries, such as tree line or the savanna-forest border, for example, are useful places to study the effects of climatic change because species may be sensitive to small changes in climate.

Causes of Spatial Heterogeneity

Landscape heterogeneity stems from environmental variation, population and community processes, and disturbance (Turner 2005). Spatial variation in state factors (e.g., topography and parent material) and interactive controls (e.g., disturbance and dominant plant species) determine the natural matrix of spatial variability in ecosystems (Holling 1992). Human activities are an increasing cause of changes in the spatial heterogeneity of ecosystems.

Detection and Analysis of Spatial Heterogeneity

Remote sensing provides a set of tools to determine the structure and some aspects of the functioning of heterogeneous landscapes. Much of the spatial heterogeneity of interest occurs at spatial scales that cannot be observed from a single point on the ground. Remote sensing provides a suite of techniques – from low-technology aerial observation and photography to repeated satellite imagery – that allow us to visualize ecosystems across a large area all at once, to see them synoptically. Recent developments in remote sensing have transformed our ability to analyze ecosystem heterogeneity, and ongoing developments will continue to do so. For example, the integration of aircraft-based LIDAR (light detection and ranging, which is used to measure topography, canopy height, and vegetation structure) with high-spectral, high-spatial resolution spectrometry (which can measure aspects of canopy chemistry and physiological stress) allows highly resolved measurements of spatial variation in plant structure and chemistry, more or less simultaneously across thousands of hectares (Asner et al. 2007). When applied to

natural terrestrial ecosystems, this approach can be used to detect, map, and analyze directly spatial heterogeneity in ecosystem structure and aspects of ecosystem functioning (Vitousek et al. 2009a). This approach can also be applied to understanding the distribution, dynamics, and consequences associated with biogeochemical hot spots, such as those associated with termite mounds in African savannas (Levick et al. 2010) and nitrogen-fixing biological invaders in Hawaiian rainforests (Hall and Asner 2007).

State Factors and Interactive Controls

Differences in abiotic characteristics and associated biotic processes account for the basic matrix of landscape variability. Temperature, precipitation, parent materials, and topography vary independently across Earth's surface. Some of these state factors, such as rock type, exhibit sharp boundaries and can therefore be classified into distinct patches. Others, including climate variables, vary more continuously and generate gradients in ecosystem structure and functioning, although amplifying feedbacks among processes controlled by these underlying gradients often create sharp boundaries in ecosystem structure and functioning. Analysis of these landscape classes and gradients shows that different factors control spatial pattern at different spatial scales. Regional-scale patterns of vegetation, net primary production (NPP), soil organic matter, litter quality, and nutrient availability in grasslands, for example, correlate with regional gradients in precipitation and temperature (Fig. 13.3; Burke et al. 1989). In contrast, topography, soil texture, and land-use history explain most variability at the scale of a few kilometers (Burke et al. 1999). Broad elevational and aspect-related patterns of ecosystem processes in tropical forests on the Hawaiian Islands are also governed largely by climate with local variation reflecting the type and age of parent material (Vitousek et al. 1992, Raich et al. 1997, Vitousek 2004). The resulting differences in soils give rise to consistent differences in nitrogen cycling (Pastor et al. 1984), phosphorus cycling (Lajtha and Klein 1988), and

nitrous oxide emissions (Matson and Vitousek 1987). These comparative studies provide a basis for extrapolating ecosystem processes to regional scales based on the underlying spatial matrix of abiotic factors.

Community Processes and Legacies

Historical legacies, stochastic dispersal events, and other community processes can modify the underlying relationship between environment and the distribution of a species.

Ecosystem processes depend not only on the current environment but also on past events that influence the species present at a site (see Chap. 12). In Yellowstone National Park, for example, landscape variation in fire severity and cone **serotiny** (extent to which seeds are retained in cones) caused post-fire seedling recruitment of lodgepole pine to range from 0 to >500,000 stems ha⁻¹, which, in turn, strongly influenced post-fire productivity and nutrient cycling (see Fig. 12.14; Turner et al. 1999, Turner 2010). In arid and semi-arid ecosystems, soil processes are strongly influenced by the presence or absence of individual plants, resulting in "resource islands" beneath plant canopies (Schlesinger et al. 1990, Burke and Lauenroth 1995). The distribution of species on a landscape results from a combination of habitat requirements of a species, historical legacies (see Chap. 12), and stochastic events. Once these patterns are established, they can persist for a long time, if the species effects are strong. Fine-scale distribution of hemlock and sugar maple that developed in Michigan several thousand years ago, for example, has been maintained because each tree species produces soil conditions that favor its own persistence (Davis et al. 1998).

Disturbance

Natural disturbances are ubiquitous in ecosystems and create spatial patterning at many scales. The **patch dynamics** of a landscape reflect cycles of disturbance and post-disturbance

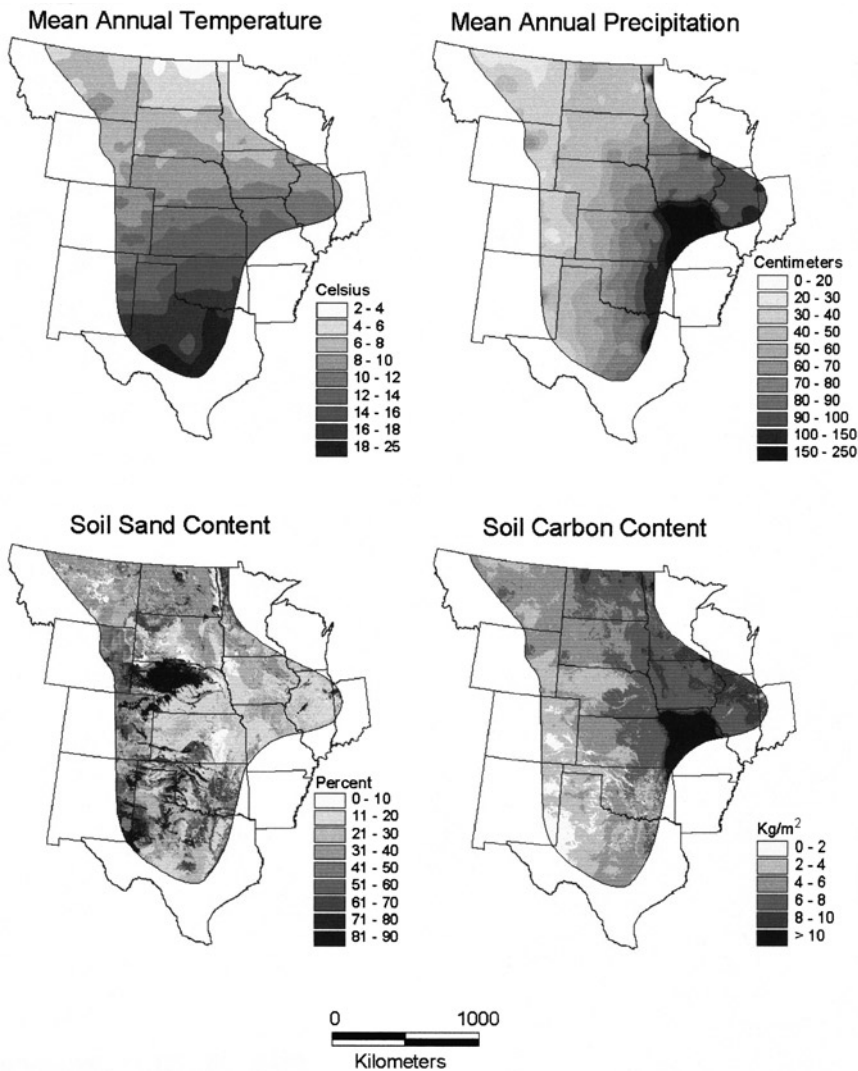


Fig. 13.3 Regional patterns of air temperature, precipitation, soil sand (a measure of the coarseness of soil texture), and soil carbon content across the Great Plains of the U.S. (Burke et al. 1989). Soil carbon content was modeled

based on regional databases of the environmental variables using the CENTURY model. Soil carbon content varies regionally in ways that are predictable from climate and soil texture. Figure kindly provided by Indy Burke

succession (see Chap. 12; Pickett and White 1985, Turner 2010). Under relatively stable conditions, this generates a **shifting steady-state mosaic**, in which the vegetation at any point in the landscape is always changing but, averaged over a large enough area, the proportion of the landscape in each successional stage remains relatively constant (Bormann and Likens 1979). Although every point in the landscape may be at a different successional stage, the landscape as a

whole may be close to steady state (Turner et al. 1993). Shifting steady-state mosaics develop (1) in environmentally uniform areas, where disturbance is the main source of landscape variability, (2) when disturbances are small relative to the size of the landscape, and (3) when the rate of recovery is similar to the return time of the disturbance (Fig. 13.4). When disturbances are small and recovery is rapid, most of the landscape will be in mid- to late-successional stages. In the

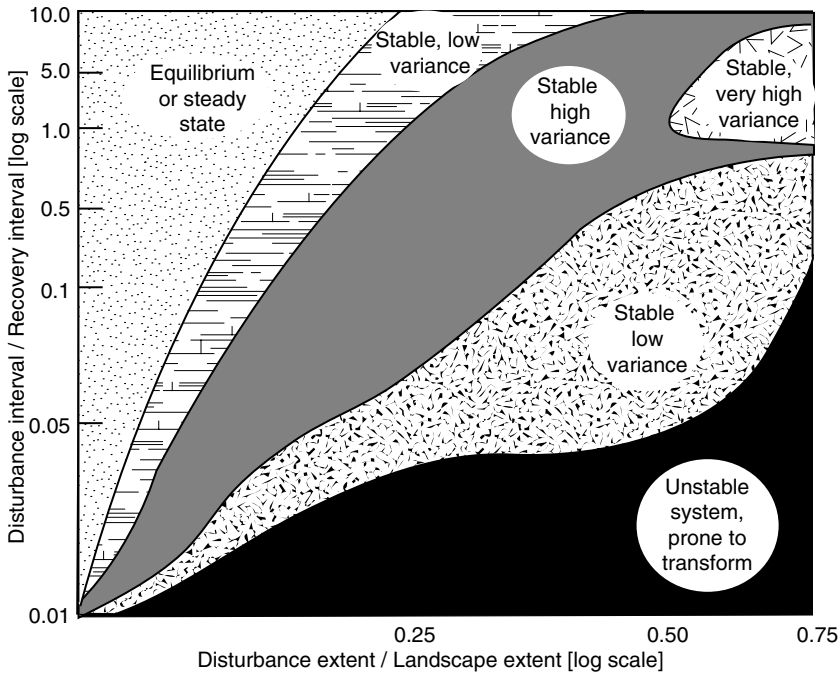


Fig. 13.4 Effect of disturbance size (relative to the size of the landscape) and disturbance frequency (relative to the time required for the ecosystem to recover) on the stability of landscape processes. Landscapes are close to steady state when disturbances are small (relative to the size of the study area) and when they are infrequent

(relative to the time required for ecosystem recovery). As disturbances become more frequent or larger, the landscape becomes more heterogeneous, and individual patches are increasingly likely to shift to different successional trajectories. Redrawn from Turner et al. (1993)

primary tropical rainforests of Costa Rica, for example, the regular occurrence of treefalls results in maximum tree age of only 80–140 years (Hartshorn 1980). Gap-phase disturbance contributes to the maintenance of the productivity and nutrient dynamics of the forest. Light, and sometimes nutrient availability, increases in tree-fall gaps, providing resources that allow species with higher resource requirements to grow quickly and maintain themselves in the forest mosaic (Chazdon and Fetcher 1984, Brokaw 1985). Disturbances by animals in grasslands and shrublands can also generate a shifting steady-state mosaic. Gophers, for example, disturb patches of California serpentine grasslands, causing patches to turn over every 3–5 years (Hobbs and Mooney 1991).

Large-scale infrequent disturbances alter the structure and processes of some ecosystems over large areas. These disturbances create

non-steady-state mosaics in which large expanses of the landscape are in the same successional stage. After Puerto Rico’s Hurricane Hugo in 1989, for example, most of the trees in the hurricane path were broken off or blown over or lost a large proportion of their leaves, resulting in a massive transfer of carbon and nutrients from vegetation to the soils. The large pulse of high-quality litter increased decomposition rates substantially over large areas (Scatena et al. 1996).

Fire can also create large patches of a single successional stage on the landscape (Johnson 1992). In 1988, wildfires burned about a third of Yellowstone National Park. Fires of this magnitude and intensity recur every few centuries (Schoennagel et al. 2004). Long-term human fire suppression has increased the proportion of late-successional communities in many forests characterized by ground fires (e.g., ponderosa pine or sequoia in the western U.S.). This results in a

more homogeneous and spatially continuous, fuel-rich environment in which fires can burn large areas. Forests that are characterized by stand-replacing crown fires (e.g., lodgepole pine in Yellowstone) quickly regenerate enough fuel to burn again. Fire suppression therefore has little effect on the fire regime of these forests.

Even large disturbed areas are often internally quite patchy, creating a **functional mosaic**, that is, a landscape with functionally important differences among patches. Fires, for example, usually produce islands of unburned vegetation and patches of varying burn severity that often differ dramatically in the density of regenerating trees, productivity, and rates of nitrogen cycling (Turner 2010). Unburned islands act as seed sources for post-fire succession and protective cover for wildlife, greatly reducing the effective size of the disturbance (Turner et al. 1997). In many cases, patches become less distinct as succession proceeds, so spatial heterogeneity may decline with time in non-steady-state mosaics (see Fig. 12.14b; Turner 2010).

Human-induced disturbances alter the natural patterns and magnitude of landscape heterogeneity. The signature of human influence is readily detectable in landscape patterns (Cardille and Lambois 2010). Isolated land-use changes may augment landscape heterogeneity by creating small patches within a matrix of largely natural vegetation. However, human activities have transformed as much as 75% of the ice-free terrestrial surface (see Fig. 1.8; Turner et al. 1990, Ellis and Ramankutty 2008). We have cleared or selectively harvested forests; converted grasslands and savannas to pastures or agricultural systems; drained wetlands; flooded uplands; and irrigated drylands. As land-use change becomes more extensive, the human-dominated patches become the matrix in which isolated fragments of natural ecosystems are embedded, reducing landscape heterogeneity and causing a qualitative change in landscape structure and functioning. These contrasting impacts of human actions on landscape heterogeneity are illustrated by the practice of shifting agriculture.

Shifting agriculture is a source of landscape heterogeneity at low population densities but

reduces landscape heterogeneity as human population increases. Shifting agriculture, also known as slash-and-burn agriculture or swidden agriculture, involves the clearing of forest for crops followed by a fallow period during which forests regenerate, after which the cycle repeats (Fig. 13.1). Shifting agriculture is practiced extensively in the tropics and in the past played an important role in clearing the forests of Europe and eastern North America. Small areas of forest are typically cleared of most trees and burned to release organically bound nutrients. Crops are planted in species mixtures, with multiple plantings and harvests (Vandermeer 1990). As soil fertility drops, and insect and plant pests encroach, often within 3–5 years, the agricultural plots are abandoned, and the forest regenerates. The regenerating forests provide fuel and may be managed to provide fruits and other useful products for 20–40 years until the cycle repeats. Shifting agriculture generates landscape heterogeneity at many scales, ranging from different aged patches within a forest to different crop species within a field. With moderate human population densities that allowed long enough fallow periods and judicious selection of land for cultivation, shifting agriculture persisted for thousands of years without any progressive change in biogeochemical cycles (Ramakrishnan 1992, Palm et al. 2005).

As population density increases, land becomes scarcer, and the fallow periods are shortened or eliminated, leading to a more homogeneous agricultural landscape. Under these conditions, nutrient and organic matter losses during the agricultural phase cannot be recouped, and the system degrades, requiring larger areas to provide enough food. As the landscape becomes dominated by active cropland or early successional weedy species, the seed sources of mid-successional species are eliminated, preventing forest regrowth and further reducing the potential for landscape heterogeneity. In northeast India, for example, this shifting agriculture appears unsustainable when the rotation cycle declines below 10 years (Table 13.1; Ramakrishnan 1992, Palm et al. 2005).

Table 13.1 Comparison of ecosystem processes among several agricultural systems in Northeast India^a

Ecosystem	Nitrogen input (g N m ⁻² year ⁻¹) ^b	NPP (g m ⁻² year ⁻¹) ^c	Litterfall (g m ⁻² year ⁻¹) ^c	Soil erosion (g m ⁻² year ⁻¹) ^d
Natural forest	15.5	2,360	118	800
Shifting agriculture				
5-year cycle	5.7	550	48	6,900
10-year cycle	9.2	670	71	3,000
30-year cycle	10.9	1,480	98	1,500
Mixed crop	–	100	–	100
Intensive agriculture				
Coffee	12.4	50	–	1,200
Tea	28.4	100	–	2,600
Ginger	21.3	190	–	20,000

^aNote that the natural forest, which was an undisturbed sacred grove, had a higher productivity and litterfall than any of the managed ecosystems, even though the annual nitrogen inputs in litterfall were less than many of the intensively managed crops. When the rotation cycle of shifting agriculture became shorter than 10 years, there was a substantial drop in nitrogen cycling and litterfall and an increase in erosion. The continuous cropping systems (mixed and intensive) were less productive than the shifting agriculture, even for the crop phase. Data from Ramakrishnan (1992)

^bNitrogen inputs are from natural litterfall in the natural forest and the fallow phase of shifting agriculture but from fertilizer in the intensive agriculture

^cValues are grams dry matter for the fallow phase for shifting agriculture

^dValues are for the total rotational cycle

Interactions Among Sources of Heterogeneity

Landscape heterogeneity and disturbance history interact to influence further disturbance.

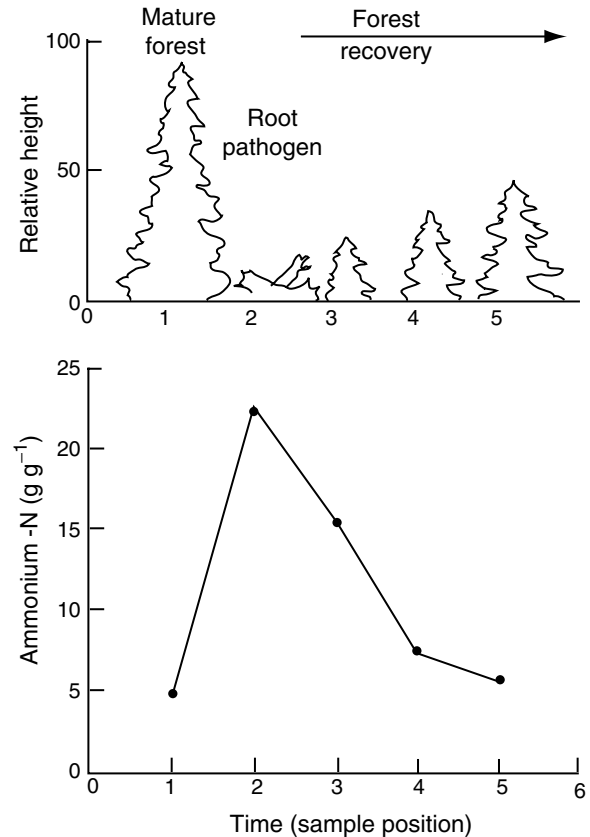
Disturbance is more than a simple overlay on the spatial patterns governed by environment because even slight variations in topography or edaphic factors can influence the frequency, type, or severity of natural disturbances and the probability that land will be cleared by people. Slope and aspect of a hillside affect solar irradiance, soil moisture, soil temperature, and evapotranspiration rate. These factors, in turn, contribute to variation in biomass accumulation, species composition, and fuel characteristics. Different parts of the landscape therefore differ in susceptibility to fire. The resulting mosaic of patch types with different flammabilities can prevent a small, locally contained fire from moving across large areas. Slope and aspect can also directly influence the exposure of ecosystems to fire spread because fire generally moves uphill and tends to halt at ridgetops. Elevation and topographic position also influence the susceptibility of forest trees to windthrow (Foster 1988). Alternatively, a wildfire can spread

across a large, highly connected landscape, even if started by a small ignition source. An untended campfire resulted in the largest fire in the history of Colorado, the Hayman fire in 2002 (Graham 2003).

Patchiness created by disturbance and other legacies influences the probability and spread of disturbance, thereby maintaining the mosaic structure of landscapes. The spread of fire, for example, creates patches of early successional vegetation in fire-prone ecosystems that are less flammable than late-successional vegetation (Rupp et al. 2000). In this way, past disturbances create a legacy that governs the probability and patch size of future disturbances. The effectiveness of these disturbance-generated early successional firebreaks depends on climate. At times of extreme fire weather, almost any vegetation will burn (Turner 2010).

Past history of insect or pathogen outbreaks also generates a spatial pattern that determines the pattern of future outbreaks. In mountain hemlock ecosystems of the Northwestern U.S., low light and nutrient availability in old-growth stands make trees vulnerable to a root pathogen. The resulting tree death increases light, nitrogen

Fig. 13.5 Transect of tree height and net nitrogen mineralization rate across a disturbance caused by root pathogens in a hemlock stand in the Northwestern U.S. Nitrogen mineralization increases dramatically beneath trees recently killed by the pathogen (position 2). As trees recover (positions 3, 4, and 5), net nitrogen mineralization declines toward rates typical of undisturbed forest (position 1). Data from Matson and Boone (1984)



mineralization, and nutrient availability, making the regenerating forest resistant to further attack (Matson and Boone 1984; Fig. 13.5). The infections tend to move through stands in a wave-like pattern, attacking susceptible patches and creating resistant patches in their wake (Sprugel 1976), just as described for fire. Similarly, hurricanes that blow down large patches of trees generate early successional patches of short-statured trees that are less vulnerable to windthrow in the next hurricane. Even the fine-grained steady-state mosaics that characterize gap-phase succession are self-sustaining because young trees that grow in a gap created by treefall are less likely to die than are older trees. In summary, those disturbances that reduce the probability of future disturbance generate a stabilizing (negative) feedback that tends to stabilize the disturbance regime of a landscape, resulting in a shifting steady-state mosaic with a characteristic patch size and return interval. Any long-term trend in

climate or soil resources or extreme events that alters disturbance regime will probably alters the characteristic distribution of patch sizes and shapes on the landscape.

Interactions among processes that are controlled at different scales lead to nonlinear and sometimes catastrophic consequences (Peters et al. 2004). A wildfire starts, for example, when lightning strikes a tree whose structure and chemistry support combustion under ambient weather conditions. Fire spread, however, depends on the arrangement of plant canopies within a stand. Fire may then spread from one stand to another if there is high connectivity among stands, again leading to a nonlinear increase in combustion, once this threshold is passed. Finally, hot extensive fires create their own winds, which can greatly accelerate fire spread. Desertification, shrub encroachment into grasslands, and disease epidemics follow similar nonlinear changes in rates of spread, as new controls come into play at

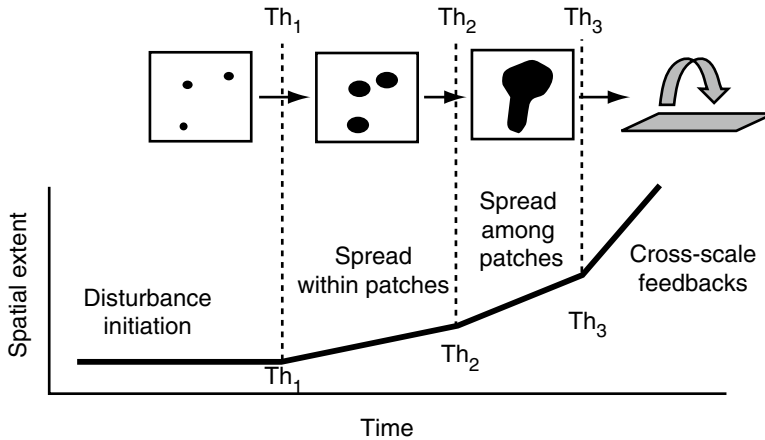


Fig. 13.6 Cross-scale interactions that influence the non-linear spread of disturbance across a landscape. Disturbances (e.g., fire, drought, disease epidemics) are often controlled by different processes at different scales (e.g., at scales of individuals, patches, landscapes, and regions).

progressively larger scales (Fig. 13.6). The changes that occur at progressively larger scales can be either amplifying or stabilizing. Predicting the consequences of these **cross-scale linkages** requires an understanding of the predominant controls at each scale of interest.

Human activities that create novel small-scale disturbances have the potential to produce unanticipated effects at larger scales. The cultivation of extensive areas of drought-sensitive crops on marginal lands in the U.S. in the 1920s created a landscape matrix of cultivated, drought-susceptible patches interspersed with small patches of native grassland (Peters et al. 2004). Hot, dry weather combined with strong winds in the 1930s resulted in reduced plant cover, high plant mortality, and localized wind erosion on the cultivated patches. At the landscape scale, these small dust storms became aggregated among patches to generate massive dust storms (“black blizzards”) that disturbed intervening uncultivated patches and spread to affect much of the country (see Fig. 3.1; Peters et al. 2004, Schubert et al. 2004). The impact was extensive enough to reduce rainfall, intensifying the drought. Blowing soil from the Great Plains was documented as far as the east coast, over 1,500 km away.

Disturbances that increase the probability of other disturbances complicate predictions

This produces thresholds (Th_1, Th_2, \dots) and changes in temporal responses as new processes exert control at each scale. Amplifying feedbacks cause upward shifts in the curve. Stabilizing feedbacks cause downward shifts in the curve. Redrawn from Peters et al. (2004)

of landscape pattern. Insect outbreaks that kill trees in a fine-scale mosaic, for example, are often thought to increase the overall flammability of the forest, although the evidence for this pattern is sparse, and insects sometimes reduce fire risk by reducing fuel density (Turner 2010, Simard et al. 2011). The public concern about large fires after insect outbreaks then creates public pressure for salvage logging of insect-killed stands. This logging creates patches of clearcuts that are intermediate in size between those created by insects and those that might have been produced by a catastrophic fire. It is difficult to predict in advance what patterns of patch structure will develop. Rule-based models that define conditions under which particular scenarios are likely to occur provide a framework for predictions in the face of multiple potential outcomes (Starfield 1991).

Human activities create amplifying and stabilizing feedbacks to disturbances that alter the patch structure and functioning of landscapes. In principle, the effect of human-induced disturbances, such as land clearing, on landscape structure is no different than that of any other disturbance. However, the novel nature and the increasingly extensive occurrence of human disturbances are rapidly altering the structure of many landscapes. The construction of a road



Fig. 13.7 Maps of fires caused by naturally and human-caused fires in Alaska. The human-caused fires mirror the road and river transportation corridors, indicating the

importance of human access in altering regional fire regime. Redrawn from Gabriel and Tande (1983)

through the tropical wet forests of Rondonia, Brazil, for example, created a simple linear disturbance of negligible size. The sudden increase in human access, however, led to rapid clearing of forest patches that were much larger than natural treefall gaps or the hand-cleared patches created by shifting agriculture. Similarly, road access is the major factor determining the distribution of fire ignitions in the boreal forest of interior Alaska (Fig. 13.7). In general, road access is one of the best predictors of the spread of human-induced disturbances in relatively natural landscapes (Dale et al. 2000).

Socioeconomic factors, such as farmer income, interact with site characteristics to influence human impacts on landscape pattern. Heterogeneous landscapes are often converted to fine-scale mosaics of agricultural and natural vegetation, whereas large areas suitable for mechanized agriculture are more likely to be deforested in large blocks. In northern Argentina, for example, patches of dry deciduous forests on the eastern slopes of the Andes were converted to small patches of cropland, or modified by grazing into thorn-scrub grazing lands and secondary forests (Fig. 13.8; Cabido and Zak 1999). On the adjacent plains, however, larger parcels were initially deforested for grazing and more recently converted to mechanized agriculture. Large holdings on the plains are owned by companies that make land-use decisions based on the global economy. Small family producers in the mountains maintain a more traditional lifestyle that involves smaller, less frequent changes in land use (Zak et al. 2008).

Disturbance is increasingly used as a management tool to generate stand and landscape structures that more closely mimic those of natural ecosystems. Forest harvest varies from 0% to 100% tree removal, and the sizes and shapes of clearcuts can be altered from the standard checkerboard pattern to mimic more natural disturbances (Franklin et al. 1997). Forest harvest regimes can also be designed to retain some of the functional attributes of late-successional forests, such as the filtering function of riparian vegetation, the presence of large woody debris, and the retention of a few large trees as seed source and nesting habitat. Protection of these features can significantly reduce the ecological impact of forest harvest. Prescribed fire is increasingly used as a management tool, particularly in areas where a century of “Smoky the Bear” policy of complete fire suppression led to unnaturally large fuel accumulations in some ecosystems. Prescribed fires are typically lit under weather conditions where fire intensity and severity are low, so the fire can be readily controlled. In populated regions, vegetation may be physically removed as a substitute for fire because prescribed fires are considered unsafe. Natural fire, prescribed fire, and physical removal of vegetation probably differ in their impacts on ecosystem processes due to differences in the quantity of organic matter and nutrients removed; these differences affect subsequent regrowth.

Ecologists are only beginning to understand the long-term consequences of different disturbance regimes for the structure and functioning of ecosystems and landscapes. As this understanding

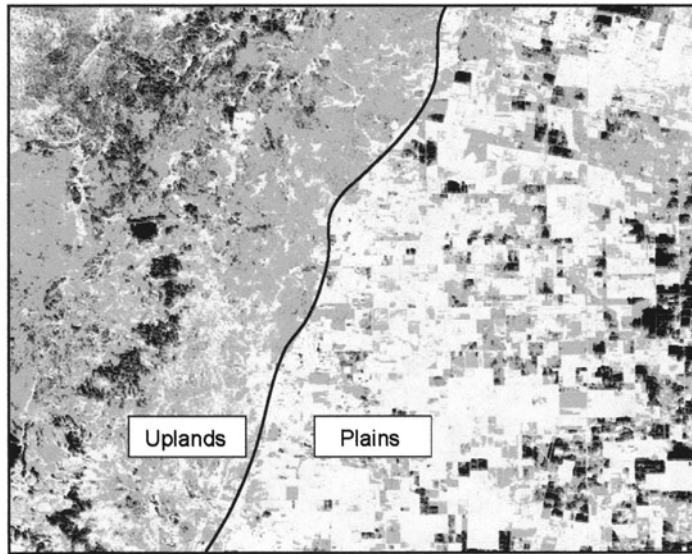


Fig. 13.8 Satellite-based map of the Cordoba region of Northern Argentina in 1999, showing semi-natural vegetation (*black*), lands that have been modified by grazing (*gray*) and croplands (*white*). The plains to the east are more suitable for mechanized agriculture and are large land holdings with large areas converted to croplands. Lands to the west are more mountainous and less

suitable for mechanized agriculture. They are owned by small farmers, each of whom maintains a heterogeneous mosaic of land use. The proportion of area converted to cropland is greater in large land holdings suitable for intensive agriculture (Cabido and Zak 1999). Figure kindly provided by Marcelo Cabido and Marcelo Zak

improves, more informed decisions can be made in using disturbance as a tool in ecosystem management (see Chap. 15). Management of disturbance regime can recreate landscape structures in which natural disturbance regimes can again come into play or can mimic the ecological effects of disturbance under conditions in which the natural disturbance pattern has unacceptable societal consequences.

Patch Interactions on the Landscape

Interactions among patches on the landscape influence the functioning of individual patches and the landscape as a whole. Landscape patches interact through lateral movement of water, energy, nutrients, or organisms across boundaries from one patch to another. This occurs through topographically controlled interactions, transfers through the atmosphere, biotic transfers, and the spread of disturbance. These transfers are critically important to the long-term sustainability of

ecosystems because they represent losses from donor ecosystems and subsidies to recipient ecosystems. Large changes in these transfers constitute changes in inputs and outputs of resources and therefore alter the functioning of ecosystems.

Topographic and Land–Water Interactions

Topographically controlled redistribution of materials is the predominant physical pathway by which materials move between ecosystems (Fig. 13.9). Gravity is a potent force for landscape interactions. It causes water to move downhill, carrying dissolved and particulate materials. Gravity is also the driving force for landslides, soil creep, and other forms of soil movement (see Chap. 3). These topographically controlled processes transfer materials from gopher mounds to the surrounding grass matrix, from uplands to lowlands, from terrestrial to aquatic systems, and from freshwater ecosystems

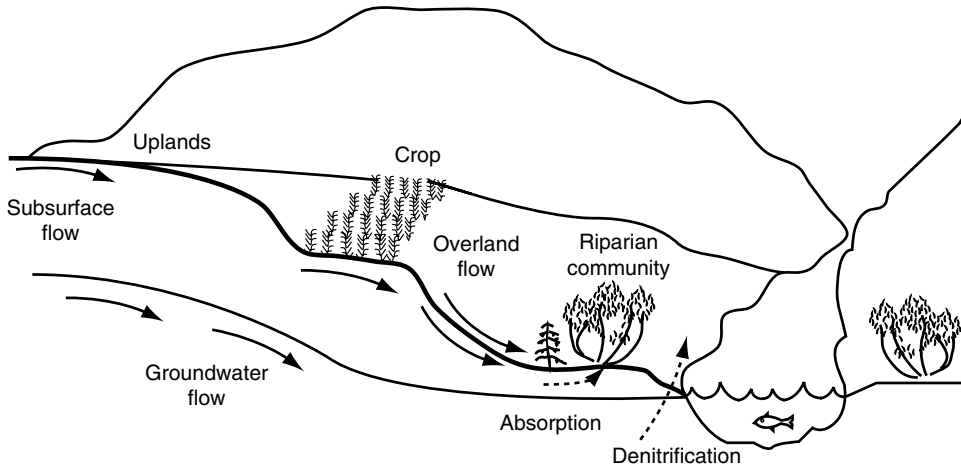
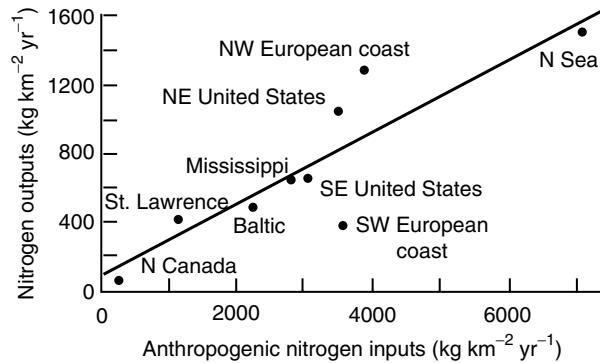


Fig. 13.9 Topographically controlled interactions among ecosystems in a landscape via erosion and solution transfers in subsurface flow or groundwater. Riparian forest trees absorb nutrients primarily from well-aerated soils, whereas denitrification requires anoxic conditions,

which generally occur below the water table. Nitrogen absorption and denitrification are the most important mechanisms by which riparian zones filter nitrogen from groundwater between upland ecosystems and streams

Fig. 13.10 Relationship between the total nitrogen input to the major watersheds of the world and nitrate loading in rivers. Redrawn from Howarth et al. (1996a)



to estuaries and the ocean (Naiman et al. 2005, Yoo et al. 2005).

The nature of donor ecosystems and their management govern the transfer of dissolved materials. Regions with intensive agriculture and those receiving substantial nitrogen deposition transfer substantial quantities of nitrate and phosphorus to rivers, lakes, and groundwater (Carpenter and Biggs 2009). Nitrate loading in rivers, for example, correlates closely with the total nitrogen input to the major watersheds of

the world (Fig. 13.10; Howarth et al. 1996a). At more local scales, the patterns of land use and urbanization influence the input of nutrients to lakes and streams. These increased fluxes of dissolved nitrogen have multiple environmental consequences, including health hazards, acidification, eutrophication, and reduced biodiversity of downstream freshwater and marine ecosystems (Howarth et al. 1996a, Nixon et al. 1996).

Erosion moves particulate material containing nutrients and organic matter from one

ecosystem and deposits it in another. Erosion ranges in scale from silt suspended in flowing water to movement of whole mountainsides in landslides. The quantity of material moved depends on many physical factors, including slope position, slope gradient, the types of rocks and unconsolidated material underlying soils, and the types of erosional agents (e.g., amount and intensity of rainfall events; see Chap. 3). The biological characteristics of ecosystems are also critical. Vegetation type, root strength, disturbance, management, and human development can be as important as the vertical gradient or parent material. Forest harvest on steep slopes in the Northwestern U.S., for example, has increased the frequency of landslides. Similarly, upland agriculture often increases sedimentation and the associated transfer of nutrients and contaminants (Comeleo et al. 1996, Syvitski et al. 2005). Proper management of up-slope systems through use of cover crops, reduced tillage, and other management practices can reduce erosional transfers of materials.

Landscape pattern influences the transfer of materials among ecosystems. In managed and unmanaged landscapes, ecosystems interact with one another along topographic sequences, with nutrients leached from uplands providing a nutrient subsidy to mid-slope or lowland ecosystems (Shaver et al. 1991). The configuration of these ecosystems in the landscape determines the pattern of nutrient redistribution and their outputs to groundwater and streams. Riparian vegetation zones, including wetlands and floodplain forests, act as filters and sediment traps for the water and materials moving from uplands to streams (Fig. 13.9). The dominance of riparian zones by disturbance-adapted plants that tolerate soil deposition and have rapid growth rates contributes to their efficiency as landscape filters. Riparian zones play a particularly crucial role in agricultural watersheds, where they remove fertilizer-derived nitrogen and phosphorus and eroding sediments. The fine-textured, organic-rich soils and moist conditions characteristic of most riparian areas also promote denitrification of incoming nitrate. Plant uptake and denitrification together account for the decline in nitrate con-

centration as groundwater flows from agricultural fields through riparian forests to streams. Phosphorus is retained in riparian areas primarily by plant and microbial absorption of nutrients and by physical adsorption to soils because phosphorus has no pathway of gaseous loss.

The high productivity and nutrient status of riparian vegetation and the presence of water cause riparian areas to be intensively used by animals, including livestock in managed ecosystems. People also use riparian areas intensively for water, gravel, transportation corridors, and recreation. Long-term elevated inputs from heavily fertilized agricultural areas or from wetlands used for tertiary sewage treatment (i.e., to remove the products of microbial decomposition) can saturate the capacity of riparian areas to filter nutrients from groundwater. Overexploitation of riparian areas can increase sediment and nutrient loading to streams and reduces shading, making freshwater ecosystems more vulnerable to changes in land use within the watershed (Correll 1997, Lowrance et al. 1997, Naiman and Décamps 1997).

In some cases, landscape pattern has no apparent effect on ecosystem processes. During severe fire weather, for example, all stands burn, and landscape patterns of differential flammability are relatively unimportant (Turner et al. 1994). Landscape pattern is most likely to be important when there is a distinct directionality of patch interaction (e.g., nutrient flow from land to water) and when disturbances are of low-to-moderate intensity (Turner 2010).

The properties of recipient ecosystems influence their sensitivity to landscape interactions. The vulnerability of ecosystems to inputs from other patches in the landscape depends largely on their capacity to sequester or transfer the inputs. Riparian areas, for example, may have a higher capacity to retain a pulse of nutrients or transfer them to the atmosphere by denitrification than do upland late-successional forests. Streams characterized by frequent floods are less likely to accumulate sediment inputs than are slow-moving streams and rivers because floods flush sediments from river channels of steep stream reaches. Lakes on calcareous substrates or those that

receive abundant groundwater input due to a location low in a watershed are better buffered against inputs of acidity and nutrients than are oligotrophic lakes on granitic substrates or lakes high in a watershed that receive less groundwater input (Webster et al. 1996).

Estuaries, the coastal ecosystems located where rivers mix with seawater, are a striking example of the way in which ecosystem properties influence their sensitivity to inputs from the landscape. They are among the most productive ecosystems on Earth (Howarth et al. 1996b, Nixon et al. 1996). Their high productivity stems in part from the inputs they receive from land and from the physical structure of the ecosystem, which is stabilized by the presence of sea grasses and other rooted plants. This tends to dampen wave and tidal energy, reducing resuspension and increasing sedimentation. Salinity and other geochemical changes that occur as the waters mix lead to flocculation and settling of suspended particles. Nutrient absorption by the rooted vegetation and phytoplankton, burial by sedimentation, and denitrification in anoxic sediments function as sinks for nutrients flowing from upstream watersheds, just as in riparian zones. The stability of the landscape on the Mississippi River Delta, for example, depends on regular delivery of sediments from upstream to replace soils removed by tidal erosion. Channels, levees, and other engineering solutions to flood control and water management may reduce the short-term probability of flooding but also eliminate the sediment supply that builds and maintains these barrier islands that protect the coast from larger storms. The drainage of wetlands to support urban development in New Orleans caused widespread subsidence of the land surface and reduced the capacity of the wetlands to store water from storm surges. Together this shift from dependence on natural landscape interactions to engineered alternatives contributed to the catastrophic impact of Hurricane Katrina in New Orleans in 2005 (Kates et al. 2006). Many estuaries, including the Gulf of Mexico near the entrance of the Mississippi River, are becoming saturated by nutrient enrichment within their watersheds,

resulting in harmful phytoplankton blooms, loss of sea grass, and increasing frequency of anoxia or hypoxia that create dead zones that kill fish and benthic invertebrates such as shrimp (see Fig. 9.1; Rabalais et al. 2002).

Atmospheric Transfers

Atmospheric transport of gases and particles links ecosystems over large distances and coarse spatial scales. Gases emitted from managed or natural ecosystems are processed in the atmosphere and can be transported for distances ranging from kilometers to the globe. Once deposited, they can alter the functioning of the recipient ecosystems (Fig. 13.11), just as with topographically controlled transfers.

In areas downwind of agriculture, NH_3 and NO_x can represent a significant fraction of nitrogen deposition. Dutch heathlands, for example, receive at least 10-fold more nitrogen deposition than would occur naturally. The magnitude of these inputs is similar to the quantity of nitrogen that annually cycles through vegetation, greatly increasing the openness of the nitrogen cycle. Areas downwind of industry and fossil fuel combustion receive nitrogen largely as NO_x . Sulfur gases, including SO_2 , are also produced by fossil fuel combustion, although improved regulations have reduced these emissions and deposition relative to NO_x .

The large nitrogen inputs to ecosystems have important consequences for NPP, nutrient cycling, trace gas fluxes, and carbon storage. Chronic nitrogen deposition initially reduces nitrogen limitation by increasing nitrogen cycling rates, foliar nitrogen concentrations, and NPP. Above some threshold, however, the ecosystem becomes saturated with nitrogen (Fig. 13.12; Aber et al. 1998). As excess nitrate and sulfate leach from the soil, they carry with them cations to maintain charge balance, inducing calcium and magnesium deficiency in vegetation (Driscoll et al. 2001). In southern Sweden, for example, over half of the plant-available cations have been lost from the upper 70 cm of soil in the past half-century, due at least in part to chronic exposure

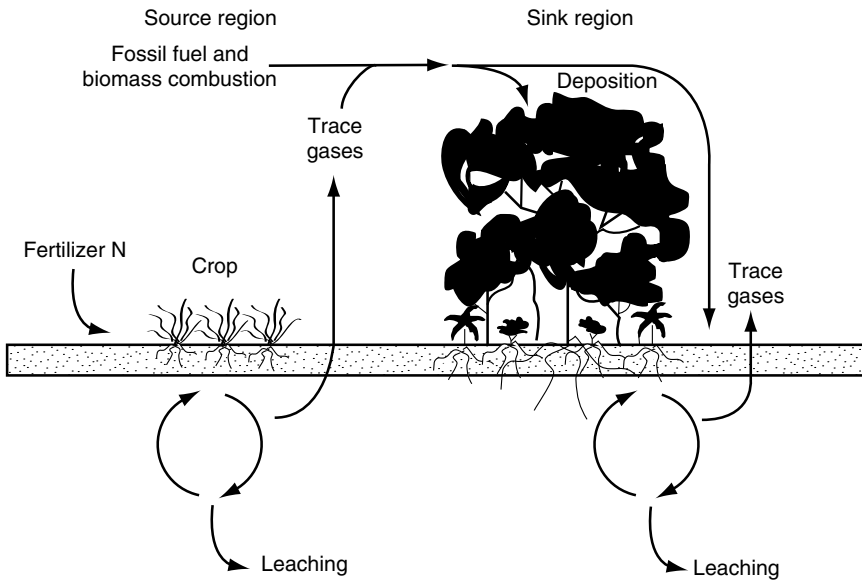
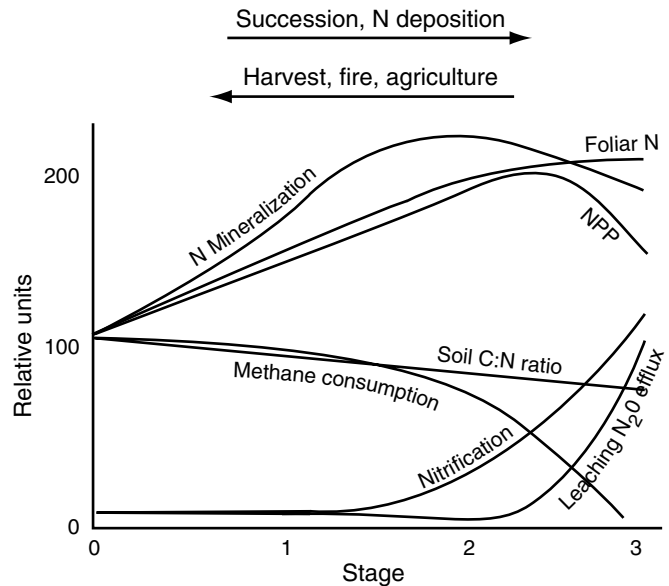


Fig. 13.11 Atmospheric transfers of gases, solutions, and particulates among ecosystems. Inputs come from fossil fuel and biomass combustion and from trace gases originating from natural and managed ecosystems

Fig. 13.12 Changes hypothesized to occur as forests undergo long-term nitrogen deposition and nitrogen saturation. Redrawn from Galloway et al. (2003)



to acid precipitation (Hallbacken 1992). The exchange complex becomes more dominated by manganese, aluminum, and hydrogen ions, increasing soil acidity and the likelihood of aluminum toxicity. Together this suite of soil changes often enhances frost susceptibility, impairs root

development, and promotes herbivory, leading to forest decline in many areas of Europe and the Northeastern U.S. (Schulze 1989, Aber et al. 1998). The major surprise, however, has been how resilient some forests have been to acid rain, often retaining most of the nitrogen inputs within

the ecosystem for decades and sustaining their productivity and carbon storage (Magnani et al. 2007, de Vries et al. 2009, Janssens et al. 2010).

In other forests, half of the nitrogen inputs are lost in streamflow (Lovett et al. 2000). The vulnerability of ecosystems to acid rain depends in part on the magnitude of inputs (related to distance from pollution sources and amount of precipitation received) and initial soil acidity, which in turn depends on parent material and species composition. For example, in the Northeastern U.S., forest productivity has declined in sites with granitic bedrock, particularly at high elevations where soil pools of base cations are smallest (Likens et al. 1996, Fahey et al. 2005). This is associated with calcium loss from soils and reduced growth and increased mortality of sugar maple, a calcium-sensitive species and important canopy dominant. Calcium addition to a watershed caused increases in mycorrhizal colonization, tissue calcium, and growth of sugar maple seedlings, particularly at high elevations (Juice et al. 2006). Acid rain also increases nitrogen inputs to streams and reduces the acid-neutralizing capacity of lakes (Aber et al. 1998, Carpenter et al. 1998, Driscoll et al. 2001). The increases in lake acidity are most pronounced in watersheds whose bedrock is poor in cations. In these lakes, acidity reduces the size, survival, and density of fish, in part through reductions in their food supply (Driscoll et al. 2001).

Nearly all research on the transport, deposition, and ecosystem consequences of anthropogenic nitrogen has been conducted in the Temperate Zone. Further increases in nitrogen deposition will, however, likely occur primarily in the tropics and subtropics (Galloway et al. 1995), where plant and microbial growth are often limited by elements other than nitrogen. These ecosystems might therefore show more immediate nitrogen loss in trace gases or leaching in response to nitrogen deposition (Matson et al. 1998). On the other hand, soil properties such as high clay content or cation exchange capacity may allow tropical soils to sequester substantial quantities of nitrogen before they become leaky.

Biomass burning transfers nutrients directly from terrestrial pools to the atmosphere and then to downwind ecosystems.

Biomass combustion releases a suite of gases that reflect the elemental concentrations in vegetation and fire intensity. About half of dry biomass consists of carbon, so the predominant gases released are carbon compounds in various stages of oxidation, including carbon dioxide, methane, carbon monoxide, and smaller quantities of non-methane hydrocarbons. The atmospheric role of these gases varies. CO_2 and CH_4 are greenhouse gases, whereas carbon monoxide and non-methane hydrocarbons react in the troposphere to produce ozone and other atmospheric pollutants that can affect downwind ecosystems (see Chap. 2). Nitrogen is also released in various oxidation states, including nitrogen oxides (NO and NO_2 , together known as NO_x) and ammonia (NH_3). The proportional release of these forms also depends on the intensity of the burn, with NO_x typically accounting for most of the emissions. Sulfur-containing gases, organic soot and other aerosol particles, elemental carbon, and many trace species of carbon, nitrogen, and sulfur also have important regional and global effects. Satellite and aircraft data show that these gases and aerosols in biomass burning plumes can be transported long distances.

Windblown particles of natural and anthropogenic origins link ecosystems on a landscape. The role of the atmosphere as a transport pathway among ecosystems varies among elements. For some base cations (Ca^{2+} , Mg^{2+} , Na^+ , and K^+) and for phosphorus, dust transport is the major atmospheric link among ecosystems. At the local-to-regional scale, dust from roads or rivers can alter soil pH and other soil properties that account for regional zonation of vegetation and land-atmosphere exchange (Walker et al. 1998). At the global scale, Saharan dust is transported across the Atlantic Ocean and deposited on the Amazon by tropical easterlies. Although the annual input of dust is small, it contributes substantially to soil development over the long term (Okin et al. 2004). Similarly, dust from the Gobi desert is deposited in wet forests of the Hawaiian Islands at the rate of $1.25 \text{ g m}^{-2} \text{ year}^{-1}$. In old soils, that is, those >2 million years old, dust input can be the largest source of phosphorus (Chadwick et al. 1999, Vitousek 2004). In the

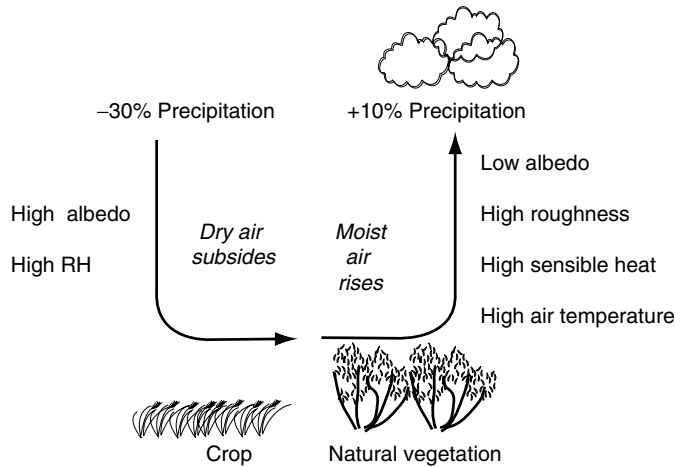


Fig. 13.13 Effects on regional climate of conversion from heathland to barley croplands in southwestern Australia. The heathland absorbs more radiation (low albedo) and transmits a larger proportion of this energy to the atmosphere as sensible heat than does adjacent croplands. This causes air to rise over the heathland and draws in moist air (high relative

humidity [RH]) laterally from the irrigated cropland; this causes subsidence of air over the cropland, just as with the air circulation of sea breezes (see Chap. 2). Rising moist air increases precipitation by 10% over heathland, whereas subsiding dry air reduces precipitation by 30% over the cropland. Data from Chambers (1998; see Fig. 4.1)

Western U.S., the building of railroads between 1860 and 1900 combined with intense cattle and sheep grazing in the American Southwest increased dust loads in the atmosphere to result in reduced duration of snow cover in the San Juan Mountains (Painter et al. 2007, Neff et al. 2008). Similarly, large Asian dust storms can travel as far as the Western U.S., causing faster and earlier snow melt with less water available for irrigation, cities, and ski resorts in the Rocky Mountains.

Land–atmosphere exchange of water and energy in one location influences downwind climate. The ocean and large lakes moderate the climate of adjacent land areas by reducing temperature extremes and increasing precipitation (see Chap. 2). Human alteration of the land surface is now occurring so extensively that it also has significant effects on downwind ecosystems. Conversion of Australian heathlands to agriculture has, for example, increased precipitation over heathlands and reduced it by 30% over agricultural areas (Fig. 13.13; see Fig. 4.1). Deforestation in the Amazon reduces regional evapotranspiration. This reduction in water recycling reduces the moisture available for precipitation elsewhere in the basin, making the climate less favorable for tropical rainforests (Foley et al.

2003b). At a global scale, the clearing of land for agriculture has reduced regional albedo and evapotranspiration, leading to greater sensible heat flux (Chase et al. 2000, Foley et al. 2003b, Field et al. 2007). At all spatial scales the atmospheric transfer of heat and water vapor from one ecosystem to another strongly affects ecosystem processes in downwind ecosystems. The climatic impacts on downwind ecosystems of reservoirs, irrigation of arid lands, and land-use change are seldom included in assessments of the potential impacts of these management projects.

Movement of Plants and Animals on the Landscape

The movement and dispersal of plants and animals link ecosystems on a landscape. Large animals typically consume forage from high-quality patches and deposit feces and urine where they rest or sleep. Sheep in New Zealand, for example, often spend nights on ridges, moving nutrients upward and counteracting the downward nutrient transport by gravity. Marine birds transfer so much phosphorus from marine foods to the land that the **guano** deposited in their traditional nesting areas

has served as a major source of phosphorus for fertilizer. **Anadromous fish**, that is, marine fish that enter freshwater to breed, also transport marine-derived nutrients to terrestrial ecosystems. These fish carry the nutrients up rivers and streams, where they become an important food item for terrestrial predators, which transport the marine-derived nutrients to riparian and upland terrestrial ecosystems (Willson et al. 1998, Helfield and Naiman 2001). The enhanced tree growth supported by these marine-derived nutrients, in turn, provides more shade, less streambank erosion, larger coarse woody debris, and therefore potentially better salmon habitat than in streams that lack salmon (Helfield and Naiman 2001). Similarly, insects that feed on seaweed and other marine detritus are an important food source for spiders on islands, merging marine and terrestrial food webs (Polis and Hurd 1996).

Animals also transfer plants, especially as seeds, on fur and in feces. Many plants have evolved life history strategies to take advantage of this efficient form of dispersal. This dispersal mechanism has contributed to the spread of invasive plants. Feral pigs, a non-native herbivore in Hawaiian rainforests, for example, transfer seeds of invasive plants such as the passion vine, which alters patterns of nutrient cycling. Similarly, the alien bird white eye spreads the alien nitrogen fixer *Morella faya* (Woodward et al. 1990), which alters the nitrogen status of native ecosystems (Vitousek et al. 1987). Thus, invasions of both plants and animals from one ecosystem to another can contribute to a variety of ecosystem changes.

Animals that move among patches can have effects that differ among patch types. Edge specialists such as deer, for example, may concentrate their browsing in one habitat type but seek protection from predators and deposit nutrients in another (Seagle 2003). Predator–prey dynamics may also structure nutrient heterogeneity based on where predation occurs and carcasses are deposited, for example when moose feed on nitrogen-rich aquatic vegetation and are killed by wolves in upland sites (Bump et al. 2009). At a larger scale, migratory birds move seasonally among different ecosystem types. Lesser snow geese, for example, overwinter in the Southern

U.S. and breed in the Canadian Arctic. Populations of this species have increased by more than an order of magnitude as a result of increased use of agricultural crops (rice, corn, and wheat) on the wintering grounds and reduced hunting pressure. This species now exceeds the carrying capacity of its summer breeding grounds and has converted productive arctic salt marshes into unvegetated barrens (Jefferies and Bryant 1995).

People are an increasing cause of lateral transfers of materials among ecosystems, through addition of fertilizers, pesticides, etc., introduction of propagules of invasive species, removal of crops and forest products, and diversion of water. The resulting nutrient inputs to aquatic systems occur in locations where riparian zones and other ecological filters are often degraded or absent. The nutrient transfers in food from rural to urban areas are substantial. Food imports to Europe are a significant component of the European carbon and especially nitrogen balance (Ciais et al. 2008), and food imports are the major source of nitrogen to coastal watersheds (Driscoll et al. 2003). Water diversion by people has substantially altered rates and patterns of land-use change in arid areas at the expense of rivers and wetlands (see Chap. 4). As water becomes increasingly scarce in the coming decades, pressures for water diversion are likely to increase.

Disturbance Spread

Patch size and arrangement determine the spread of disturbance across a landscape.

Disturbance is a critical interactive control over ecosystem processes that is strongly influenced by horizontal spread from one patch to another. Fire and many pests and pathogens move most readily across continuous stretches of disturbance-prone vegetation. Fuelbreaks of nonflammable vegetation, for example, reduce fire risk at the urban–wildland interface. Fires create their own fuelbreaks because post-fire vegetation is generally less flammable than that which precedes a fire. Theoretical models suggest that, when less than half of the landscape is disturbance-prone, severity is more important than frequency in

determining the impacts of disturbance. When large proportions of the landscape are susceptible to disturbance, however, the frequency of disturbance becomes increasingly important (Gardner et al. 1987, Turner et al. 1989). The size of patches also influences the spread of disturbance. Landscapes dominated by large patches tend to have a low frequency of large fires, which in turn generate large patches. Landscapes with small patches have greater edge-to-area ratio, so fires tend to spread more frequently into less flammable vegetation (Rupp et al. 2000). In this way, landscapes tend to sustain their characteristic disturbance regime, until modified by other factors (e.g., climate or land-use change).

Patchy agricultural landscapes are less prone to spread of pests and pathogens than are large continuous monocultures. Intensive agriculture has reduced landscape patchiness in several respects. The average size of individual fields and the proportion of the total area devoted to agriculture have generally increased, as has the use of genetically uniform varieties. This can lead to rapid spread of pests across the landscape.

Human Land-Use Change and Landscape Heterogeneity

Human modification of landscapes has fundamentally altered the role of ecosystems in regional and global processes. Much of the land-use change has occurred within the last two to three centuries, a relatively short time in the context of evolution or landscape development. Since 1700, for example, the land area devoted to crop production has increased 466% and now accounts for about 10–20% of the ice-free terrestrial surface (Ellis and Ramankutty 2008). Many areas of the world are therefore dominated by a patchwork of agricultural fields, pastures, and remnant unmanaged ecosystems. Similar patchworks of cut and regenerating forest interspersed with small areas of old-growth forest are common on every continent. Human-dominated landscapes supply large amounts of food, fiber, and other ecosystem services to society. Two general patterns of land-use change emerge: (1) **extensification**, that is,

the increase in *area* affected by human activities, and (2) **intensification**, that is, the increase in *inputs* applied to a given area of land or water.

Extensification

Land-use changes include both land-use conversions and modifications (Meyer and Turner 1992). **Land-use conversion** involves a human-induced change in ecosystem type to one dominated by different physical environment or plant functional type, for example, the change from forest to pasture or from stream to reservoir. **Land-use modification** is the human alteration of an ecosystem in ways that significantly affect ecosystem processes, community structure, and population dynamics without radically changing the physical environment or dominant plant functional type. Examples include alteration of natural forest to managed forest, savanna management as grazing lands, and alteration of traditional low-input agriculture to high-intensity agriculture. In aquatic ecosystems, this includes the alteration of flood frequency by dams and levees or the stocking of lakes for sport fishing. Both types of land-use change alter the functioning of ecosystems, the interaction of patches on the landscape, and the functioning of landscapes as a whole.

Deforestation is an important conversion in terms of spatial extent and ecosystem and global consequences. Forests cover about 25% of the terrestrial surface, 2–3 times the total agricultural land area (see Fig. 1.8, Table 6.6). Globally, forest area has decreased about 15% (i.e., by 9 million km²) since preagricultural times. Much of the European and the Indian subcontinents, for example, were prehistorically blanketed by forests, but over the last five to ten centuries have supported extensive areas of agriculture. Similarly, North America was once contiguously wooded from the Atlantic seaboard to the Mississippi River, but large areas of this forest were cleared by European settlers at rates similar to those that now characterize tropical forests (Dale et al. 2000).

Today, conversion of forests to pasture or agriculture is one of the dominant land-use changes

in the humid tropics. The magnitude of this land-use change is uncertain, but that uncertainty is diminishing as both the technology and the applicability of remote sensing improve (Chambers et al. 2007). As recently as the 1990s, only the largest clearings could be monitored accurately via remote sensing – however, newly developed tools and analyses permit the detection of areas of selective logging as well as those of clearing and conversion. For example, Asner et al. (2010) used a multi-scale approach with aircraft-based LIDAR and satellite systems to evaluate carbon stocks and losses in a 4.3 million hectare region of the Peruvian Amazon, with a spatial resolution of 0.1 ha. Their analysis demonstrated that an amount of carbon equivalent to just over 1% of standing biomass in this relatively remote area was lost to land-use change in a decade and that inclusion of selective logging in the analyses increased the calculated amount of carbon lost by nearly 50%. On a finer spatial scale, repeated LIDAR measurements of forest structure can be used to estimate rates of treefall gap formation and filling directly, on a landscape scale (Kellner et al. 2009). In time, these direct measurements of forest turnover will be applied to larger and more heterogeneous areas (Kellner and Asner 2009). These tools will become increasingly important as efforts to retain or sequester carbon in biomass become more widespread.

The trajectory of landscape change caused by deforestation depends on both the nature of the original forests and the land use that follows. Primary forests are likely to persist longer in remote regions such as much of Amazonia and Central Africa than elsewhere. The permanent or long-term conversion of forests to managed ecosystems involves burning or removal of most of the biomass and often leads to large losses of carbon, nitrogen, and other nutrient elements from the system. Logging, in contrast, removes only the commercially valuable trees and may cause less carbon and nutrient loss from soils. The nutrient losses that accompany deforestation can alter adjacent ecosystems, particularly aquatic ecosystems, and influence the atmosphere and climate through changes in trace gas fluxes and water and energy exchange (see Chap. 4). They

may also affect forest regrowth after disturbance (Davidson et al. 2004).

Reforestation of abandoned agricultural land through natural succession or active tree planting is also changing landscapes, particularly in the Eastern U.S., Europe, China, and Russia. In the Eastern U.S., for example, much of the land that was originally cleared reverted to forest dominated by native species (see Fig. 12.2). In Chile, however, plantations of rapidly growing exotic trees such as *Pinus radiata* are replacing primary forests (Armesto et al. 2001). These plantations have low diversity and a quite different litter chemistry and pattern of nutrient cycling than do the primary forests that they replace. In addition, some tropical areas are now experiencing a “forest transition,” in which the past net forest decline has been reversed, and overall forest cover is increasing, similar to patterns that occurred across much of the temperate zone in the twentieth century (Rudel et al. 2005).

The characteristics of the regenerating forests also depend on the previous types of land use (Foster et al. 1996, 2010). Long-term and intensive agricultural practices can compact the soil, alter soil structure and drainage capability, deplete the soil organic matter, reduce soil water-holding capacity, reduce nutrient availability, deplete the seed bank of native species, and introduce new weedy species. The forests that regenerate on such land may therefore differ substantially from the original forest, or from those that regrow on less-intensively managed lands (Motzkin et al. 1996). Grazing intensity and accompanying land management practices also influence potential revegetation, with more intensively grazed systems often taking longer to regain forest biomass. Natural reforestation under these conditions may proceed slowly or not at all.

Use of grasslands, savannas, shrublands, and cleared forests for cattle grazing is the most extensive modification of natural ecosystems occurring today, and, like deforestation, it can now be monitored and analyzed by remote sensing. Globally, thousands of square kilometers of savanna are burned annually to maintain productivity for cattle grazing. Although both fire and grazing are natural components of mesic

grasslands, changes in the frequency or severity of burning and grazing alters ecosystem processes (Knapp et al. 1998). Burning releases nutrients and stimulates the production of new leaves that have a higher protein content and are more palatable to grazers. Conversely, grazers reduce fire probability by reducing the accumulation of grass biomass and leaf litter. Fire and browsers both prevent establishment of most trees, which might otherwise convert savannas to woodlands or forests. When fire frequency increases substantially, however, the loss of carbon and nitrogen from the system can reduce soil fertility and water retention and (and therefore productivity). Fire can also affect regional trace-gas budgets and deposition in downwind ecosystems and the transfer of nutrients and sediments to aquatic ecosystems.

Expansion of marine fishing has altered marine food webs globally, with cascading effects on most ecosystem processes. The area of the world's ocean that is actively fished has increased substantially, in part because technological advances allow fish and benthic invertebrates to be harvested more efficiently and stored for longer times before returning to markets. Most of Earth's continental shelves, the most productive marine ecosystems, are now actively fished, as are the productive high-latitude open ocean basins. Removal of fish has cascading effects on pelagic ecosystems because fish predation has large top-down effects on the biomass, and species composition of zooplankton, which in turn impact primary productivity by phytoplankton and the recycling of nutrients within the water column (see Chap. 10; Pauly et al. 1998). Harvesting of benthic invertebrates, such as clams, crabs, and oysters, also has large ecosystem effects because of direct habitat disturbance and the effects of these organisms on detrital food webs and benthic decomposition. The globalization of marine fisheries has a broader impact than we might expect because many large fish are highly mobile and migrate for thousands of kilometers (Berkes et al. 2006). Large changes in these fish populations therefore have ecological effects that diffuse widely throughout the ocean and even into freshwater ecosystems in the case of anadromous fish.

Intensification

Intensification of agriculture often reduces landscape heterogeneity and increases the transfer of nutrients and other pollutants to adjacent ecosystems. Agricultural intensification generally involves the use of high-yield crop varieties combined with tillage, irrigation, industrially produced fertilizers, and often pesticides and herbicides. Intensification has allowed food production to keep pace with the rapid human population growth (see Fig. 8.1; Evans 1980, Naylor 2009). Although this practice has reduced the areal extent of land required for agriculture, it has nearly eliminated some ecosystem types that would naturally occupy areas of high soil fertility. Intensive agriculture is most developed on relatively flat areas such as floodplains and prairies that are suitable for irrigation and use of large farm machinery. The high cost of this equipment requires that large areas be cultivated, largely eliminating natural patterns of landscape heterogeneity (Fig. 13.8).

Agricultural intensification generates biogeochemical hot spots that alter ecosystem processes in ways that impact the local, regional, and global environment (Matson et al. 1997). The large regular inputs of nutrients required to sustain intensive agriculture (see Fig. 8.1) increase the emissions of nitrogen trace gases that play a significant role in the global nitrogen cycle and link these ecosystems with downwind ecosystems (see Chaps. 9 and 14).

Nutrient loading on land increases non-point sources of pollution for neighboring aquatic ecosystems (Strayer et al. 2003, Carpenter and Biggs 2009). Phosphorus additions on land have particular large impacts in lakes for at least two reasons. First, primary production of most lakes is limited most fundamentally by phosphorus and therefore responds sensitively to even small phosphorus additions. Second, much of the phosphorus added to agricultural fields is chemically fixed, so more phosphorus is often added to fields than is absorbed by crops. On the North China Plain, for example, three times more phosphorus is added than is removed in crops. Large additions represent a massive reservoir of phosphorus

that will continue to enter aquatic ecosystems long after farmers stop adding fertilizer. Phosphorus inputs from human sewage and livestock manure have similarly long-lasting effects. In some cases, farmers can “mine” past fertilizer addition to meet crop needs. Many farms in the upper Midwest corn belt, for example, now apply less phosphorus than is removed in crops, and depend on the legacy of previous phosphorus applications (Vitousek et al. 2009b).

Land-use change has caused greater ecological impact during the twentieth century than any other global change. Understanding and projecting future changes in land use are therefore critical to predicting and managing future changes in the Earth System. Land-change scientists have developed effective interdisciplinary collaborations among climatologists, geographers, ecologists, agronomists, and social scientists to evaluate the rates, causes, and consequences of land-use and land-cover change (Lambin et al. 2003). These collaborations permit the development of plausible scenarios for future land-use/land-cover change. Optimistic scenarios that assume that the growing human population will be fed rather than die from famines, wars, or disease epidemics project continued large changes in land use, particularly in developing countries (MEA 2005). What actually occurs in the future is, of course, uncertain, but these and other scenarios suggest that land-use change will continue to be the major cause of global environmental change in the coming decades. Ecologists working together with policy makers, planners, and managers have the opportunity to develop approaches that will minimize the impact of future landscape changes (see Chap. 15). This vision must recognize the large effects of land-use change on landscape processes, their consequences on local-to-global scale, and the relationship with human activities and behaviors.

Extrapolation to Larger Scales

Extrapolation of ecosystem processes to large spatial scales requires an understanding of the role of spatial heterogeneity in ecosystem processes. Efforts to estimate the cumulative effect

of ecosystem changes at landscape to regional and global scales have contributed to increased recognition of the importance of landscape processes in ecosystem dynamics. Estimates of annual carbon sequestration, for example, require that rates measured (or modeled) in a few locations be extrapolated over large areas or (increasingly) that methods be developed that can measure carbon pools over large areas in ways that account for spatial heterogeneity. These estimates are economically and politically important in international negotiations to reduce human impacts on the climate system.

Many approaches to spatial extrapolation have been used, each with its advantages and disadvantages (Miller et al. 2004, Turner and Chapin 2005). A useful starting point is to multiply the rates typical of the most widespread land-cover type by the area of concern to give a “back-of-the-envelope” estimate of regional pools and fluxes. This might suggest whether a process of potential interest (e.g., deforestation effects on regional precipitation) warrants more careful consideration. A “paint-by-numbers” approach identifies potentially important patch types and estimates the flux or pool for the entire area by multiplying the average value for each patch type (e.g., the yield of major types of crops or the carbon stocks of different forest types) times the areal extent of that patch type. This provides a more realistic approximation that can guide process-based research. This approach requires the selection of representative values of processes and accurate estimates of the area of each patch type. This extrapolation approach can be combined with empirical regression relationships (rather than a single representative value) to estimate process rates for each patch type. Carbon pools in a given forest type, for example, might be estimated as a function of temperature or NDVI rather than assuming that a single value could represent the carbon stocks of all sites. Improvements in satellite remote sensing technologies and the development of multi-scale sampling that assimilates satellite sensors, aircraft sampling, and ground-based analyses have allowed the development of sampling strategies that incorporate spatial variation in both the state factors and patch dynamics (Asner et al. 2010).

Process-based models can also be used to estimate fluxes or pools over large areas or under novel conditions. These estimates are based on maps of input variables for an area (e.g., maps of climate, elevation, soils, and satellite-based indices of leaf area or more sophisticated measures of ecosystem structure and functioning) and a model that relates input variables to the ecosystem properties simulated by the model (Box 13.1; Potter et al. 1993, VEMAP-Members 1995, Running et al. 2004). Regional evapotranspiration, for example, can be estimated from satellite data on vegetation structure and maps of temperature and precipitation that are used as inputs to an ecosystem model (Running et al. 1989). Estimates from ecosystem models are sensitive to the quality, quantity, and uncertainty of the input data and to the validity and degree of generality of the relationships assumed by the models. The generality of relationships used in ecosystem models can then be tested through comparisons of model output with field data and through intercomparisons of models that differ in their structure but use the same input data (Cramer et al. 2001).

Any extrapolation exercise requires consideration of biogeochemical hot spots with high process rates. Regional extrapolation of methane flux at high latitudes, for example, should consider beaver ponds (Roulet et al. 1997) and thermokarst lakes (Walter et al. 2006) because they have very high fluxes relative to their area, just as analyses of savannas need to consider the distribution of termite mounds. Similarly, estimates of NEP require differentiation between young and old forests because forest age is an important determinant of NEP (see Chap. 12).

Processes that are strongly influenced by interactions among patches on a landscape cannot be extrapolated to large scales without explicitly considering these interactions. The effects of climate change on wildfire risk to communities, for example, is strongly influenced by fire spread, which depends on the configuration of ecosystems on the landscape. Spatially explicit models that incorporate the spread of disturbance among patches on a landscape are critical for projections of long-term changes in vegetation and disturbance regime (Gardner et al. 1987, Rupp et al. 2000, Perry and Enright 2006).

Box 13.1 Spatial Scaling Through Ecological Modeling

The complexity of ecological controls over all the processes that influence ecosystem carbon balance makes long-term projections of terrestrial carbon storage a daunting task. Making these projections is, however, critical to assessing the relative role of different terrestrial ecosystems in the global carbon balance. Experiments that test multiple environmental effects on terrestrial carbon storage are difficult to design. Modeling of complex combinations of environmental–biotic interactions extends what can be learned from a limited amount of empirical information. Ecosystem models have, for example, been used to identify key controls over net ecosystem carbon balance (NECB) to assess the role of the biosphere in regulating atmospheric CO₂ concentration under different scenarios of fossil fuel emissions and climate change (IPCC 2007).

Many of key processes regulating NECB involve changes occurring over decades to centuries. The temporal resolution of the models must therefore be coarse, with **time steps** (the shortest unit of time simulated by the model) of a day, month, or year. Use of relatively long time steps reduces the level of detail that can be considered. The short-term pulses of decomposition associated with drying and wetting cycles or grazing by soil fauna, for example, are subsumed in the shape of the annual temperature and moisture response curves of decomposition and in the decomposition coefficients. Only the more general controls such as temperature, moisture, and chemistry can still be observed with an annual time step.

The basic structure of a model of NECB must include the pools of carbon in soils and vegetation. It must also include carbon fluxes

(continued)

Box 13.1 (continued)

from the atmosphere to plants (GPP or NPP), from plants to the atmosphere (plant respiration, harvest, and combustion), from plants to soil (litterfall), and from soil to the atmosphere (heterotrophic respiration and disturbance). Models differ in the detail with which these and other pools and fluxes are represented. Plants, for example, might be considered a single pool, or be separated into different plant parts (leaves, stems, and roots), functional types of plants (e.g., trees and grasses in a savanna), or chemical fractions such as cell wall and cell contents. Under some circumstances, certain fluxes (e.g., fire and leaching) are ignored. There is no single “best” model of NECB. Each model has a unique set of objectives, and the model structure must be designed to meet these objectives, and results must be interpreted in light of the objectives and the assumptions that are built into the model. We briefly describe how three models incorporate information about controls over NEP, emphasizing how the differences in model structure make each model appropriate to particular questions or ecosystems. NEP models ignore carbon fluxes associated with disturbance and leaching.

Perhaps the biggest challenge in model development is deciding which processes to include. One approach is to use a hierarchical series of models to address different questions at different scales (Reynolds et al. 1993). Models of leaf-level photosynthesis and of microclimate within a canopy have been developed and extensively tested for agricultural crops, based on the basic principles of leaf biochemistry and the physics of radiation transfer within canopies. One output of these models is a regression relationship between environment at the top of the canopy and net photosynthesis by the canopy. This environment–photosynthesis regression relationship can then be incorporated into models operating at larger temporal and spatial scales to simulate NPP, without explicitly including all the details of biochemistry and radiation transfer. This hierarchical

approach to modeling provides an opportunity to **validate** the model output (i.e., to compare the model predictions with data obtained from field observations or experimental manipulations) at several scales of temporal and spatial resolution, providing confidence that the model captures the important underlying processes at each level of resolution.

The Terrestrial Ecosystem Model (TEM; Fig. 13.14) was designed to simulate ecosystem carbon budgets for all locations on Earth at 0.5° longitude \times 0.5° latitude resolution (60,000 grid cells) for time periods of a century or more (McGuire et al. 2001). TEM has a relatively simple structure and a monthly time step, so it can run efficiently in large numbers of grid cells for long periods of time. Soil, for example, consists of a single carbon pool. The model assumes simple universal relationships between environment and ecosystem processes based on general principles that have been established in ecosystem studies. The model assumes, for example, that decomposition rate of the soil carbon pool depends on the size of this pool and is influenced by the temperature, moisture, and C:N ratio of the soil. The model incorporates feedbacks that constrain the possible model outcomes. The nitrogen released by decomposition, for example, determines the nitrogen available for NPP, which in turn governs carbon inputs to the soil and therefore the pool of soil carbon available for decomposition. The model is validated by comparison of model output with global patterns of carbon pools and fluxes in natural ecosystems (McGuire et al. 2001), making the model useful in simulating regional and global patterns of soil carbon storage under historical or potential future climatic conditions.

CENTURY (Fig. 13.14) was originally developed to simulate changes in soil carbon storage in grasslands in response to variation in climate, soils, and tillage (Parton et al. 1987, Parton et al. 1993). It has since been adapted to most global ecosystem types. In CENTURY,

(continued)

Box 13.1 (continued)

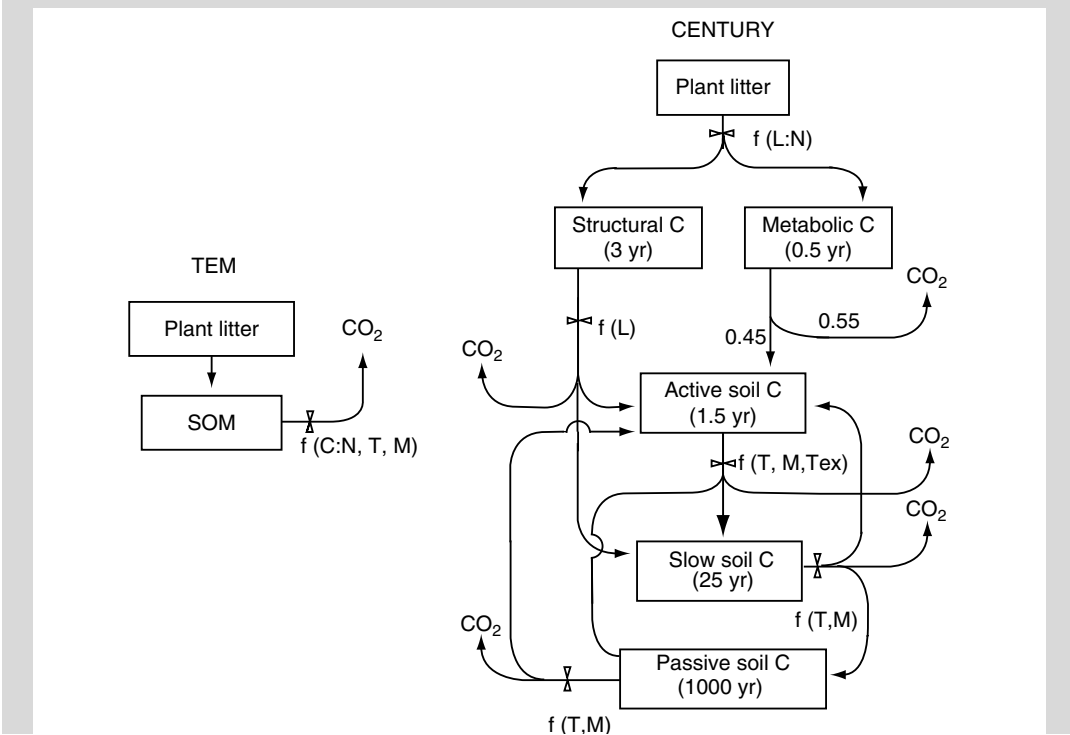


Fig. 13.14 Diagrammatic representation of the decomposition portion of two terrestrial ecosystem models: TEM (McGuire et al. 1995b) and CENTURY (Parton et al. 1987). Inputs from the vegetation component of these models are shown as plant litter. Arrows indicate the fluxes of carbon from litter to other pools and even-

tually to CO₂. The bow-ties indicate controls over these fluxes (or the partitioning of the flux between two pools) as functions (f) of C:N ratio (C:N), lignin (L), lignin: N ratio (L:N), temperature (T), and moisture (M). In CENTURY, we show representative residence times of different carbon pools in grassland soils

the soil is subdivided into three compartments (active, slow, and passive soil carbon pools) that are defined empirically by turnover rates observed in soils. The active pool represents microbial biomass and labile carbon in the soil with a turnover time of days to years. The slow pool consists of more recalcitrant materials with a turnover time of years to decades. The passive pool is humified carbon that is stabilized on mineral surfaces with a turnover time of hundreds to thousands of years. The detailed representation of soil pools in CENTURY enables it to estimate changes in decomposition under situations where a change in disturbance regime or climate alters the decomposition of some soil pools more than others. A change in climate, for example, primarily affects the active and slow

pools, with the passive pool remaining protected by clay minerals, whereas tillage enhances the decomposition of all soil pools.

How do we know whether the patterns of NEP estimated by global-scale models are realistic? A comparison of model results with field data for the few locations where NEP has been measured provides one reality check. At these sites, measurements of NEP over several years spanning a range of weather conditions provides a measure of how that ecosystem responds to variation in climate. This allows a test of the model's ability to capture the effects of ecosystem structure and climate on NEP.

The seasonal and interannual patterns of atmospheric CO₂ provide a second reality check for global models of NEP. Atmospheric transport

(continued)

Box 13.1 (continued)

models describe the patterns of redistribution of water, energy, and CO₂ through Earth's atmosphere. These transport models can be run in inverse mode to estimate the spatial and temporal patterns of CO₂ uptake and release from the land and ocean that are required to produce the observed patterns of CO₂ concentration in the atmosphere (Fung et al. 1987, Tans et al. 1990). The global patterns of CO₂ sources and

sinks estimated from the atmospheric transport models can then be compared with the patterns estimated from ecosystem models. Any large discrepancy between these two modeling approaches provides hints about processes or locations where either the ecosystem or the atmospheric transport models have not adequately captured the important controls over carbon exchange and transport.

Summary

Spatial heterogeneity within and among ecosystems is critical to the functioning of individual ecosystems and entire regions. Landscapes are mosaics of patches that differ in ecologically important properties. Some patches, for example, are biogeochemical hot spots that are much more important than their area would suggest. The size, shape, connectivity, and configuration of patches on a landscape influence their interactions. Large patches, for example, may have a smaller proportion of edge habitat. The shape and connectivity of patches influences their effective size and heterogeneity in ways that differ among organisms and processes. The distribution of patches on a landscape is important because it determines the nature of transfers of materials and disturbance among adjacent patches. The boundaries between patches have unique properties that are important to edge specialists. Boundaries also have physical and biotic properties that differ from the centers of patches, so differences among patches in edge-to-area ratios, due to patch size and shape, influence the average rates of processes in a patch.

State factors, such as topography and parent material, govern the underlying matrix of spatial variability in landscapes. This physically determined pattern of variability is modified by biotic processes and legacies in situations where species strongly affect their environment. These landscape patterns and processes in turn influence disturbance regime, which further modifies the

landscape pattern. Humans are exerting increasing impact on landscape patterns and change. Land-use decisions that convert one land-surface type to another (e.g., deforestation, reforestation, shifting agriculture) or that modify its functioning (e.g., cattle grazing on rangelands) influence both the sites where those activities occur and the functioning of neighboring ecosystems and the landscape as a whole. Human impacts on ecosystems are becoming both more *extensive* (i.e., impacting more area) and more *intensive* (i.e., having greater impact per unit area).

Ecosystems do not exist as isolated units on the landscape. They interact through the movement of water, air, materials, organisms, and disturbance from one patch to another. Topographically controlled movement of water and materials to downslope patches depends on the arrangement of patches on the landscape and the properties of those patches. Riparian areas, for example, are critical filters that reduce the transfer of nutrients and sediments from upland ecosystems to streams, lakes, estuaries, and the ocean. Aerial transport of nutrients, water, and heat strongly influences the nutrient inputs and climate of downwind ecosystems. These aerial transfers among ecosystems are now so large and pervasive as to have strong effects on the functioning of the entire biosphere. Animals transport nutrients and plants at a more local scale and influence patterns of colonization and ecosystem change. The spread of disturbance among patches influences both the temporal dynamics and the average properties of patches

on a landscape. The connectivity of ecosystems on the landscape is rarely incorporated into management and planning activities. The increasing human impacts on landscape interactions must be considered in any long-term planning for the sustainability of managed and natural ecosystems.

Review Questions

1. What is a landscape? What properties of patches determine their interactions in a landscape?
2. How do fragmentation and connectivity influence the functioning of a landscape?
3. Give examples of spatial heterogeneity in ecosystem structure at scales of 1 m, 10 m, 1 km, 100 km, and 1,000 km. How does spatial heterogeneity at each of these scales affect the way in which these ecosystems function? In other words, if heterogeneity at each scale disappeared, what would be the differences in the way in which these ecosystems function.
4. What are the major natural and anthropogenic sources of spatial heterogeneity in a landscape? How do these sources of heterogeneity influence the way in which these landscapes function? How do interactions among these sources of heterogeneity affect landscape dynamics?
5. What is the difference between a shifting steady-state mosaic and a non-steady-state mosaic? Give examples of each.
6. What is the difference between intensification and extensification? What has been the role of each in ecosystem and global processes?
7. Which ecosystem processes are most strongly affected by landscape pattern? Why?
8. What properties of boundaries influence the types of interactions that occur between patches within a landscape?
9. Describe how patches within a landscape interact through (1) the flow of water, (2)

transfers of materials through the atmosphere, (3) movement of animals, and (4) the movement of disturbance. What properties of landscapes and patches influence the relative importance of these mechanisms of patch interaction?

10. What issues must be considered in extrapolating processes measured at one scale to larger areas? How does the occurrence of hot spots influence approaches to spatial scaling?

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