CHAPTER 8

ECOSYSTEM PROCESSES IN HETEROGENEOUS LANDSCAPES

Understanding the patterns, causes, and consequences of spatial heterogeneity for ecosystem function remains a research frontier in both landscape and ecosystem ecology (Lovett et al. 2005; Chapin et al. 2012). The term, *ecosystem*, was introduced by Tansley (1935) to describe the characteristic and persistent interactions of organisms (plants, animals, and microbes) with their abiotic environment (e.g., water, temperature, radiation) within well-defined landscape boundaries (Likens 1995). Although ecosystems may appear to be discrete (e.g., ponds and watersheds), they do not exist in isolation. Interactions among ecosystems occur as a function of the heterogeneity of the landscape. *Ecosystem ecology* focuses on the flow of energy and matter between organisms and their environment, thus emphasizing pools (i.e., amounts or stocks), fluxes (i.e., rates), and the factors that control pools and fluxes. The spatial dimensions of ecosystem ecology may encompass bounded systems like watersheds, complex landscapes of diverse habitats, or even the biosphere itself; temporally, ecosystem science may cross scales ranging from seconds to millennia (Carpenter and Turner 1998). Ecosystem process rates vary across landscapes at multiple scales, and this variation can be difficult to quantify, explain, and predict. Transfers of matter and energy

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among patches (i.e., losses from donor ecosystems and subsidies to recipient ecosystems) are often important to long-term ecosystem sustainability (Polis and Hurd 1995; Naiman 1996; Carpenter et al. 1999; Chapin et al. 2012).

Ecosystem studies address questions about the capture of light energy by plants, its conversion into organic matter, and its transfer to other organisms; and questions about nutrient cycling, in which essential elements such as phosphorus and nitrogen cycle repeatedly between living and nonliving parts of ecosystems (Golley 1993; Carpenter 1998). From initial descriptions of the structure and function of diverse ecosystems, ecosystem ecology moved toward increasingly sophisticated analyses of function, including food web dynamics, biogeochemistry, regulation of productivity, and structure–function relationships (Golley 1993; Pace and Groffman 1998). Ecosystem ecology cannot be exhaustively reviewed here; interested readers are referred to Frank Golley's history of ecosystem research (1993) and two outstanding ecosystem ecology texts (Chapin et al. 2012; Weathers et al. 2013). From ecosystem studies, ecology has gained an excellent understanding of the mechanisms underlying many processes and how ecosystems develop and change through time. However, understanding patterns, causes, and consequences of spatial heterogeneity in ecosystem function remains a frontier.

When landscape ecologists study ecosystem processes, they often emphasize the causes and consequences of spatial heterogeneity in the rates of ecosystem processes (e.g., net primary productivity or nitrogen mineralization), and how landscape composition and configuration may influence the horizontal movement of materials such as water, nutrients, or sediments. The landscape also provides an ideal template for exploring linkages between organisms and ecosystem processes because the transfer of nutrients within and between ecosystems is often mediated by the actions of organisms (e.g., Jones and Lawton 1995; Seagle 2003; Holtgrieve et al. 2009). In spite of its importance, ecosystem function has received somewhat less attention in landscape ecology relative to other foci, such as disturbance dynamics and organism distributions, but a growing number of studies are now filling this gap.

Why has spatial heterogeneity in ecosystem function remained a research frontier? Determining the patterns, causes, and effects of ecosystem function across landscapes is conceptually young (Jenerette and Wu 2004; Lovett et al. 2005; Massol et al. 2011). In part, this is because of scale complexity; many rates are controlled by microbial dynamics that operate at extremely fine spatial and temporal scales and are difficult to measure (e.g., see discussion of nitrogen mineralization by Schimel and Bennett 2004). It is challenging to work across such a wide range of scales, and process studies are also technically demanding and expensive. Linking microbial mechanisms to landscape patterns of ecosystem processes is particularly difficult (Smithwick 2006). Further, landscape-level estimates of ecosystem function may require integration of multiple types of ecosystem, such as upland forests, wetlands, and lakes (e.g., Burcher et al. 2007; Buffam et al. 2011), which are often studied independently by scientists trained in different disciplines (e.g., freshwater or terrestrial ecology). Nonetheless, understanding ecosystem function in heterogeneous landscapes is important for many aspects of global change, and it offers the potential to enhance linkages between species and ecosystem dynamics for a more complete understanding of landscape function.

CONCEPTUAL FRAMEWORKS: ECOSYSTEM PROCESSES IN HETEROGENEOUS LANDSCAPES

Theoretical Development

Clearly, ecosystem processes are spatially heterogeneous. The basic causes of this variation have been well known for a long time (Jenny 1941); a primary factor driving heterogeneity is the abiotic template, which includes climate, topography, and substrate. In addition, ecosystem processes vary with the species assemblage, disturbance events (including their long-term legacies), and the activities of humans (Chapin et al. 1996; Amundson and Jenny 1997). As with other topics covered in this text, pattern–process interactions are reciprocal. Ecosystem processes affect landscape patterns, as when nutrient mineralization rates influence plant distributions, or patterns of net primary production influence the amount, quality, and location of suitable habitat for an animal population. Landscape patterns also affect ecosystem processes, as when the composition and configuration of land cover in a watershed influence nutrient loadings to wetlands, streams, and lakes, or when the landscape mosaic of habitats affects the redistribution of nutrients by mobile animals. Despite recognizing these reciprocal interactions, ecology has lacked a general theory of ecosystem function that is spatially explicit.

An early conceptual approach for considering interactions among different ecosystem types identified the importance of boundaries—their permeability and/or resistance to the flow of material and energy—on spatial fluxes within complex landscape (Wiens et al. 1985). *Boundaries* were defined as locations where the rates or magnitudes of ecosystem transfers (e.g., energy flow, nitrogen exchange) could change abruptly in relation to those within individual patches (Wiens et al. 1985). Fluxes of materials, energy, and organisms may be driven by resource gradients or by active vectors (e.g., wind, herbivores, etc.) that move materials or energy against existing gradients (Wiens et al. 1985). This seminal paper touched on many themes, including ecosystem–community interactions, which have received considerable subsequent theoretical attention.

The importance of integrating food webs and landscape ecology was recognized by Polis et al. (1997), who observed that subsidies of nutrients and detritus from one habitat to another could increase productivity. This forward-thinking review explicitly recognized the role of landscape variables and boundary features. Polis et al. (1997) noted, "the movement of nutrients, detritus, prey, and consumers among habitats is ubiquitous in diverse biomes and is often a central feature of population, consumer-resource, food web and community dynamics.... The message is clear: Ecosystems are closely bound to one another, be they stream and lake, pelagic and intertidal zones, farms and the sea, forest and river, or ocean and desert."

A conceptual framework based on metapopulation and metacommunity concepts was introduced by Loreau et al. (2003). The *meta-ecosystem* was defined as a set of ecosystems connected by spatial flows of energy, materials, and organisms across ecosystem boundaries. Loreau and colleagues were motivated by the need for a theoretical framework for a spatial ecology that would link community and ecosystem dynamics, and they distinguished a meta-ecosystem from a landscape in several ways. First, they considered that meta-ecosystems need not be continuous and occurring within the same physical, geographic space; in other words, the local ecosystems that comprised a meta-ecosystem could be discrete and distant from each other, as islands surrounded by a sea with which they have few interactions. Second, they argued that a landscape is a physical entity with a characteristic spatial scale, whereas meta-ecosystems can be defined at different scales depending on the organisms, ecosystems, and processes considered. However, landscapes may also be defined across a wide range of scales depending on the processes being considered (see Chap. 1), so this distinction seems artificial. Third, they asserted that a landscape can be studied from a variety of perspectives, including one that is purely descriptive and centered on pattern, whereas the meta-ecosystem concept focused on "the properties of the higher-level, spatially extended dynamic system that emerges from movements at landscape to global scales" (Loreau et al. 2003:675). Again, this distinction seems a bit artificial, although it recognizes that landscape ecology is a broader field. Loreau et al. (2003) then presented a simple meta-ecosystem model of source–sink dynamics among ecosystems, assuming a closed system; results demonstrated strong constraints on local ecosystems because of the spatial coupling among ecosystems. A subsequent body of work has extended these ideas into theoretical frameworks for spatial ecosystem ecology (e.g., Loreau and Holt 2004; Gravel et al. 2010; Massol et al. 2011; Leroux and Loreau 2012). This work is valuable for its ability to apply theory that is well developed in population ecology to material fluxes between ecosystems, although it remains somewhat disconnected from the landscape ecology literature and the large body of empirical work in ecosystem ecology.

A significant theoretical study of spatial linkages between nutrient dynamics and biotic communities was conducted by Jenerette and Wu (2004), who modeled plant–nitrogen interactions. They linked biogeochemistry and plant-community dynamics to assess these interactions on ecosystem function and to understand why nitrogen fixers may be unable to alleviate sustained nitrogen limitation in terrestrial ecosystems. The landscape was represented as a grid, and the spatial model included three layers of data for each grid cell: (1) vegetation type, which could be nitrogen fixers, nonfixers, or unvegetated; (2) nitrogen content, which summed the nitrogen concentration in vegetation and soils; and (3) net primary production, which was determined by the vegetation and nitrogen content. Results demonstrated that these interactions could generate self-organizing spatial patterns, and that the system could regulate productivity and nitrogen content independently of external nitrogen supplies. Importantly, the fine-scale dynamics (cell to cell) could be very different from behavior of the whole, spatially integrated system (Jenerette and Wu 2004).

Increasing recognition of the need to strengthen the conceptual foundation for ecosystem processes in landscapes led to the 10th biennial Cary Conference, organized in 2003 by ecosystem ecologists at the Institute for Ecosystem Studies (Lovett et al. 2005). The central question of this conference was, when do we need to deal with spatial heterogeneity as it affects ecosystem processes, and when can we safely ignore it? Strayer et al. (2003a) had presented a logical approach to answer this question for ecosystem modeling. However, the many different types of entity (e.g., mass, energy, information, organisms) that move simultaneously within and among ecosystems (Reiners and Driese 2001, 2004), and the many different ecosystems juxtaposed in different landscapes, continue to make it difficult to identify general principles.

A Practical Framework

Given these difficulties, it is not surprising the ecologists have approached ecosystem function across heterogeneous landscapes in two general ways (Turner and Chapin 2005) that differ conceptually and practically. One is focused on understanding landscape patterns of biomass and process rates, such as net primary production, decomposition, and nutrient cycling rates. Such studies aim to explain why rates are high in some places and low in others and to predict how these patterns might respond to changing drivers. A second approach emphasizes lateral (i.e., horizontal) fluxes of matter, recognizing that the composition and configuration of the landscape play key roles in mediating these fluxes. Land–water interactions are good examples of such lateral fluxes, and many landscape studies have asked how nutrients derived from land are transported to aquatic systems. Both approaches relate to ecosystem processes in heterogeneous landscapes, but they differ in their relative emphasis on vertical or horizontal fluxes, and practically, they differ in how they are studied.

Thus, two general classes of ecosystem process can be considered (Turner and Chapin 2005). *Point processes* represent rates measured at a particular location

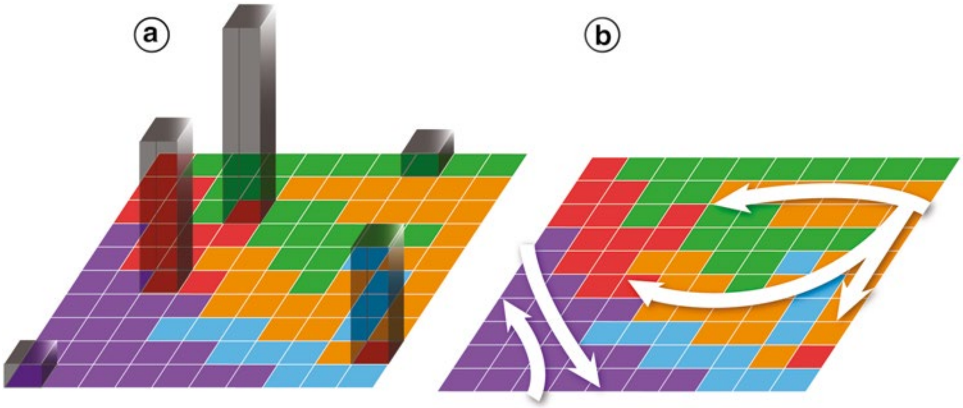


FIGURE 8.1.

Schematic illustration of two general classes of ecosystem processes (**a**) point processes and (**b**) lateral transfers.

ADAPTED FROM TURNER AND CHAPIN (2005).

(Fig. 8.1a), ignoring lateral transfers if they can be assumed to be small relative to the measured response. Examples of point processes include site-specific measurements of net primary production, net ecosystem production, denitrification, or nitrogen mineralization. *Lateral transfers* are flows of materials, energy, or information from one location to another represented in a two-dimensional space (Fig. 8.1b). Examples of lateral transfers include the flow of nitrogen or phosphorus from land to water, or the movements of nutrients across a landscape by herbivores.

Spatial heterogeneity can also be considered from the perspective of the *drivers* of ecosystem processes (biotic and abiotic forces external to the ecosystem) and/or for the ecosystem response variables (e.g., pools or fluxes of materials and energy) altered by changes in ecosystem drivers (Fig. 8.2). Drivers, which vary in space and time, may include soils, topography, climate, and disturbances, which act together to alter pools or fluxes of matter or energy. The combined effect of variation in drivers may be measured by spatial variation in *occurrence* of ecosystem processes, i.e., presence or absence of denitrification (Fig. 8.2a) or spatial variation in the *magnitude* of process rates, i.e., whether denitrification is high or low (Fig. 8.2b, columns). The term, *hot spot*, is often used to identify locations where the magnitude of a flux is especially high (McClain et al. 2003). For lateral transfers, one can also consider the actual pathways of flow (Fig. 8.2b, arrows), much as movement trajectories are tracked for an animal. For both point processes and lateral transfers, an aggregate measure of the function of the heterogeneous system (e.g., average net primary production across the landscape or the total amount of phosphorus delivered from a watershed to a lake) can be assessed. Because many different facets of spatial variation can be considered, it is important to be explicit about the ecosystem process as well as the driver or response for which spatial heterogeneity

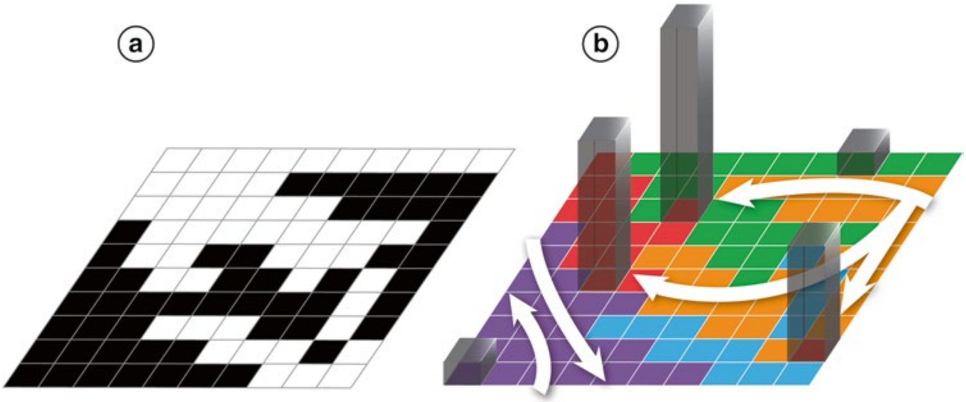


Figure 8.2.
Spatial heterogeneity can be considered in: (**a**) the occurrence of a process, (**b**) the magnitude of the rate or flux (columns), the actual flow paths (arrows) and the template, which is usually multivariate.
Adapted from Turner and Chapin (2005).

is being considered. Using this framework, we next consider a variety of point processes (those related to biomass, carbon cycling, landscape biogeochemistry, landscape limnology) and lateral fluxes (wind-driven transport, land–water interactions, mobile animals) in heterogeneous landscapes.

POINT PROCESSES (VERTICAL FLUXES)

Biomass, Net Primary Production, and Carbon

Early Approaches and Insights

Global and regional variation in *net primary production* (the rate at which organic matter, or carbon, is produced by plants; see Table 8.1 for key terms) on land and in water has long been appreciated by biologists (Leith and Whittaker 1975; Box 1978). Ecologists gained tremendous insights into patterns of biomass and net primary production (NPP) with the advent of remote imagery. Since the first Landsat satellite was launched in 1972, estimation of terrestrial plant production has been an important application of satellite remote sensing (Running 1990). Understanding and predicting such patterns became more urgent as scientists strived to understand the global carbon cycle; tried to quantify carbon sinks, sources, and fluxes; and began to grapple with predicting possible consequences of global warming.

New views of spatiotemporal patterns of vegetation and NPP that were produced in the 1980s by remote sensing scientists caught the attention of ecologists. For example, data from the Advanced Very High Resolution Radiometer (AVHRR)

TABLE 8.1.
TERMS USED IN STUDIES OF CARBON CYCLING AND THEIR DEFINITIONS (BASED ON CHAPIN ET AL. 2006 AND HICKE ET AL. 2012A).

Term	Sample units	Definition
Carbon stock or density	g C, g C m^{-2} or Mg C ha^{-1}	Reservoirs of carbon in vegetation and soil pools, including live and dead tree stems, foliage, roots, and soil organic matter
Carbon fluxes	g C m^{-2} year^{-1} or Mg C ha^{-1} year^{-1}	Rates of transfer among carbon pools, including those in the ecosystem and atmosphere
Gross primary production (GPP)	g C m^{-2} year^{-1}	Total amount of atmospheric C fixed by plants
Autotrophic respiration (R_a)	g C m^{-2} year^{-1}	Release of C to the atmosphere by plants
Net primary production (NPP)	g C m^{-2} year^{-1}	GPP – R_a; the net amount of C fixed by plants and available for subsequent use by heterotrophs. Sometimes distinguished by above- or below-ground (ANPP or BNPP, respectively)
Heterotrophic respiration (R_h)	g C m^{-2} year^{-1}	Release of C by microbes through decomposition of organic matter
Net ecosystem production (NEP)	g C m^{-2} year^{-1}	NPP – R_h; the net rate of C accumulated by the ecosystem or lost to the atmosphere. NEP is positive when an ecosystem is a carbon sink and negative when an ecosystem is a carbon source
Net ecosystem exchange (NEE)	g C m^{-2} year^{-1}	Exchange of C between the ecosystem and the atmosphere; NEE is positive when there is a net transfer of C to the atmosphere and may be the same magnitude (but opposite in sign) as NEP
Net biome production (NBP)	g C m^{-2} year^{-1}	Rate of flux of C to and from ecosystems; NBP includes NEP as well as losses of C through such processes as combustion and leaching (e.g., of dissolved inorganic or organic carbon)

CARBON STOCK OR DENSITY REPRESENTS AN AMOUNT; ALL OTHER TERMS BELOW ARE RATES AND THUS REQUIRE TIME.

satellite, which provided daily images of the earth at a resolution of 1.1 km, were used to generate vegetation maps for Africa (Tucker et al. 1985), North America (Goward et al. 1985), and the globe (Justice et al. 1985). These maps relied on the dimensionless *normalized difference vegetation index* (*NDVI*), a ratio of the difference between near-infrared (NIR, 0.725–1.1 m) and red (RED, 0.58–0.68 m) portions of the spectrum: NDVI = (NIR – RED)/(NIR + RED). The value of the NDVI is directly related to the presence of photosynthesizing vegetation, providing an indirect measure for mapping vegetation status and growth (Jensen 1996). NDVI has proven to be quite useful, as it relates well to *leaf area index* (*LAI*) (Sellers 1985, 1987) and, in turn, to NPP (Goward et al. 1987). LAI—the ratio of leaf area to ground area, usually reported as m^2/m^2—is a useful index for a variety of ecosystem processes, including the interception of light and water by the vegetation, attenuation of light through the canopy, transpiration, photosynthesis, and nitrogen content. Ecologists estimating ecosystem processes across landscapes routinely measure LAI, in part because it can be well estimated for large areas by satellite imagery (Running 1990).

Vegetation indices derived from satellite data offered new ways of exploring spatial variation in ecosystem structure and function at broad scales. For example, Riera et al. (1998) hypothesized that variability in vegetation cover and biomass should be related to topographic relief and to land use/land cover at the spatial extent of full Landsat Thematic Mapper (TM) images (~185 km swath). The *simple ratio vegetation index* (*SR*) [defined as the ratio between TM3 (the reflectance in band 3, 0.63–0.69 m, corresponding to the red portion of the spectrum), and TM4 (the reflectance in band 4, 0.76–0.90 m, the near-infrared) of the Landsat TM sensor] and the NDVI were compared across 13 study sites representing a wide range of biomes in North America. Marked differences in landscape heterogeneity were observed among the landscapes. Desert and grassland landscapes had low mean NDVI and low overall heterogeneity, whereas forested landscapes had high mean NDVI but also low overall heterogeneity. Spatial heterogeneity was greatest for those landscapes that had intermediate values of the vegetation indices (Riera et al. 1998).

Ecologists began combining remote imagery and other spatial data with ecosystem simulation models to predict spatiotemporal patterns of NPP in the late 1980s. Early advances were driven by the need to link global models, such as the general circulation models (GCMs) used to simulate the global climate, with changes in vegetation. Running et al. (1989) were among the first to integrate biophysical data obtained from many sources and use these data to execute an ecosystem model over a large landscape. They used a 28-×55-km coniferous forest landscape in western Montana, USA, and built a simple GIS in which climate and soil data were stored. The model required an LAI estimate for each grid cell, and this estimate was obtained from satellite imagery. In addition, the model required soil water-holding capacity for each grid cell and daily meteorological data. The ecosystem model FOREST-BGC (Running and Coughlan 1988) was then run in each of the 1200 grid cells representing the landscape to predict spatial patterns of annual evapotranspiration and net photosynthesis. The resulting estimates of LAI, evapotranspiration, and photosynthesis (Fig. 8.3) demonstrated the power of these new integrative methods for producing spatially explicit projections of variation in ecosystem processes and offered insights into interactions among the controls on these processes (Running et al. 1989).

Extensive empirical studies were also conducted during the 1980s and 1990s on regional patterns of primary production, the accumulation of soil organic matter, and

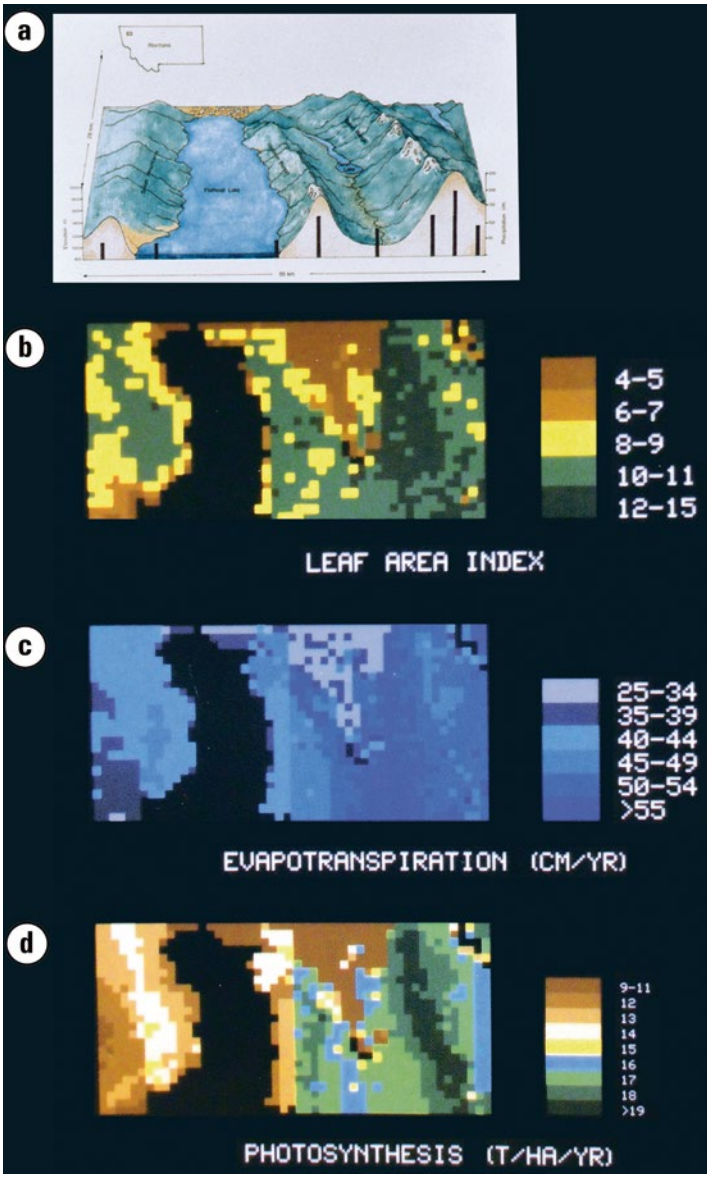


FIGURE 8.3.
(**a**) Schematic diagram showing prominent physiographic features of a 1540-km^2 study area in western Montana in which Running et al. (1989) combined satellite imagery, GIS, and an ecosystem simulation model to predict patterns of ecosystem processes. Maps of (**b**) leaf area index (LAI), (**c**) annual evapotranspiration, and (**d**) annual net photosynthesis for the 28 × 55 km study area using 1.1-km grid cells. LAI was estimated by satellite, microclimate data were extrapolated from a model, and ecosystem processes were simulated with the FOREST-BGC model. From Running et al. (1989) and reproduced with permission from the Ecological Society of America.

biogeochemical cycling; studies from the Great Plains region of North America nicely illustrate this approach. Using an extensive data set containing measurements of aboveground net primary production (ANPP) from 9500 sites throughout the Central Grassland region of the United States, Sala et al. (1988) evaluated (1) the spatial and temporal pattern of annual production for the region and (2) the importance of climatic variables as determinants of the pattern of ANPP when the site-level data were aggregated to major land resource areas. Results demonstrated that general trends in processes like net primary productivity and decomposition could be predicted reasonably well by broad-scale variability in temperature, precipitation, and soils (Sala et al. 1988). The analyses by Sala et al. (1988) confirmed the importance of water availability as a control on ANPP, with the regional spatial pattern of production reflecting the east–west gradient in annual precipitation. ANPP was lower in the drier western part of the region and higher in the more moist eastern areas, but the spatial pattern shifted eastward during dry years and westward during wet years (Fig. 8.4). The analyses revealed an interaction between precipitation and soil-water holding capacity. When annual precipitation was <370 mm, sandy soils with low soil-water holding capacity were predicted to be more productive than loamy soils with high water-holding capacity. The opposite pattern was predicted when precipitation was >370 mm. This occurs because bare-soil evaporation is lower in sandy soils than in loamy soils because water penetrates more deeply into the soil; runoff is also lower in the sandy soils. Sala et al. (1988) also observed from their empirical analysis that a model will need to include a larger number of variables to account for the spatial pattern of the same process as the scale of analysis becomes finer. The pattern of the process at the coarse scale constrained the pattern at the finer scale; thus, variability at the finer scale will be accounted for by factors at that scale plus the factors that determine the pattern at the coarse scale. Temporal relationships between precipitation and ANPP in arid regions also show promise for mapping changes in shrub canopy cover and other ecological state changes characterized by shifts in plant functional types and/or ANPP (Williamson et al. 2012).

Many landscape studies of biomass and productivity now integrate data from multiple sources, including forest inventories, intensive plot measurements, and remote sensing (e.g., Van Tuyl et al. 2005; Zhang et al. 2007), in an attempt to understand ANPP and carbon fluxes at regional scales. For example, landscape studies have become increasingly important for understanding how carbon storage and fluxes vary with climate warming. Using Landsat imagery and high-resolution repeat aerial photography, Fraser et al. (2014) found evidence that the "greening" of the western Canadian arctic between 1985 and 2011 was driven by increased temperature. This greening was driven by increased cover of erect dwarf and tall shrubs and decreased cover of lichens. A 4 °C increase in winter temperature over the past 30 years was associated with warmer soils and enhanced nutrient mineralization rates and explained this vegetation change. However, multiple drivers were important; local increases in shrub growth were also attributable to disturbances caused by wildfire, exploratory gas wells, and drained lakes (Fraser et al. 2014).

Spatially extensive field measurements of biomass or ANPP may be combined with statistical models to explain variability and extrapolate patterns to the landscape. For example, in the western portion of the Greater Yellowstone Ecosystem, aboveground net primary production (ANPP) was sampled in 90 forest stands stratified by forest type, stand age, and elevation class (Hansen et al. 2000). Forest type and elevation explained 89 % of the variation in ANPP. The landscape

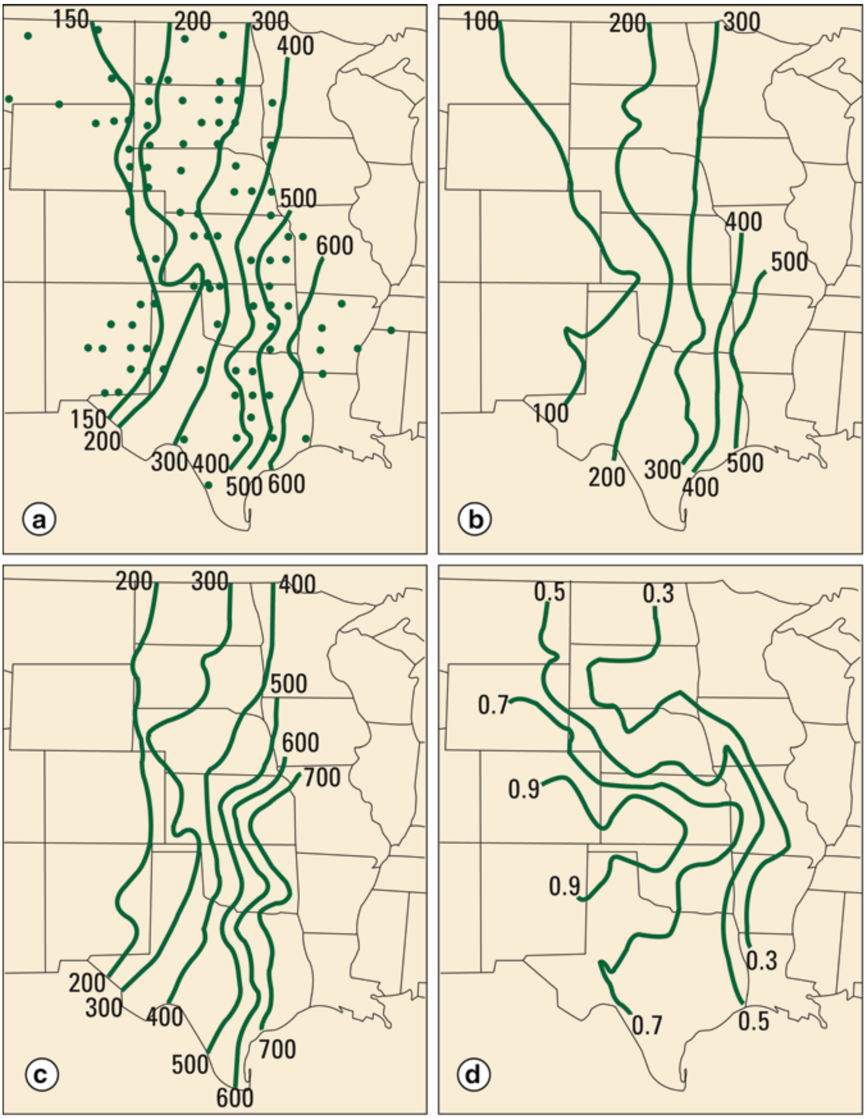


Figure 8.4.

Isopleths of aboveground net primary production (ANPP, g/m^2) for the Central Grassland region of the USA (**a**) during years of average precipitation, (**b**) during relatively dry years, (**c**) during relatively wet years. (**d**) Isopleths show the relative variability in production between favorable and unfavorable years, estimated as: (ANPP$_{wet}$ – ANPP$_{dry}$)/ANPP$_{average}$.

Adapted from Sala et al. (1988).

extrapolation revealed that most (72 %) of the landscape was relatively low in ANPP, but hotspots of ANPP (>4.5 Mg ha^{-1} year^{-1}) occupied about 6 % of the study landscape (Fig. 8.5a). In another study in Yellowstone, areas that burned in the 1988 Yellowstone Fires were sampled in 1999 to determine how ANPP varied

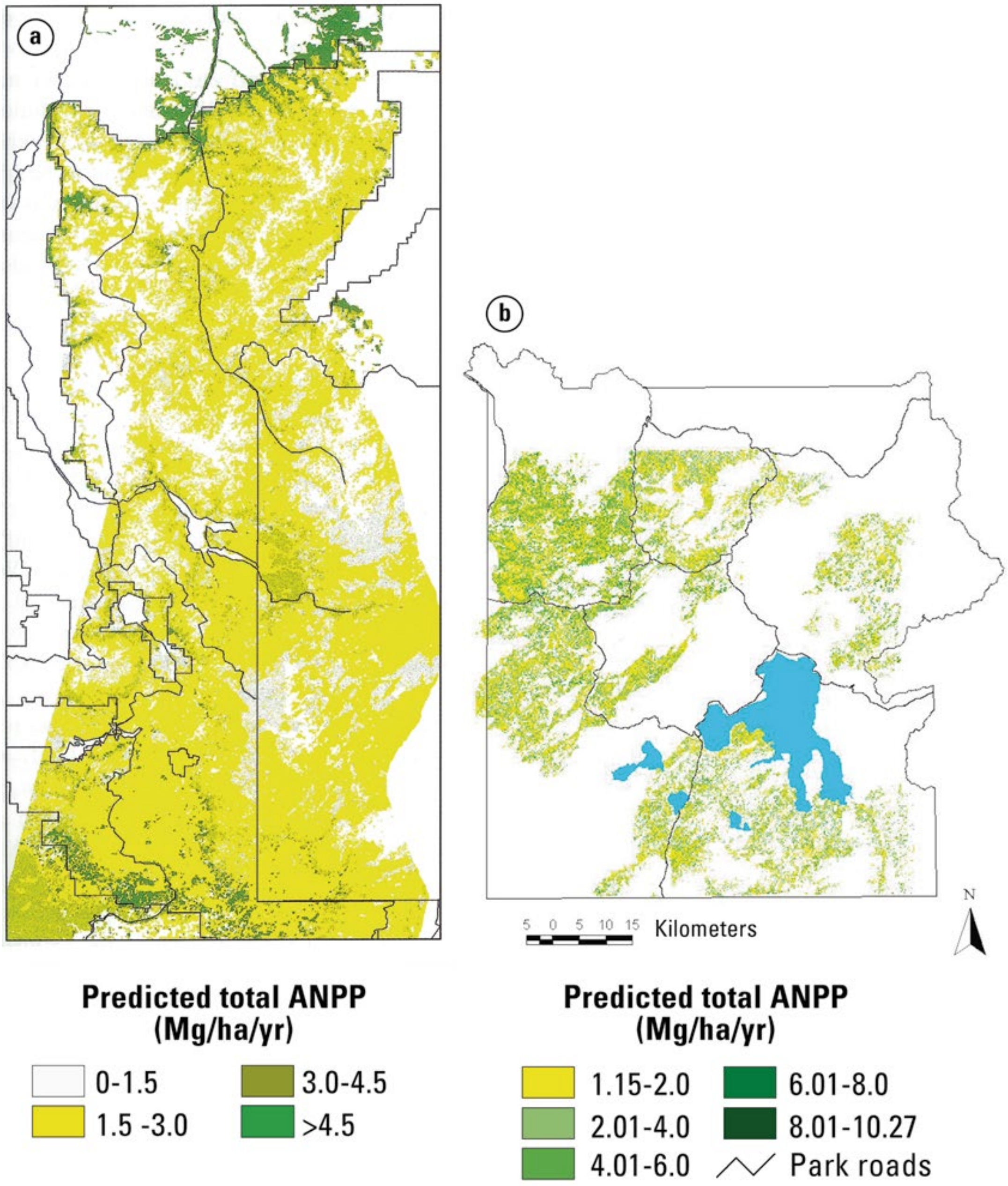


FIGURE 8.5.

Landscape maps of aboveground net primary production (ANPP) in (**a**) the western portion of Greater Yellowstone in forests of different type and age, and (**b**) in young postfire forested areas of Yellowstone National Park that burned in the 1988 Yellowstone Fires.

ADAPTED FROM HANSEN ET AL. (2000) AND TURNER ET AL. (2004B).

across the landscape in young postfire stands of the same age (Turner et al. 2004b). This study found a fine-grained mosaic of variability in ANPP in the 10-year-old forests (Fig. 8.5b); about 68 % of the burned landscape had relatively low ANPP (<2.0 Mg ha^{-1} year^{-1}), but areas of high ANPP (>4 Mg ha^{-1} year^{-1}) occupied 10 % of the burned landscape. The spatial variability in this essential ecosystem process rate was striking, given that these were young forests of the same age, and strongly related to landscape patterns of tree density, which was a legacy of the fire (see Chap. 6).

Landscape Heterogeneity and Regional Carbon Dynamics

Understanding the influence of landscape heterogeneity for regional estimates of carbon cycling is an important area of research. Studies of how primary productivity and carbon fluxes are responding to rapid recent warming in the Arctic provide a nice example of the need to understand landscape patterns of driving variables. Permafrost structures much of the boreal landscape and exerts strong control on carbon fluxes (e.g., Turetsky 2004). Future carbon stores in high-latitude ecosystems will depend on the mosaic of permafrost persistence and thaw across the landscape because processes like photosynthesis and respiration are enhanced by permafrost thaw (Belshe et al. 2012). To assist with upscaling of ecosystem process measurements in tundra, Lee et al. (2011) characterized the spatial heterogeneity of carbon fluxes created by permafrost thaw and *thermokarst* development (i.e., the irregular surface of marshy areas and small hummocks that forms as permafrost thaws). Using replicated sampling grids, they found relationships between carbon flux measurements (annual gross primary production, annual respiration, and annual net ecosystem exchange) and surface subsidence, soil thaw depth, and aboveground biomass, along with spatial structure in all variables. This information informed a model for predicting carbon exchange of the entire landscape and within particular patches (Belshe et al. 2012). Such studies also highlight the danger of quantifying regional carbon fluxes in heterogeneous landscapes from single flux-tower sites because vegetation and topoedaphic conditions may drive variability in fluxes (Emanuel et al. 2011; Sturtevant and Oechel 2013). Even in urban settings, carbon fluxes depend on the surrounding land-use matrix (Groffman et al. 2006a). Carbon fluxes can and do vary with landscape context; incorporating landscape variability into regional estimates of biomass, productivity, and carbon flux remains an important research challenge.

As drivers of landscape pattern and change, disturbance and recovery are fundamentally linked to regional carbon balance and must be considered in regional carbon studies (Bradford et al. 2008; Kurz et al. 2008; Flannigan et al. 2009). Disturbances release carbon stored in biomass to the atmosphere, either quickly, as with combustion during a fire, or over decades, as trees killed by insects, disease, or drought decompose. Forests again become carbon sinks as the vegetation recovers from disturbance, and net losses and gains of carbon over a region may balance over long time periods. For example, much of the carbon lost during fire is regained once a stand has recovered (e.g., Kashian et al. 2006; Campbell et al. 2012), with little net effect on atmospheric carbon over the fire cycle. In subalpine conifer forests of western North America, carbon is usually recovered in about 100 years (Bradford et al. 2008; Smithwick et al. 2009). Moreover, significant amounts of stable carbon (e.g., charcoal) remain in the ecosystem following fire and can persist for centuries, suggesting that wildland fires could be a significant long-term sink for some carbon that would otherwise cycle back to the atmosphere (DeLuca and Aplet 2008). Soil charcoal plays other roles, as well, such as stimulating nitrification, which can enhance growth of vegetation following fire (DeLuca et al. 2006). Because fire regimes are changing in many places, understanding effects of increased fire frequency, size, and severity on net carbon storage is of importance. If fires reoccur before carbon stocks have recovered, a forest that used to store carbon over the long term may switch from a sink to a source (Kashian et al. 2006; Smithwick et al. 2009). For example, a short-interval fire in Alaska eliminated the accumulated dead wood biomass in a black spruce forest and substantially reduced forest carbon storage (Brown and Johnstone 2011). Understanding how future fire regimes may affect landscape carbon dynamics is an important research priority.

Biotic disturbances like forest pathogens and insect outbreaks also affect carbon cycling, and Hicke et al. (2012a) provide an excellent review of disease-induced changes in carbon stocks and fluxes. Forest primary productivity is reduced immediately following insect or pathogen attack, and repeated growth reductions can lead to tree mortality. However, in the years following the attack, primary productivity can increase rapidly because growth of surviving vegetation is enhanced (Hicke et al. 2012a). Across landscapes, there is great uncertainty about net effects on carbon cycling because consequences depend on the type of pest or pathogen, the severity of the outbreak or attack (such as the amount of tree mortality), time since disturbance, and spatial extent of the disturbed area. Progress in understanding how carbon stocks and fluxes vary over space and time and how they respond to disturbances is sorely needed.

Landscape ecologists also recognized that primary production changes with land-use change. For example, annual net primary production in the Georgia, USA, landscape increased from 2.5 to 6.4 Mg ha^{-1} between 1935 and 1982 (Turner 1987b). These changes were associated with widespread abandonment of croplands followed by natural succession to pine and increased urbanization in some areas. Low NPP through the 1960s reflected persistent effects of poor agricultural practices, which had caused fertility of the land to decline (Turner 1987b). The importance of spatial and temporal variation in NPP for regional and global patterns of carbon dynamics has also been recognized. Secondary forests in regions that experienced widespread cropland abandonment could serve as important terrestrial sinks for global carbon (Delcourt and Harris 1980), although ongoing land-use changes may counter this effect. Levy et al. (2004) simulated global carbon balance between 1770 and 1990 with and without land-use change. In the absence of land-use change, terrestrial carbon storage was predicted to increase by 145 Pg carbon. However, when land-use change was represented, the terrestrial system became a net source of 97 Pg carbon. Thus, land use shifted the terrestrial system from a sink to a source of carbon (Levy et al. 2004). Understanding how future climate and land use will interact to influence carbon balance is of high priority.

Estimates of regional carbon storage and fluxes should account for the entire mosaic of different ecosystem types within a region, but this is not always done. In regional studies, terrestrial ecologists often consider only the terrestrial ecosystems, aquatic ecologists focus on the surface waters, and wetlands may be few and ignored by both groups. However, these ecosystems process and store carbon differently, and the whole suite of systems must be considered to understand the function of intact landscapes. One study that integrated aquatic and terrestrial components to generate a complete regional carbon budget was done for the 6400 km^2 Northern Highlands Lake District of northern Wisconsin (Buffam et al. 2011). Estimates of carbon stocks and fluxes were obtained from field surveys, tower-based CO_2 flux measurements, modeling, and published literature. Results found that landscape C storage was dominated by peat-containing wetlands and lake sediments, which covered only 20 % and 13 % of the landscape, respectively, but stored >80 % of the total carbon on the landscape. The largest regional carbon flux, however, was an accumulation of carbon into aggrading forests that were still recovering from nineteenth and twentieth century harvest, but C fluxes into wetlands and from surface waters were still of consequence (Buffam et al. 2011). Carbon pools and fluxes were spatially heterogeneous but showed strikingly different landscape patterns, as locations of greatest C density are not necessarily the locations where annual fluxes are greatest (Fig. 8.6), underscoring the need to consider both stocks and flux rates when studying landscape C cycling.

The potential role of landscape configuration in regional carbon studies is intriguing. Productivity and carbon fluxes are often predicted at points (or grid cells) because the vertical flux is usually dominant. However, several studies have reported interesting effects when landscape pattern and patch characteristics are considered. It is commonly assumed that carbon dynamics can be measured or modeled within homogenous patches, then summed to predict over broader scales, but Smithwick et al. (2003) found that might not always be the case. Edge-induced variation in light levels, wind exposure, and tree mortality in fragmented forest landscapes lead to errors in the additive approach (Smithwick et al. 2003). Similarly, Robinson et al. (2009) used field data and Biome-BGC to demonstrate that within-patch and landscape heterogeneity, as well as habitat fragmentation, had a strong effect of forest carbon cycling and storage. Vitousek et al. (2009), using advances in remote sensing, found that fine-scale patterns of topography affected community structure and N concentration levels as a consequence of human disturbance and the recent

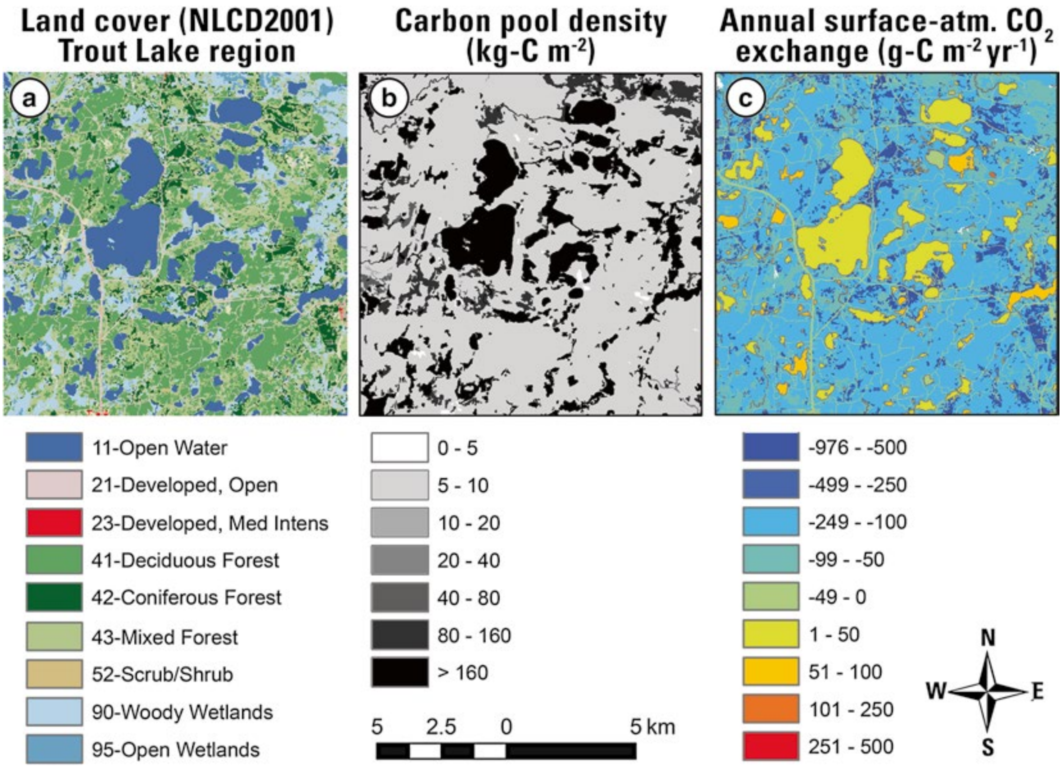


FIGURE 8.6.

Map of spatial variation in carbon pools and fluxes for an 18 × 18 km region of the Northern Highlands Lake District in northern Wisconsin, USA. (**a**) Land cover. (**b**) Pool sizes of carbon. (**c**) Average annual surface-atmosphere fluxes of carbon.

ADAPTED FROM BUFFAM ET AL. (2011).

introduction of invasive plants. Together these results show that point-specific studies can identify key ecosystem processes, but additional studies are required to understand the often-unexpected effects of landscape heterogeneity.

Landscape Biogeochemistry

Interest in obtaining broad-scale estimates of other biogeochemical process rates and their spatial variability increased with the emergence of landscape ecology, in part because of human intrusions into global nutrient cycles, which often make more of a given element available in a biologically active form (Mooney et al. 1987; Groffman et al. 1992; Vitousek et al. 1997b). Nitrogen (N) is a useful indicator of ecosystem function for several reasons. Nitrogen often limits primary productivity in temperate ecosystems (Vitousek and Howarth 1991; Reich et al. 1997), and the presence of nitrate in soil water and streamwater can be used as an indicator of disturbances that lead to N leaching (Bormann and Likens 1979; Vitousek and

Melillo 1979; Parsons et al. 1994). Nitrogen influences the quality of water and air, and anthropogenic modifications of the global N cycle have profound effects on the form and function of terrestrial and aquatic ecosystems (Vitousek et al. 1997b). The unprecedented production of industrially fixed N has resulted in massive global inputs of N that have resulted in N no longer limiting NPP in many ecosystems. As with carbon, N dynamics are affected by abiotic gradients and biotic interactions. For example, temperature and soil type explained a considerable amount of variation in both N mineralization rates and ANPP in cool temperate forests (Reich et al. 1997). *Nitrogen mineralization* (the production of ammonium by aerobic soil bacteria) and *nitrification* (conversion of ammonium to nitrate by aerobic soil bacteria) produce the inorganic forms of nitrogen available for plant uptake.

Spatially explicit studies of biogeochemistry were few in early landscape studies, but they quickly increased in number and began to provide insights into scale-dependent relationships between ecosystem pattern and process. For instance, Morris and Boerner (1998) quantified nitrogen mineralization and nitrification potentials in soils of hardwood forests in southern Ohio at three spatial scales: (1) the regional scale, represented by four study areas of 90–120 ha separated by 3–65 km; (2) the local scale, represented by three contiguous watersheds within each study area; and (3) the topographic scale, represented by different landscape positions within each watershed. Their results underscored the importance of understanding the patterns of variation manifested at different spatial scales. They observed no effect of spatial scale for nitrification potential in their study area, suggesting extrapolation from plot to region should be relatively easy. However, this was not the case for nitrogen mineralization potential or storage of organic carbon, which varied significantly with topographic position making this variable an important element of any extrapolation from plots to regions. Studies in other locations have confirmed the importance of topographic effects on soil nitrogen dynamics.

A regional study in southern Michigan, USA, used soil texture and natural drainage class to extrapolate rates of denitrification obtained from a landscape study (Groffman and Tiedje 1989) to an even larger area using a GIS (Groffman et al. 1992). *Denitrification* is the production of gaseous nitrogen from nitrate by soil bacteria in the absence of oxygen and is a critical process for reducing nitrate pollution in groundwater. Results from Groffman et al. (1992) revealed that spatial patterns of soil texture strongly influenced regional patterns of denitrification. Loam-textured soils occurred under 47 % of the forests in the region but accounted for 73 % of the denitrification. Sandy soils occurred under 44 % of the regional forest but produced only 5 % of the regional denitrification, and clay loam soils, which underlie 9 % of the regional forest, produced 22 % of the denitrification (Groffman et al. 1992).

Since these early studies, numerous researchers have attempted to quantify and explain spatial variability in pool size or cycling rates of different elements, and these studies span a wide range of spatial scales. Ecologists have made substantial progress in quantifying landscape patterns of process rates, but the spatial heterogeneity of the multiple factors responsible for such patterns is challenging to study and poorly understood (Turner and Chapin 2005). Nutrient pools and fluxes are influenced by multiple drivers that may differ in importance and/or interact across a wide range of scales (e.g., Reich and Oleksyn 2009). Landscape ecologists have assessed spatial dependence in nutrient pools and fluxes over a wide range of scales, from within single stands (e.g., Smithwick et al. 2005; Turner et al. 2011) to large regions (e.g., Vasquez et al. 2012).

In addition to local habitat and soil conditions, landscape configuration may influence some biogeochemical process rates. In an experimentally fragmented landscape in Kansas (USA), laboratory measurements of N-related fluxes in soils obtained from forest patches of different size revealed interesting differences attributed to patch size (Billings and Gaydess 2008). Rates of net N mineralization and gross nitrification were substantially greater in soils collected from small vs. large patches. The differences were associated with greater root biomass and root N concentration in the small patches compared to the large patches (Billings and Gaydess 2008). Results suggested that N cycling may differ in small vs. large patches, and furthermore, that gaseous losses of N from the ecosystem may relate to forest patch size (Billings and Gaydess 2008). Given the extent of habitat fragmentation worldwide, these intriguing results bear testing in other landscapes to determine how general patch size-related differences in nutrient cycling may be and to understand the causal pathways involved.

In landscapes that have a strong imprint of human activity, land-use legacies influence biomass, productivity, and nutrient pools and fluxes. Thus, landscape history matters when interpreting contemporary ecosystem process rates. In secondary forests that developed after agriculture was abandoned, soil organic matter can be substantially reduced. For example, soils in secondary forests of central New York (USA) had 15 % less organic matter and 16 % less carbon in the top 10 cm of soil than adjacent primary forest (Flinn and Marks 2007). Stand history also influences the mass, C, and N in downed coarse wood (Currie and Nadelhoffer 2002). Land-use effects are not only observed in forests. In an agricultural watershed in southern Wisconsin (USA), soil phosphorus concentrations varied with land use and showed spatial scale dependence (Bennett et al. 2005). Fertilizer applications and pasturing increased mean soil P and variance in soil P and shifted the spatial scale of variation to larger extents, and these alterations persisted through time (Bennett et al. 2005). As discussed in Chap. 2, historical agriculture can homogenize fine-scale variation in soils, thereby changing the spatial scale of variability in nutrient pools and fluxes.

Recent studies have demonstrated an important role of species interactions in structuring spatial patterns of soil nutrients and foliar nitrogen. Species interactions play out spatially on landscapes, creating opportunities to influence heterogeneity of process rates. For example, wolves can modulate landscape patterns of nutrients by configuring the distribution of ungulate carcasses (Bump et al. 2009a). Using a 50-year record that included >3600 moose carcasses from Isle Royale National Park, Michigan (USA), Bump et al. (2009a) found elevated soil nutrients, microbial biomass, and foliar nitrogen at kill sites for at least 2–3 years (Fig. 8.7). The locations of wolf-killed moose deposition varied in space and time with wolf hunting behavior, but the activities of this top predator structured the patterns of important ecosystem processes in the landscape (Bump et al. 2009a) and changed competitive dynamics between herbs and trees (Bump et al. 2009b). These and other studies of how trophic dynamics and carcasses can influence landscape patterns of ecosystem processes in soils and vegetation (e.g., Danell et al. 2002) are providing exciting new insights about ecosystem function in heterogeneous landscapes.

Identifying spatially and temporally explicit nutrient cycling rates remains challenging because the processes and the drivers vary so much in both space and time. Consider *denitrification*, a key process that removes excess nitrate from ecosystems, returning reactive nitrogen to the stable pool of nitrogen in the atmosphere. Denitrification is often highest in wetlands and inundated floodplains. However, denitrification is difficult to measure and model, in part because small areas (*hotspots*) and brief time periods (*hot moments*) can account for a high percentage of the denitrification activity that occurs in a landscape. The process is relatively well understood, but mapping and modeling spatial hotspots in the environment are difficult; it is challenging to predict the spatial pattern of drivers, such as nitrate availability and carbon substrate, along with the timing and location of the anoxic conditions required for the process. Many scientists and land managers are interested in predicting this microbial process at the landscape level because the effects of nitrate on soils, water quality, and air chemistry are substantial. Predicting rates and patterns of *methanogenesis* (anaerobic production of methane, a potent greenhouse gas) presents similar challenges. In addition, the technical training and high cost of labor and the laboratory analyses required to assess nutrient cycling in space and time can be prohibitive for many researchers.

With new sensors and rapid methodological advances, remote sensing data offer tremendous promise for scaling field measurements to the landscape and detecting evidence of nutrient limitation on net primary productivity over large areas. The biophysical and biochemical characteristics of canopy foliage are important indicators of forest ecosystem patterns and processes. Spectroscopy has long been used to develop linkages between narrow-band indices and leaf-level physiology for nondestructive measurements of foliar properties such as structure (e.g. leaf thickness), biochemistry (i.e., chlorophylls and accessory pigments, nitrogen), and water content (e.g., Carter 1998; Gao and Goetz 1994; Knapp and Carter 1998). Satellite-based spectrometers can now make many of these measurements remotely with high spectral resolution. Imaging spectroscopy (i.e., hyperspectral imagery) can be used to assess forest ecosystem function (Asner and Martin 2008) and to infer soil

FIGURE 8.7.
Illustration of how predator–prey dynamics in Yellowstone National Park, USA, are associated with spatial heterogeneity in ecosystem function. The hunting behavior of wolves influences the spatial and temporal distribution of carcasses on the landscape. *Top* and *center* photos show wolf-killed elk carcass sites in spring. Decomposing carcasses release nutrients that enhance tissue quality in grasses (*bottom*), which creates preferred grazing patches at carcass sites.

PHOTOS BY JOSEPH K. BUMP.

processes from canopy spectral reflectance (Martin and Aber 1997; Wessman et al. 1989, 1998; Ollinger et al. 2002; Ollinger and Smith 2005). For example, prediction of foliar nitrogen using hyperspectral imagery is now well established (Smith et al. 2003; Townsend et al. 2003). Continued advances in measurement technology in the future will likely open new avenues for understanding landscape patterns of nutrient stocks and fluxes.

Landscape Limnology

Spatial variability is also observed among the aquatic systems embedded in landscapes. Limnologists have long considered lakes as discrete units of study, owing in part to the natural boundary of the lake shoreline (Forbes 1887). Understanding the spatial patterns within individual lakes (e.g., patterns and processes in stratified lakes) occupied early limnologists (Forel 1892; Birge and Juday 1911; Soranno et al. 1999). Recognition of the interactions between lakes and their watershed and airshed lead to a broader view of lake ecosystems in which atmospheric inputs and catchment characteristics such as geology, land use/land cover, and topography were recognized as important influences on the chemical and trophic status of lakes (Likens 1985). Lake ecologists began to recognize spatial variation among lakes at landscape scales (Kratz et al. 1997), and the importance of the regional spatial scale for explaining variation among lakes (Cheruvelil et al. 2013). We focus here on aggregate measures of individual lakes and how lakes vary from one another, then consider land–water interactions in the next section in the chapter.

Landscape limnology refers to the spatially explicit study of lakes, streams, and wetlands and the effects of these spatial patterns on ecosystem processes across temporal and spatial scales (Soranno et al. 2010). The core principles of landscape ecology provide the foundation for landscape limnology, building on earlier arguments that landscape ecology can be usefully applied to aquatic ecosystems (e.g., Stanford 1998; Wiens 2002). Landscape limnology treats the freshwater landscape as embedded in a terrestrial and human mosaic and considers a variety of landscape ecological variables as they apply to freshwater ecosystems: (1) patch characteristics, (2) patch context, (3) patch connectivity and directionality, and (4) spatial scale and hierarchy (Soranno et al. 2010).

Some landscapes are dominated by presence of many lakes that cover a substantial proportion of the land surface (e.g., northern Sweden; northern Minnesota and Wisconsin in the US). The glacial processes that created these landscapes result in lakes that generally lie within the same geologic setting, experience the same weather, and, therefore, might be expected to be similar in their biological and chemical properties. However, lakes within such a *lake district* (regions of similar geomorphology and climate that contain many lakes) often show remarkable differences from one another, even though they are in close proximity. The many factors that can contribute to differences between lakes include lake size and depth, internal processes such as nutrient cycling and/or trophic dynamics, and the characteristics of the surrounding landscape.

A lake's *landscape position* can be measured by its hydrologic position in the regional flow system that connects adjacent lakes within a given landscape (Kratz et al. 1997) (Fig. 8.8). Many hydrologic properties of a given lake will be determined directly by landscape position. In northern Wisconsin, groundwater is an important component of the water balance of lakes; some lakes have no inflow of surface water. The amount of groundwater that enters a lake is directly influenced by the position of the lake in the landscape. Lakes higher in the flow system (which may differ in elevation by only a few meters in northern Wisconsin) have different relative sources of water than lakes lower in the flow system (Webster et al. 1996). Precipitation comprises a greater proportion of the water input to lakes higher in the landscape than to the lower lakes, which receive a greater proportion of their water input from groundwater. Groundwater typically has greater ionic strength than precipitation because of its contact with the soils and substrate; thus landscape position influences ionic concentrations in lakes (Fig. 8.9).

Soranno et al. (1999) analyzed long-term data from nine *lake chains* (lakes in a series, connected through surface or groundwater flow) from seven lake districts of diverse hydrogeomorphic setting in North America. The study asked: (1) are there predictable spatial patterns in chemical, algal, and water quality variables along lake chains, and (2) do lakes that are closer together in a chain behave more similarly through time? Results indicated that spatial and temporal patterns of lakes

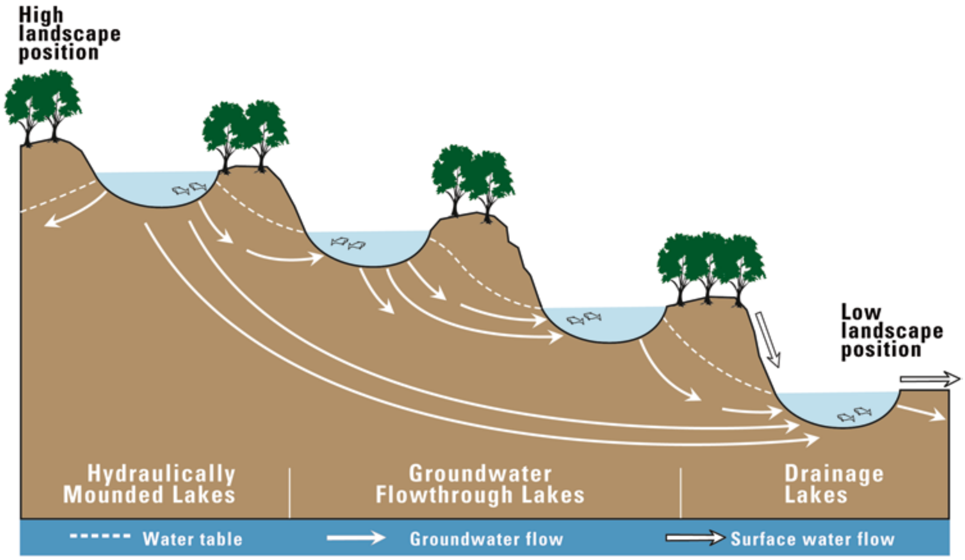


FIGURE 8.8.

Illustration of the concept of landscape position applied to lakes.

MODIFIED FROM WEBSTER ET AL. (1996).

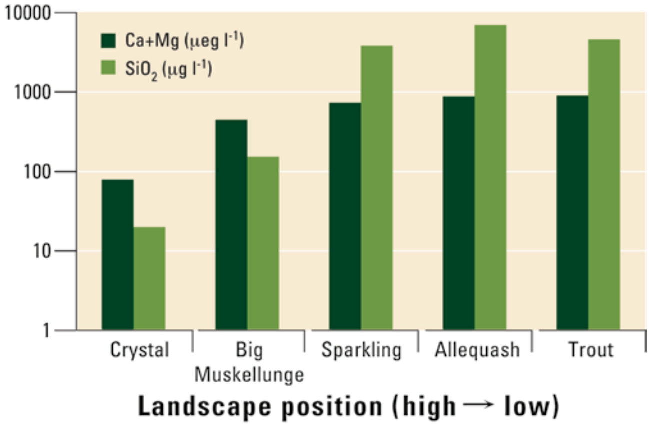


FIGURE 8.9.
The relationship between landscape position and the calcium plus magnesium and dissolved reactive silica concentrations in the five clearwater lakes of the North Temperate Long-term Ecological Research site in northern Wisconsin, USA. These five lakes lie within the same groundwater flow system. Crystal Lake is highest (i.e., headwater) and Trout Lake is lowest in the flow system.

ADAPTED FROM KRATZ ET AL. (1997).

within a lake district were organized along gradients of geology (depth of glacial till and spatial heterogeneity in soil characteristics), hydrology (water residence time and whether lakes were dominated by surface or groundwater flow), and some measure of landscape influence (e.g., ratio of watershed area to lake area). The spatial patterns along lake chains for a wide range of variables were surprisingly similar across lake districts. For example, weathering variables, alkalinity, conductivity, and calcium generally increased along lake chains, but these patterns were weaker in regions situated in calcium-rich tills or having high local heterogeneity in geologic substrate. Concentrations of particulate nutrients and measures of algal biomass increased along lake chains in drainage lakes, but not in the groundwater-dominated lakes. Regarding temporal patterns, landscape position was important in determining **synchrony** (a measure of the degree to which lake pairs within a lake district behave similarly through time [Magnuson et al. 1990]) between lake pairs only for variables related to weathering. For most variables, synchronous behavior in lakes within a lake chain was unrelated to lake spatial position.

Landscape processes that influence the amount of dissolved organic carbon (DOC) entering a lake can affect the magnitude and vertical distribution of primary production within the lake. Lakes with high concentrations of DOC tend to be tea colored, and the brown color reduces the clarity of the water and hence the light penetration. Colored DOC is derived mainly from the soils or wetlands rich in organic matter within the landscape surrounding a lake. Therefore, the position of the lake relative to sources of allochthonous (i.e., from external sources) DOC inputs can be a dominant factor determining net primary productivity within the lake (Kratz et al. 1997; Gergel et al. 1999). Interestingly, many existing lake data sets emphasize large lakes, which are often important for the human populations in a given region, but this may bias regional estimates of lake properties. In the Northern Highlands Lake District of northern Wisconsin, Hanson et al. (2007) selected a random sample of 168 lakes that spanned the full size distribution of lakes and measured a broad suite of limnological variables in each lake. The results demonstrated that most lakes were small (median lake area was 1.1 ha), although half of the surface area of water was in relatively few large lakes. Small lakes had high concentrations of DOC and lower concentrations of dissolved inorganic carbon compared to large lakes. Including small lakes in the lake survey resulted in a median DOC concentration that was about 50 % higher than it would have been without the smaller lakes (Hanson et al. 2007). Thus, all lakes need to be included in regional estimates of lake carbon; excluding small lakes will introduce bias.

Results from these studies suggest that a landscape perspective for lakes is informative and robust. This perspective argues that lakes are not isolated ecosystems but rather are embedded in a landscape matrix, with lakes interacting with one another and with the terrestrial environment. Soranno et al. (1999) argued further for an expansion of this view to encompass the set of lakes, streams, and wetlands that occur within a landscape; these aquatic systems are often treated separately (and as independent entities), yet they are often connected spatially and functionally. A landscape perspective fosters such integration, which is among the goals of landscape limnology (Soranno et al. 2010).

Studies of how lakes vary and change are also being aided by the increased availability of remotely sensed data. Indices derived from satellite data provide insights into patterns and trends in lake water clarity, which can be strongly related to lake trophic status. Landsat imagery has been used to map water clarity lakes in Wisconsin (Chipman et al. 2004), Minnesota (Olmanson et al. 2008), Maine (McCullough et al. 2012), and New Zealand (Hicks et al. 2013), although relatively few studies have yet explored the regional drivers of such patterns (Soranno et al. 2010). Understanding the drivers of interannual and among-lake variation in water clarity in lake-rich landscapes remains a key challenge in landscape limnology (Soranno et al. 2010).

LATERAL FLUXES (HORIZONTAL TRANSPORT)

Several common *vectors* (factors that facilitate transport of matter and energy across landscapes against existing gradients) often dominate ecosystem processes (see Reiners and Driese 2004 for in-depth discussion). For instance, wind (aeolian) and water (fluvial) effectively move organic matter, soils, and nutrients across many landscapes. Soluble nutrients are often moved by gravity-driven fluvial transport, and nutrients adsorbed to soils are translocated by erosion and colluvial transport. Animal locomotion is also important for moving matter and nutrients from one place to another. Within heterogeneous landscapes, nutrient pools and fluxes vary spatially, and landscape composition and configuration may affect lateral fluxes. Most examples of lateral transfers involve the transmission of matter (Reiners and Driese 2004). Here, we use three examples to illustrate these principles.

Redistribution of Litter and Organic Matter

Nutrient fluxes via litter redistribution can be extensive in some landscapes. For example, redistribution of leaf litter in a topographically and edaphically complex landscape on the Allegheny Plateau in Ohio was substantial, with some landscape positions (ridgetops and upper slopes) serving as a net source of litter, and others (side and lower slopes) serving as a net sink (Boerner and Kooser 1989). Litter movements from one cover type may even provide enough nutrients to subsidize productivity in another. Over a 3-year period in an agroforestry landscape in Guangdong Province, southeastern China, about 11 % of the litterfall in an *Acacia mangium* plantation was transported to a *Dimocarpus longan* orchard (Shen et al. 2011). The influx of windblown litter accounted for 9–59 % of the total nutrient inputs in the orchard, depending on the element. Thus, the transfer of nutrients could potentially enhance fruit production in the orchard.

Nutrient redistribution from croplands to remnant patches of natural vegetation in agricultural landscapes may lead to nutrient overenrichment in the remnants (Duncan et al. 2008). In areas of grain production in Australia, soils are nutrient poor and formerly supported semiarid woodland. Conversion to agricultural land uses was accompanied by crop fertilization and manure associated with sheep farming. Nutrients accumulated in remnant patches, but the effect varied with patch size and configuration. Small (<3 ha) patches of remnant vegetation were nutrient accumulation zones, as were the edges of large patches, especially on the windward sides of the patches (Duncan et al. 2008). Results were consistent with two different transport mechanisms. Enrichment in small remnants resulted from livestock sheltering, and enrichment in large remnants was due to wind and water movement of nutrients in soil and litter.

In lake ecosystems, airborne fluxes of nutrients represent additional important transfers of matter between ecosystems (Vander Zanden and Gratton 2011). Lakes occupy lower spots on the landscape and often receive gravity-driven inputs of matter, organisms, and nutrients. The influx of *terrestrial particulate organic carbon* (*TPOC*), such as windblown leaf litter, twigs, pollen, or insects derived from surrounding terrestrial ecosystems, can be important sources of organic matter that support lake metabolism. Many lakes are net heterotrophic systems, meaning that they require carbon inputs from outside the system (e.g., Hanson et al. 2003). The relative importance of such allochthonous inputs is greater for smaller lakes, which have higher perimeter:area ratios, than for larger lakes (Vander Zanden and Gratton 2011). Most leaf litterfall inputs occur within 10 m of the shoreline (France and Peters 1995), suggesting there will be strong effects of lake size and shape on litter inputs (Vander Zanden and Gratton 2011).

Long-range transport of soil, smoke, and dust particles from one ecosystem to another—sometimes from one continent to another—has long been recognized as a significant process capable also of transporting important nutrients around the globe (e. g., Perry et al. 1997; Prospero 1999). Dust plumes that originate in Africa are often visible in remote imagery and provide significant inputs to the landscapes of southeastern USA (Prospero 1999). Intercontinental transfers have been identified as important nutrient inputs to a variety of ecosystems.

Nutrient Loading to Aquatic Ecosystems

Land–water interactions are perhaps the best studied examples of lateral fluxes of nutrients across landscapes because problems associated with *eutrophication* (excess nutrients) are so widespread in aquatic ecosystems. A common theme underlying many studies of land–water interactions is the degree to which land uses in the uplands, and the spatial arrangement of these land uses, influence water quality (Strayer et al. 2003b). Freshwater and estuarine ecosystems act as integrators and centers of organization within the landscape, touching nearly all aspects of the natural environment and human culture (Naiman et al. 1995; Naiman 1996; Boynton et al. 1995; Correll et al. 1992). Noel Hynes, widely regarded as the father of modern stream ecology, stated, "We must not divorce the stream from its valley in our thoughts at any time. If we do, we lose touch with reality" (Hynes 1975). Land–water interactions are apparent even in relatively undisturbed landscapes. For example, studies along a toposequence of tundra, sedge, and shrub communities along a slope in Alaska revealed the importance of ecosystem adjacencies to nutrient transformation and movement (Shaver et al. 1991). The entire sequence of community types occurred along a few hundred meters, but large differences were observed in the rates of plant uptake, mineralization, and transport between ecosystems.

Improving understanding of the complex relationships between the land and water is an important goal of basic and applied research in landscape ecology. Freshwaters are degraded by increasing inputs of silt, nutrients, and pollutants from agriculture, forest harvest, and cities (Carpenter et al. 1995, 1998). Consider a watershed containing croplands or pastures. Farmers often apply fertilizers high in nitrogen and phosphorus (P) to their fields, but not all of the added N and P is taken up by the plants. When it rains, some of these nutrients are leached from the soil and transported through the watershed and into the stream by both surface and subsurface water flow. Like agricultural areas, cities and suburbs are important contributors to such "*nonpoint source*" *pollution*—that is, pollution that does not come from a single source, like a pipe, but rather is delivered from widespread areas of the landscape. Homeowners often apply as much fertilizer and pesticides per unit area to their lawns as farmers do to their crop fields, and a portion of these nutrients end up in nearby aquatic systems. Lakes and reservoirs fill more rapidly with mud from agricultural and urban land uses, and the growth of nuisance plants including toxic blue-green algae is promoted by the increased silt and nutrients. Regional changes in land use cause widespread eutrophication of many lakes on the landscape. Eutrophication also makes lakes more similar to one another, because the lakes are all dominated by species that can tolerate eutrophic conditions. Therefore, the diversity of lake types within a landscape is reduced as all lakes become eutrophic and converge to have similar species (Carpenter et al. 1995).

The nutrients most often considered in studies of land–water interactions are nitrogen and phosphorus. Economic and health concerns about excess nitrogen inputs into aquatic ecosystems are growing throughout the world (e.g., Cole et al. 1993; Mueller and Helsel 1996; Vitousek et al. 1997a, b). In rivers, nitrogen biogeochemistry is sensitive to land-use patterns, the structure of the riparian zone, and river flow regimes (Cirmo and McDonnell 1997). Coastal "*dead zones*," such as the extensive zone of hypoxia that develops each year in the Gulf of Mexico (Rabalais et al. 2002; Dodds 2006), result from excess inputs of nitrogen, mostly derived from anthropogenic activities in the watershed. Accumulation of excess phosphorus in lakes has long been recognized as a driver of eutrophication, and again, this is largely derived from human land use (e.g., Carpenter et al. 1998; Wagner et al. 2011).

Understanding the effects of land-use patterns on water quality and the spatial scales over which these effects are manifest has been an important goal of landscape ecological studies since the mid-1980s. For example, Osborne and Wiley (1988) analyzed the nitrogen and phosphorus concentration of streams in the Salt River Basin, Illinois, and used regression analysis to determine whether there was a relationship to land-use patterns mapped from aerial photos. Results demonstrated that the amount of urban land cover and its distance from the stream were the most important variables in predicting nutrient concentrations in the streamwater. Numerous studies have found significant relationships between land use and concentrations of nutrients in lakes and streams (Strayer et al. 2003b).

The impacts of human activities on sediment and nutrient budgets of watersheds are well documented (Carpenter et al. 1998). Historically, broad-scale forest clearing and conversion to agriculture or residential land use has led to increased erosion and transport of sediments and nutrients into estuaries and the lower portions of river systems. In the Chesapeake Bay basin (USA), such impacts have been documented for postsettlement times (1700s—present) both broadly for the entire Bay (e.g., Brush 1984, 1986, 1989, 1997) and specifically for selected tributaries (e.g., Jordan et al. 1997a, b). An extensive analysis of land-cover effects on stream ecosystems revealed that land cover was significantly correlated with numerous aquatic response variables, including annual nitrate flux (Strayer et al. 2003b). In a study of 210 lakes in Denmark, Nielsen et al. (2012) found that the proportion of agricultural land use in the entire watershed was best in explaining variation in lake water quality, suggesting that transport mechanisms within entire catchments are important for nutrient export to lakes. However, the spatial scale that is best for predicting ecological responses varies among response variables (Strayer et al. 2003b); predictive power declined in small watersheds, suggesting that the spatial arrangement of land-cover patches may be critical at these smaller scales.

Landscape patterns are also important for water quality in urban areas, as illustrated for Minneapolis-St. Paul by Detenbeck et al. (1993). In 33 lake watersheds in the Minneapolis-St. Paul area, landscape and vegetation patterns were obtained from aerial photographs and then compared with measured lake water quality. When lakes were embedded in a forest-dominated watershed, they were less eutrophic and had lower levels of chloride and lead. In contrast, lakes with substantial agriculture in their watersheds were more eutrophic; percent urban land use in the watershed was also positively correlated with lake phosphorus (Detenbeck et al. 1993). Wetlands were also important; when wetlands remained intact in the watersheds, less lead was present in the lake water. Along an urban to rural gradient in the Chesapeake Bay watershed, phosphorus exports were low in small, forest-dominated watersheds with low-density residential land use, and greatest in the lower watershed that was dominated by urban land use (Duan et al. 2012).

The increasing number of studies of land–water interactions that consider urban land uses also has led to a greater emphasis on the role of impervious surfaces. With increasing area devoted to roads, parking lots, and buildings, the ability of water to percolate through the soil is impeded. This decrease in perviousness of the catchment leads to a decrease in infiltration and an increase in surface runoff (Paul and Meyer 2001). As the percentage of impervious cover increases to 10–20 %, runoff doubles; with 35–50 % impervious cover, runoff triples (Paul and Meyer 2001). Understanding ecosystem processes in urban landscapes remains a topic of keen interest, as models developed in unmanaged or agricultural systems do not translate well to the urban setting (Kaye et al. 2006). Human influences such as impervious surfaces, engineered water-flow paths, landscaping choices, and irrigation all have important influences on urban biogeochemistry and land–water interactions (Kaye et al. 2006; Pickett et al. 2008).

Problems associated with nonpoint pollution have stimulated a variety of modeling studies designed to relate runoff and nutrient loading in aquatic systems to upland dynamics. In an early modeling study examining spatial variability in the loss, gain, and storage of total nitrogen, Kesner and Meentemeyer (1989) combined a simple mass-balance model with a GIS database to study N dynamics in an 11,490-ha agricultural watershed in southern Georgia, USA. Results demonstrated that it was possible to quantify and map source and sink regions of N in a watershed and that the riparian zone was critically important in buffering this watershed against excessive losses of N.

A simple model of phosphorus transformation and transport for the Lake Mendota watershed, Wisconsin, provided useful insights into the effects of land use on water quality (Soranno et al. 1996). The watershed of Lake Mendota is dominated by agricultural and urban land uses, and the lake itself has a long history of limnological study (Brock 1985; Kitchell 1992). Soranno et al. (1996) developed a GIS-based model of phosphorus loading in which phosphorus-export coefficients varied among land uses. Phosphorus is usually bound to sediments, and phosphorus delivery to the lake is attenuated by the terrestrial landscape. Soranno et al. (1996) accounted for this by weighting the contribution of phosphorus to the lake by a given grid cell by its distance from the lake. Because of the network of storm sewers serving the urban areas of Madison, Wisconsin and surrounding communities, urban areas were treated as though they were adjacent to streams. The model was then used to compare phosphorus loadings in Lake Mendota under current patterns of land use, presettlement land use, and projected future land use in which the urban area increased nearly twofold. Because rainfall events drive runoff, simulations were conducted for both high- and low-precipitation years. Results demonstrated that most of the watershed did not contribute phosphorus loading to the lake; most P came from a relatively small proportion of the watershed, ranging from 17 % of the watershed contributing during low-precipitation years to 50 % during high-precipitation years. A sixfold increase in phosphorus loading was estimated to have occurred since settlement. Results also demonstrated the importance of riparian vegetation in attenuating phosphorus runoff (Soranno et al. 1996). Ongoing research in this well-studied lake continues to yield new insights about how changes in land use and land cover influence lake hydrology, nutrient loading, and eutrophication (Carpenter et al. 2007).

Riparian corridors, including wetlands and floodplain forests, are conspicuous elements of many landscapes and important mediators of land–water interactions (Naiman and DeCamps 1997). Freshwaters are especially sensitive to changes in these adjacent lands. *Riparian buffers*—areas of relatively undisturbed vegetation along streams or adjacent to lakes—generally slow the transport of nutrients and sediments from upland agricultural–urban areas to adjacent aquatic ecosystems. Because riparian vegetation and associated microbial communities can take up large amounts of water, sediment, and nutrients from surface and groundwater draining agricultural areas within a catchment, they act as temporary storage areas that substantially reduce net discharges of nutrients into aquatic ecosystems. Disturbances to riparian zones can quickly release stored nutrients and sediments making the structure and dynamics of these landscape units an important component of management and restoration of streams in developed landscapes (Bernhardt and Palmer 2007; Craig et al. 2008; Kaushal et al. 2008).

Wetlands, floodplains, and riparian vegetation zones have been extensively altered by agricultural and urban development (Turner et al. 1998a) (Fig. 8.10).

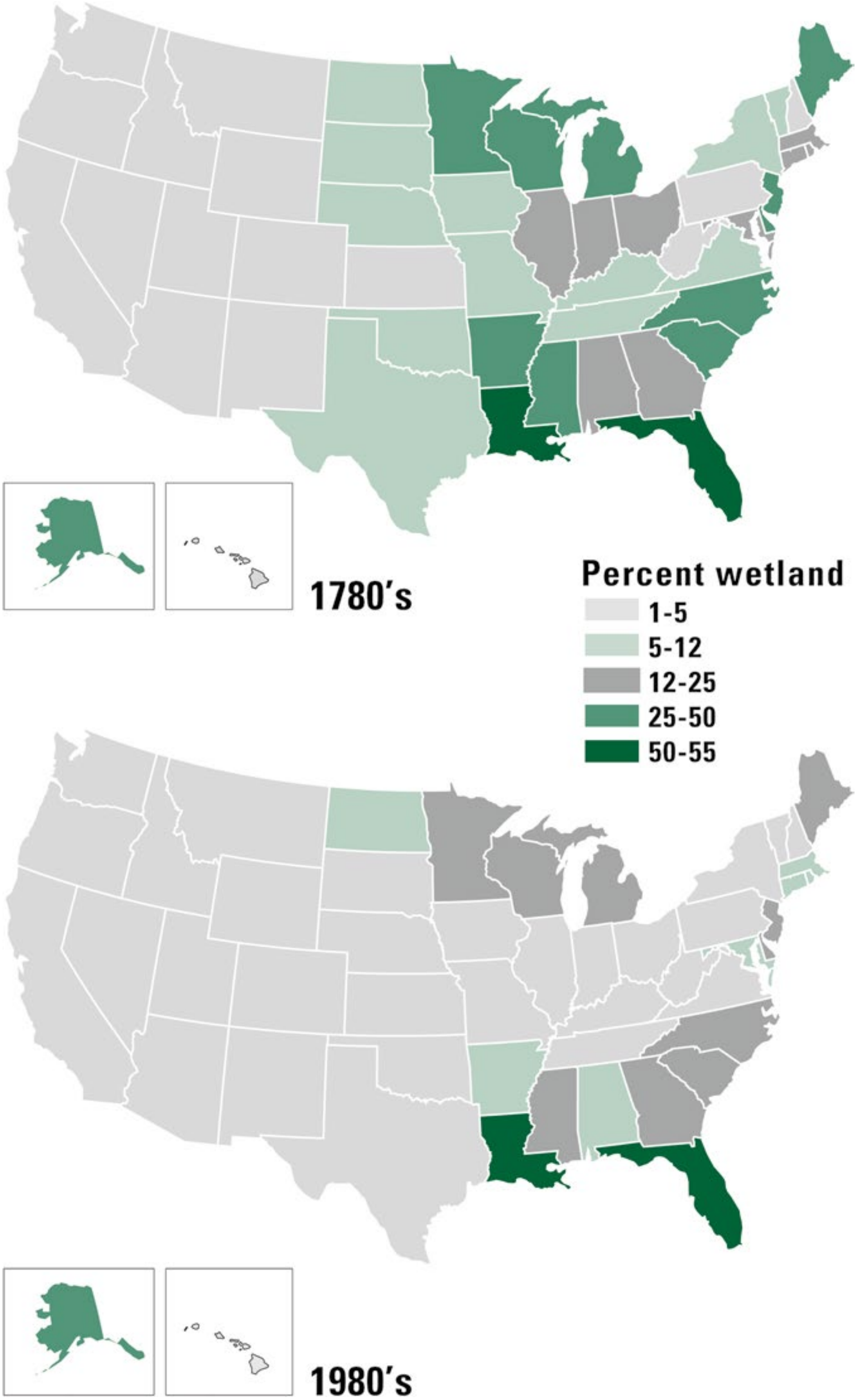


FIGURE 8.10.

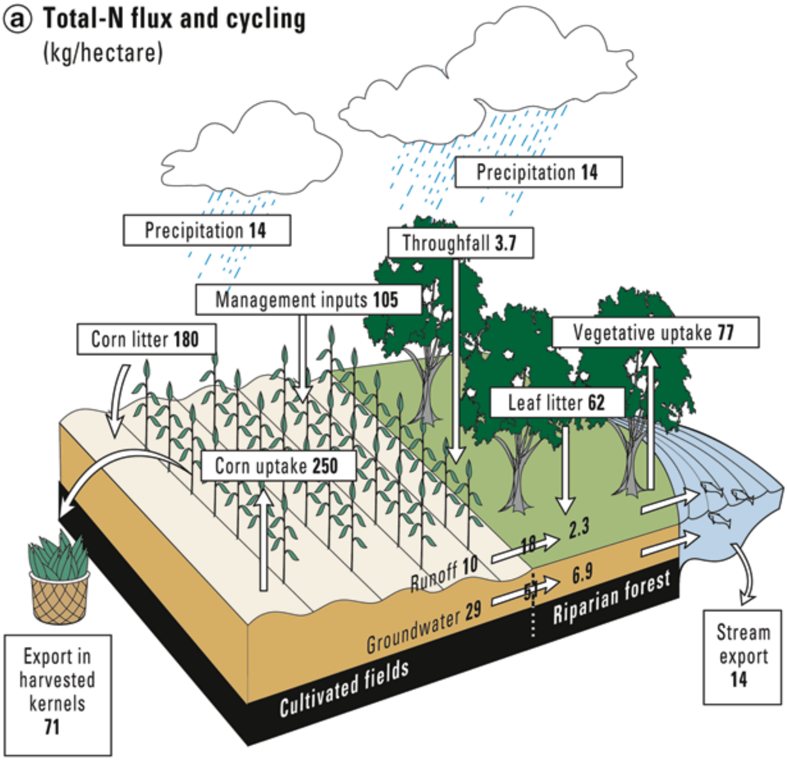
Wetland losses from the United States.

ADAPTED FROM TURNER ET AL. (1998A).

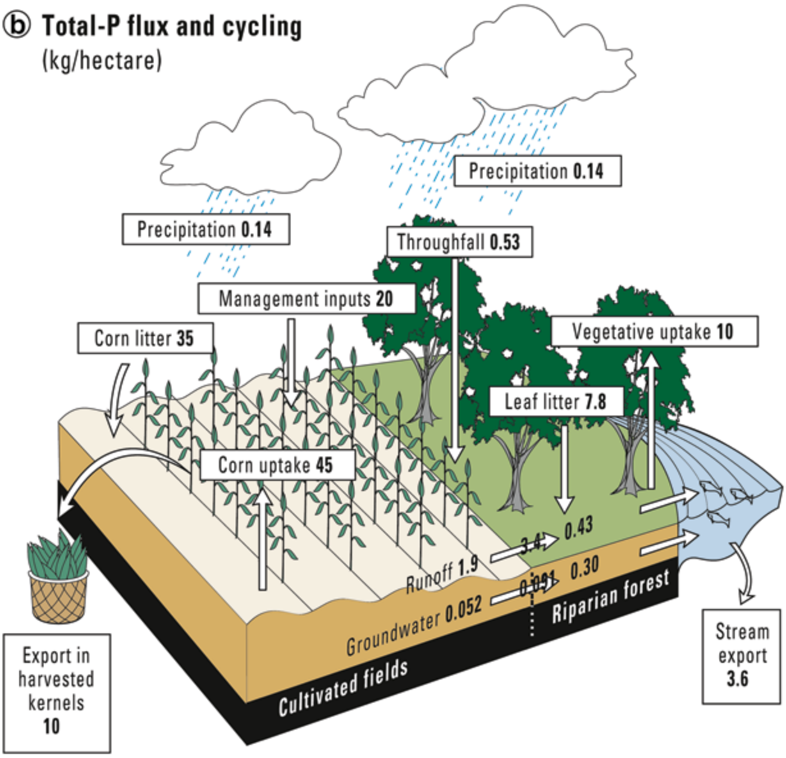
Woody riparian vegetation once covered an estimated 30–40 million ha in the contiguous United States (Swift 1974). At least two-thirds of that area has been converted to nonforest land uses, and only 10–14 million ha remained in the early 1970s. Floodplain clearing for agriculture, urbanization, and water resource development has been responsible for much of the loss of riparian forests. Since the 1970s, the total amount of forest and natural vegetation in riparian buffers has remained similar, declining by <1 % (Jones et al. 2010). A classic example of the loss of riparian forest has been described for the Willamette River, Oregon (Sedell and Froggatt 1984). Prior to 1850, the streamside forest extended up to 3 km on either side of a river characterized by multiple channels, sloughs, and backwaters. By 1967, government-sponsored programs for forest clearing, snag removal, and channelization (channel deepening and straightening) reduced the Willamette River to a single uniform channel that had lost over 80 % of its forest and land–water edge habitats. For an excellent review of the function of riparian zones, interested readers are referred to Naiman and DeCamps (1997).

In the mid-Atlantic region of the United States, studies of nutrient dynamics in mixed agricultural watersheds have nicely demonstrated the nutrient-removal function of riparian vegetation. Substantial quantities of particulate materials, organic nitrogen, ammonium-N, nitrate-N, and particulate phosphorus were removed in an agricultural watershed when waters flowing from a corn field passed across approximately 50 m of riparian forest (Peterjohn and Correll 1984) (Fig. 8.11). The effectiveness of vegetated riparian buffer strips (forest and grass) in retaining nutrients moving from adjacent agricultural lands was also examined by Osborne and Kovacic (1993). Results demonstrated that nitrogen runoff was reduced by 90 % for both forest and grassy riparian buffers, but that forest vegetation retained more nitrogen whereas grassy vegetation retained more phosphorus. This process of nutrient removal is ecologically important because it can substantially reduce cultural eutrophication. Thus, the presence and location of particular vegetation types can strongly affect the movements of materials across the landscape and help to regulate the quality of surface waters within the landscape.

The spatial pattern of riparian vegetation—i.e., variation in length, width, and gaps—influences its effectiveness as a nutrient sink. Weller et al. (1998) developed and analyzed models predicting landscape discharge based on material release by an uphill source area, the spatial distribution of riparian buffer along a stream, and retention of material within the buffer (Fig. 8.12). The buffer was modeled as a grid of cells, with each cell transmitting a fixed fraction of the material received. Variability in the riparian buffer width reduced total buffer retention and increased the width needed to meet a management goal (Weller et al. 1998). Variable-width buffers were less efficient than uniform-width buffers because transport through gaps dominated discharge, especially when buffers were narrow; average buffer width was the best predictor of landscape discharge for unretentive buffers, while the frequency of gaps was best for narrow, retentive buffers (Weller et al. 1998).



ⓐ Total-N flux and cycling (kg/hectare)



ⓑ Total-P flux and cycling (kg/hectare)

FIGURE 8.11.

Diagram of total-N flux and cycling (**a**) and total-P flux and cycling (**b**) in a study watershed from March 1981 to March 1982. All values are kg/ha of the respective habitats.

ADAPTED FROM PETERJOHN AND CORRELL (1984).

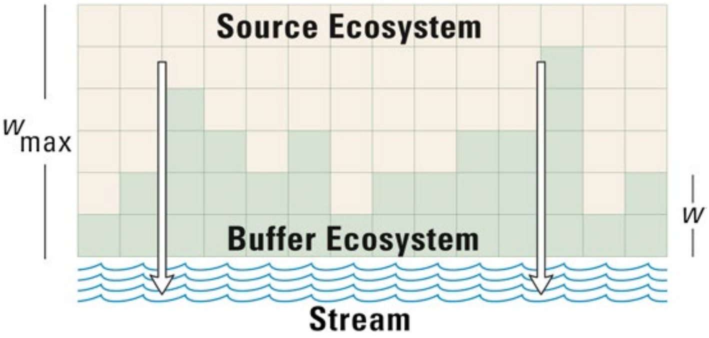


FIGURE 8.12.
Conceptual model of a landscape with a riparian buffer. The landscape is divided into a grid, and cells along the stream are occupied by the buffer ecosystem. Water and materials flow downhill from the source ecosystem, through the buffer, and to the stream. Weller et al. (1998) developed models in which the width (w) and length of the riparian buffer were varied, along with the width (w_{max}) of the entire simulated landscape, to evaluate the effectiveness of the buffer at retaining nutrients.

ADAPTED FROM WELLER ET AL. (1998).

This heuristic model offered predictions that were amenable for testing in a variety of riparian systems.

Riparian zones have a significant effect on water quality, but the spatial extent of that effect remains unclear (Fig. 8.13). That is, is it only the riparian zone that is important in maintaining water quality, or must adjacent land uses across the entire watershed be considered? Studies of such scale-dependent relationships between landscape characteristics and water chemistry have yielded mixed results. Johnson et al. (1997) found that total phosphorus in streamwater was better explained by land-use patterns within a 100-m buffer of a stream than by land use or other variables at the extent of the catchment. However, other studies have demonstrated that more distant upland land uses were as important as riparian land uses in larger watersheds (e.g., Omernik et al. 1981), or that whole-watershed predictors performed best (e.g., Nielsen et al. 2012). Responses may also differ between lotic and lentic systems. Gergel et al. (1999) found that landscape characteristics (especially proportion of wetlands) within 50-m of lakes in northern Wisconsin explained significant variability in concentrations of dissolved organic carbon (DOC); in contrast, measurements from the whole watershed always explained more variability for DOC in rivers than did measurements from the nearshore area. Within the Chesapeake Bay watershed, Weller et al. (2011) demonstrated that models that included riparian buffers better explained stream nitrate concentrations than models using only land-cover proportions. Among physiographic regions, the expected reduction in average stream nitrate concentration due to riparian buffers was greatest in the Coastal Plain (50 % of the inputs from cropland) and Piedmont

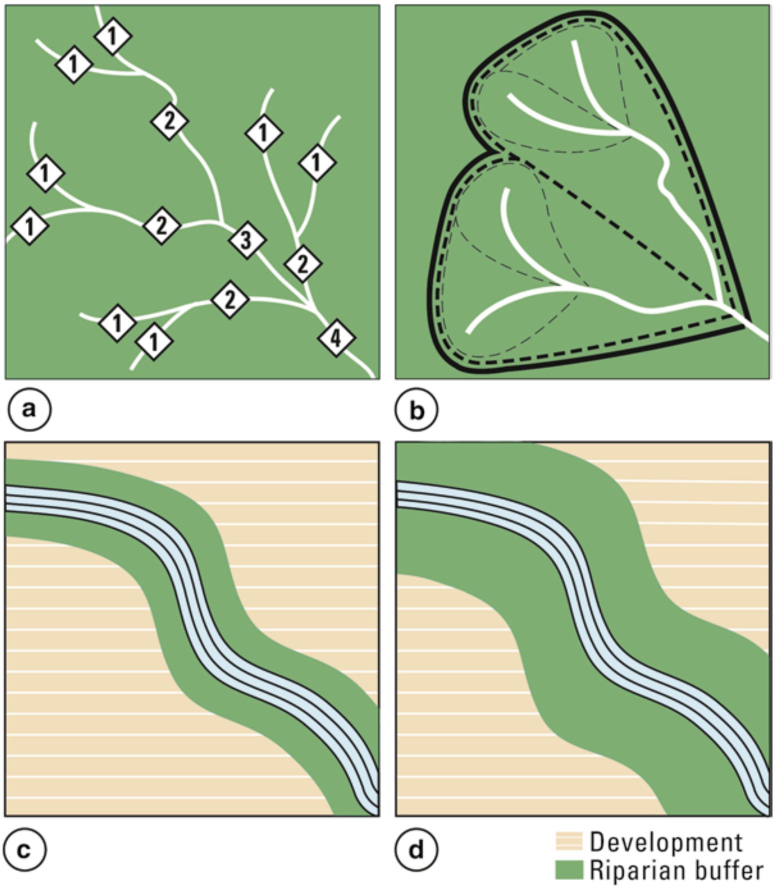


FIGURE 8.13.

Illustration of different spatial extents considered in studies of land–water interactions. (**a**) Hypothetical hierarchical drainage network with subwatersheds; numbers refer to stream order; (**b**) subwatersheds considered separately; (**c**) illustration of fixed-width buffer; and (**d**) larger fixed-width riparian buffer.

(11 %; Weller et al. 2011). In a tropical landscape in Puerto Rico, the spatial scale over which land use and land cover influenced indicators of stream water quality differed across indicators (Uriarte et al. 2011). Turbidity and dissolved oxygen respond to land use and land cover at the watershed scale, in-stream phosphorus concentration and fecal matter content responded at the subwatershed scale, and in-stream nitrogen concentration responded to riparian buffers (Uriarte et al. 2011). The variety of results from studies of watersheds and buffers in different regions underscores the need to better understand the interactions between land and water and the scales over which they are manifest.

The relative importance of spatial configuration (vs. composition) for estimating or managing nutrient loadings to lakes or streams remains unresolved. In general, configuration per se appears to be more important for explaining nutrient loading or concentrations in smaller watersheds than in larger watersheds, where effects of spatial arrangement seem to average out. A study using a grid-based surface-flow simulation model and thousands of simulated watersheds also suggested that the configuration of cover types would be most important in landscapes with intermediate relative abundances of nutrient sources or sinks (Gergel 2005). These simulations suggested an interesting set of hypotheses that relate to percolation thresholds (see Chap. 3) and could be tested empirically (Gergel 2005):

- *In watersheds with <30 % source area*: Increasing fertilizer application rates, increasing heterogeneity, or altering spatial configuration will only slightly alter variability in nutrient loading among different watersheds.
- *In watersheds with >65 % source area*: Spatial location has little impact on nutrient loading; fine-scale heterogeneity in nutrient outputs from source areas markedly affect total loading as the percentage of source area increases.
- *In watersheds with intermediate percentages of source area*: Landscape heterogeneity in sources is expected to influence loading most. Spatial configuration of sources and sinks will matter most, and source output relative to sink uptake will determine the range of source percentages for which this is true.

In sum, land–water interactions are important and complex landscape processes. Components of the landscape surrounding a lake, stream, or river strongly influence water quality. Landscape elements may serve as sources, sinks, or transformers for nutrient, sediment, and pollution loads. Land cover—such as agricultural or urban—is only part of the equation because the actual management practices used on a parcel of land can have very strong effects. Topography also influences the rate of delivery from landscape components to water bodies. When watersheds are steeply sloped and soils are highly erodible, the flux or export of nutrients and sediments to surface waters will increase. In both urban and agricultural landscapes, native vegetation can reduce nonpoint pollution and help maintain satisfactory quality of surface waters.

Mobile Animals and Species Interactions

To understand functional dynamics of entire landscapes, and especially lateral fluxes, interactions between species and ecosystem processes must be considered (Lundberg and Moberg 2003). Grazers can enhance mineral availability by increasing nutrient cycling in patches of their waste (McNaughton et al. 1988) and transport nutrients from one habitat to another (Augustine and Frank 2001; Seagle 2003). Landscape ecology offers a conceptual arena for integrating species and ecosystems that also can help unite the traditionally distinct subdisciplines of population and ecosystem ecology. In an introductory chapter in the book, *Linking Species and Ecosystems* (Jones and Lawton 1995), Grimm (1995) wrote:

> Interactions between population/community and ecosystem ecologists would be facilitated by adopting, *as a starting point*, a spatially based conception of units of study. … Whatever the scale of the investigation, a spatially based perspective places species interactions (the traditional focus of community ecology) into a context in which their effect on ecosystem processes may be assessed. Interactions between patches may be critical to larger-scale processes and include biotic interactions that occur within component subsystems.

Species and ecosystems are inherently linked, but studies in population ecology and ecosystem ecology often ignore this linkage. Landscape studies of lateral nutrient fluxes via animal movement or species interactions provide a clear mandate to bridge this divide.

A considerable body of work has identified animal-mediated movements of materials and nutrients from aquatic to terrestrial communities. Some of these involve large charismatic animals, but aquatic insects can also play important roles. The emergence of midges (Diptera: Chironomidae) and their deposition along the shorelines of Icelandic lakes offer an excellent example of lake-to-land linkages (Gratton et al. 2008). Annual midge input rates were as high as 1200–2500 kg midges ha^{-1} $year^{-1}$. As midges are about 9.2 % total N, the infall of midges was sufficient to fertilize the terrestrial vegetation along some lakes, although this effect declined with distance from the lakeshore. Further, many terrestrial consumers depended on midge-derived trophic pathways (Gratton et al. 2008; Dreyer et al. 2012). In general, insect deposition to terrestrial ecosystems shows a negative exponential decline with distance from shore (Gratton and Vander Zanden 2009), indicating a strong spatial dynamic to this interaction.

Large animals are also important nutrient transfers from water to land. Willson et al. (1998) described an expanded perspective on interactions between fish and wildlife in the Pacific coastal region of North America. Each year, millions of anadromous fish (e.g., salmon, char, and smelt) move from the ocean into numerous freshwater streams to spawn. These fishes provide an important seasonal resource base for a variety of terrestrial predators and scavengers, including bald eagles (*Haliaeetus leucocephalus* and brown and black bears (*Ursus arctos* and *Ursus americanus*, respectively). The anadramous fishes typically die after spawning, and the nutrient subsidies provided by their carcasses to the streams are well recognized. What was surprising, however, was the potential fertilization effects of salmon carcasses on the terrestrial ecosystems (Willson et al. 1998). The predators congregate and feed along the spawning streams in great numbers, then carry salmon, living or dead, onto stream banks and tens of meters into the forests (Fig. 8.14). Marine-derived nutrients, which can be identified by isotopic markers,

Figure 8.14.
Illustration of the movement of nutrients from a stream to fish, bears, and then deposited in the uplands and absorbed into the terrestrial biota.

pass from the bodies of the salmon into the soil and then into the riparian and upland vegetation, with the nutrients probably then moving up the terrestrial food chain. Willson et al. (1998) reported potential additions of P from bear-carried fishes of approximately 6.7 kg/ha, which is similar to the P application rate of commercial fertilizers for evergreens and trees! In southwestern Alaska, bears feeding on salmon increased soil ammonium concentration threefold and nitrous oxide fluxes by 32-fold (Holtgrieve et al. 2009). The consequences of this water-to-land fertilizer effect for terrestrial food webs could have substantial implications for the spatial patterns of ecosystem processes in these forested landscapes. Large mobile consumers can be very important in generating landscape heterogeneity in nutrient cycling.

In terrestrial landscapes, animals that feed in one place but excrete wastes in another location can be important vectors of nutrient transport. The movement of nutrients by large grazers has been recognized for some time, particularly in landscapes such as the Serengeti that harbor large numbers of native ungulates (McNaughton et al. 1988; Seagle and McNaughton 1992). Significant nutrient transfers from croplands to nearby forests by grazers have also been documented (Seagle 2003; Murray et al. 2013). The central-place foraging of birds and bats also results in high concentrations of guano in caves and nesting areas and caves (Stoker 1926; Bird et al. 2007).

Feeding activities of mobile animals can cascade through ecosystems to influence landscape patterns. A set of studies in the boreal forest landscape has demonstrated fascinating links among spatial patterns of plant species distributions and biomass, the foraging dynamics of moose (*Alces alces*), and rates of nutrient cycling (McInnes et al. 1992; Jeffries et al. 1994; Pastor et al. 1997). Studies on Isle Royale, an island located in Lake Superior and well known for long-term studies of moose and wolves, demonstrated how selective foraging by moose on hardwood species allows unbrowsed or lightly browsed conifers to dominate the boreal landscape (McInnes et al. 1992). Moose prefer to browse upon deciduous tree species such as birch (*Betula lutea*) and aspen (*Populus tremuloides*), as well as balsam fir (*Abies balsamea*), rather than on white spruce (*Picea glauca*). In areas of Isle Royale where fences (exclosures) were built to prevent moose from browsing, the deciduous trees have persisted and grown larger. However, outside the exclosures, where moose were allowed to browse, white spruce was the only tree species that could grow above the browsing height of a moose. Moose browsing on balsam fir and the deciduous trees prevented saplings of these preferred forage species from growing into full-sized trees. The browsing of moose also opened up the forest canopy and reduces tree biomass, allowing more light to reach the forest floor and stimulating more production of shrubs and herbaceous species.

Understanding the spatial heterogeneity of ecosystem processes in this boreal landscape requires forging a linkage between the feeding ecology and population dynamics of moose and the function of the ecosystem, all within the context of a landscape. By selectively foraging on specific plant species, moose and other large herbivores influence ecosystem dynamics—changing plant community composition, biomass, production, and nutrient cycling (McInnes et al. 1992). Soils in areas dominated by spruce received less litter, and the nutritional quality of the litter, especially its nitrogen content, declined for the decomposers. This decrease in litter quantity and quality leads to a decline in microbial processes that in turn determine nitrogen availability for the living plants. Conifer litter depresses the availability of soil nitrogen, which limits net primary production in boreal forests.

Moen et al. (1997, 1998) developed a simulation model to predict how alternative moose foraging strategies affect the net annual energy balance and density of moose, and the spatial distribution of browse across the landscape. Simulations were conducted at fine resolution (grid cells of 1 m^2 over an 8-ha landscape), and results have demonstrated how moose "create" their own landscape by their patterns of foraging and the feedbacks of those patterns on vegetation structure and composition. Because moose are highly mobile and can forage all around the landscape, interactions between moose and vegetation create a mosaic of nutrient cycling regimes in these boreal forests resulting in complex spatial and temporal patterns of browsing, conifer density, and soil nitrogen distribution across the landscape (Pastor et al. 1999).

Continued study of this system included a recent decline in the moose population and how that affected browse availability and consumption and soil fertility over an 18-year time frame (De Jager and Pastor 2009). When the moose population declined rapidly, patterns of available and consumed browse became decoupled, in contrast to earlier years. Soil nitrogen availability shifted from repeated to random patterns (De Jager and Pastor 2009).

In sum, species interactions produce strong and persistent patterns of nutrient cycling and accumulation in the landscape. Continued study of spatial interactions of plants and animals is both interesting and necessary if we are to understand ecosystem dynamics at landscape scales.

STATE OF THE SCIENCE: CHALLENGES AND OPPORTUNITIES

Empirical and modeling studies of spatial heterogeneity in ecosystem processes have demonstrated several important points. First, spatial variation in abiotic variables (temperature, precipitation, soils, and topographic position) often produces substantial spatial variation in ecosystem processes. This heterogeneity must be understood because the abiotic template is a powerful driver and constraint of ecosystem dynamics. Second, abiotic factors vary over multiple spatial scales, and ecologists are still striving to determine the scales that are appropriate for developing predictive relationships. Considering these factors hierarchically may enhance our understanding of how they vary. Third, understanding the implications of the dynamic landscape mosaic for ecosystem processes remains a frontier in ecosystem and landscape ecology.

Many empirical studies have taken a comparative approach using integrative measurements, such as nutrient concentrations in aquatic ecosystems, as indicators of how spatial heterogeneity influences the end result of lateral fluxes (Strayer et al. 2003b). Most of these studies focus on nutrients, such as nitrogen or phosphorus, related to surface water quality. Variation in topography, the amount of impervious surfaces (e.g., pavement), and the extent of agricultural and urban land uses have all been related to the concentration or loading of nutrients in waters. However, the particular aspects of spatial heterogeneity that are significant or the spatial scales over which that influence is most important have varied among studies (Gergel et al. 2002). The lack of consistency among the comparative studies may arise, in part, from the need to measure multiple variables changing in space and time and from our limited understanding about how materials actually flow laterally across heterogeneous landscapes.

Additional challenges remain. Scaling microbially regulated processes to entire landscapes remains especially difficult (e.g., Smithwick 2006). Understanding feedbacks from changing vegetation to water, carbon, nitrogen, and phosphorus cycles is an important research need in landscape and global ecology (Wassen et al. 2013). In similar vein, understanding interactions among different vectors remains limited; in semiarid African savannas, nitrogen and phosphorus delivery to riparian zones and the subsequent fate of those nutrients is affected not only by seasonality, hillslope hydrology, but also by fire, flooding, herbivory, and physical disturbance by animals (e.g., wallows; Jacobs et al. 2007). Understanding spatial interactions among interacting drivers and ecosystem elements remains limited.

A landscape perspective continues to offer the opportunity to better link populations and ecosystem processes and services (Lundberg and Moberg 2003); organisms exist in heterogeneous space and they use, transform, and transport matter and energy. Augustine and Frank (2001) demonstrated such an effect by grazers redistributing soil N at every spatial scale from individual plants to landscapes. Seagle (2003) hypothesized that the juxtaposition of land uses with different forage nutrient concentrations interacts nonlinearly with deer behavior to effect nutrient transport of sufficient magnitude to alter ecosystem nutrient budgets. Terrestrial predators, herbivores, and piscivores have all been shown to influence spatial patterns of nutrient pools and fluxes. Considering habitat use and movement patterns of species in a spatial context will continue to provide a wealth of opportunities for enhancing the linkage between species and ecosystems and enhance functional understanding of landscape mosaics.

What can be concluded about when space matters for ecosystem function? Strayer et al. (2003a) proposed a useful conceptualization of model complexity relative to inclusion of spatial and temporal heterogeneity. However, a general understanding of lateral fluxes in landscape mosaics has remained elusive, despite promising conceptual frameworks developed for particular systems (e.g., semiarid landscapes; Ludwig et al. 2000). Spatial heterogeneity is expected to be important for ecosystem processes under several conditions (Turner and Chapin 2005). For point processes, spatial heterogeneity must be considered when it is necessary to know the average rate of a process over an area that is spatially heterogeneous. This is of particular importance when there is a nonlinear relationship between the process and a driver that is spatially variable. Although this is largely a sampling issue—knowing how to stratify measurements spatially based on the important driver(s)—it is *not* trivial. Spatial heterogeneity also matters when one wants to understand or predict the spatial pattern of process rates. One may want to identify locations that are qualitatively different in their processing rates from other areas, or use the spatial pattern or spatial scale of variation as a response variable of direct interest. For lateral transfers, spatial pattern (composition and configuration) is a required predictor variable if the occurrence or rate of a lateral transfer responds directly to spatial heterogeneity. That is, the transfer of materials from one location or patch to another location or patch is modified by the spatial structure of the landscape. Spatial heterogeneity also matters if the spatial patterns themselves generate lateral transfers, as when differences in land cover alter local energy and water balances and influence weather. Finally, lateral transfers may produce, amplify, or moderate heterogeneity in patterns, as when the movement of nutrients from one place to another produces different species distributions or process rates.

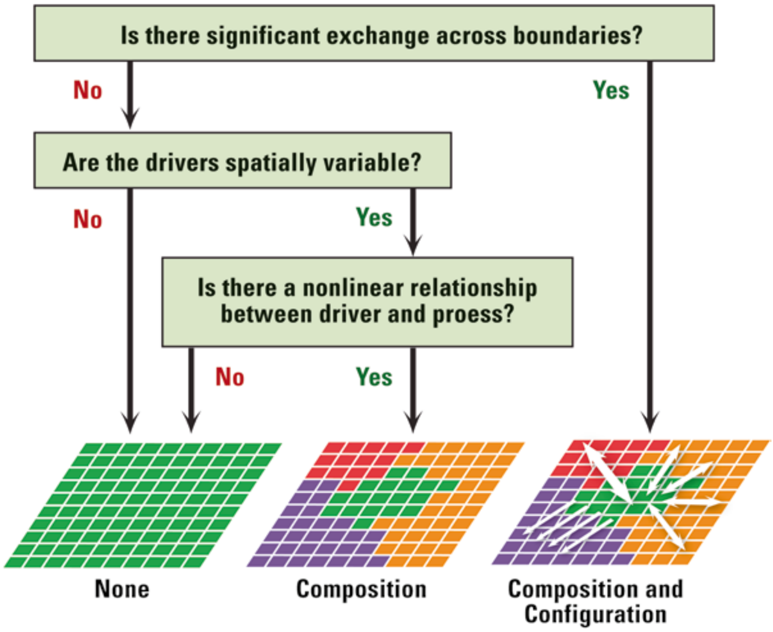


FIGURE 8.15.
Decision tree for deciding whether space should be included in studies of ecosystem function in heterogeneous landscapes that lead to three different general approaches to dealing with spatial heterogeneity: (*left*) assume spatial homogeneity, (*center*) consider composition only using a mosaic approach, which is often multivariate; and (*right*) consider composition, configuration and interacting elements.

ADAPTED FROM TURNER AND CHAPIN (2005) AND LOVETT ET AL. (2005).

A decision tree that emerged from the Cary Conference on ecosystem function in heterogeneous landscapes can provide a useful guideline for ecologists seeking to determine whether a spatially explicit approach is needed for studies of ecosystem dynamics (Fig. 8.15; Lovett et al. 2005). If there are no lateral fluxes, no spatially variable drivers, and no nonlinearities, then perhaps spatial heterogeneity can be safely ignored. If there are nonlinearities, then at a minimum, differences in landscape composition must be considered. And if lateral fluxes are important, both composition and configuration will be required (Fig. 8.15). Much still remains to be learned about ecosystem processes in heterogeneous landscapes. The successful integration of ecosystem ecology with landscape ecology promises a much more complete understanding of how landscapes function than has been developed to date.

SUMMARY

Determining the patterns, causes, and effects of ecosystem function across landscapes is a key topic in ecosystem and landscape ecology because transfers of nutrients and energy among patches are often important for ecosystem sustainability. When landscape ecologists study ecosystem processes, they typically emphasize the causes and consequences of spatial heterogeneity in determining rates of ecosystem processes (e.g., net primary productivity, nitrogen mineralization); the influence of landscape position on ecosystem function; and the horizontal movement of materials (such as water, nutrients, or sediments) across the landscape and how these movements might differ with alternative spatial arrangements of land cover.

The abiotic template is a powerful constraint on ecosystem function, but ecology has lacked a general theory of ecosystem function that is spatially explicit. From a landscape perspective, conceptual frameworks have been proposed that emphasize the importance of boundaries, including their permeability and resistance to flows; subsidies of nutrients and detritus from one habitat to another; extensions of metapopulation and metacommunity concepts to metaecosystems; and distinctions between explaining variation in process rates that are largely vertical fluxes vs. processes that are lateral transfers. In all studies, it is important to be explicit about the ecosystem process as well as the driver or response for which spatial heterogeneity is being considered.

For point processes (i.e., vertical fluxes), much research in landscape ecology has focused on patterns of biomass, net primary production, and carbon, as well as landscape patterns of nutrient biogeochemistry. Strong influences of natural disturbance and land-use/land-cover change on the spatial structure of many nutrient pools and fluxes have been identified. Biotic interactions are also important. Many studies integrate data from a multiple sources and often combine empirical study with modeling. Spatial variability is also observed among the aquatic systems embedded in landscapes, and landscape limnology refers to the spatially explicit study of lakes, streams, and wetlands and the effects of these spatial patterns on ecosystem processes across temporal and spatial scales. Landscape limnology treats the freshwater landscape as embedded in a terrestrial and human mosaic and considers a variety of landscape ecological variables as they apply to freshwater ecosystems: (1) patch characteristics, (2) patch context, (3) patch connectivity and directionality, and (4) spatial scale and hierarchy (Soranno et al. 2010). A landscape perspective also fosters a view of land–water interactions that encompasses sets of lakes, streams, and wetlands occurring together as a connected unit within a landscape.

For lateral fluxes (horizontal transport), research has emphasized aeolian fluxes, such as litter redistribution, land–water interactions, and nutrient transport by mobile animals. Land–water interactions are perhaps the best studied examples of lateral fluxes of nutrients across landscapes because problems associated with eutrophication are so widespread in aquatic ecosystems. Components of the landscape surrounding a lake, stream, or river directly determine water quality and availability—a critical concern as natural landscapes continue to be affected by agricultural and urban development. Elements of the landscape may serve as sources, sinks, or transformers for nutrient, sediment, and pollution loads. A common theme underlying many studies of land–water interactions is the degree to which land uses in the uplands, and the spatial arrangement of these land uses, affect water quality in streams and lakes. Riparian vegetation zones, including wetlands and floodplain forests, are conspicuous elements of many landscapes and important mediators of land–water interactions. The primary emphasis of studies of land–water interactions has been the movement of materials from the terrestrial components of the landscape influences the aquatic components. However, recent studies also have shown that movements of materials and nutrients from the water into terrestrial communities are also significant. These observations provide a strong imperative for ecologists to better understand the reciprocal interactions between land and water and the scales over which they are manifest.

Species and ecosystems are inherently linked, but studies in population ecology and ecosystem ecology often ignore this linkage. Landscape studies of lateral nutrient fluxes as a function of animal movement or species interactions effectively bridge this divide. In terrestrial landscapes, animals that feed in one place but excrete wastes in another location can be important vectors of nutrient transport. Species interactions produce strong and persistent patterns of nutrient cycling and accumulation in the landscape. Continued study of spatial interactions of plants and animals is both interesting and necessary if we are to understand ecosystem dynamics at landscape scales.

Understanding the implications of the dynamic landscape mosaic for ecosystem processes remains a frontier in ecosystem and landscape ecology. We do not have a well-developed theory of ecosystem function that is both spatially explicit and general enough to be widely applicable. However, the library of empirical studies has grown tremendously. New empirical studies are still needed to test hypotheses about nutrient pools, fluxes, and transfers among diverse landscape elements and for upscaling process rates. These challenging issues reinforce the importance of landscape ecology as a conceptual framework for understanding ecosystem function.

DISCUSSION QUESTIONS

1. A daunting challenge in studying spatial variation in ecosystem function and the factors that control the rates of ecosystem processes is balancing data needs (e.g., spatial extent of the study and the ideal number of measurements) with logistical difficulties

and actual cost (e.g., person-hours required for collecting and processing samples and the costs of running laboratory analyses). Consider an extensive landscape of your choice. Develop a field sampling design to describe the spatial variation of an ecosystem attribute or process rate (e.g., NPP, LAI, nitrogen mineralization, denitrification, phosphorus accumulation) of your choice. Then answer the questions below.

   (a) *Response variables*. What variables did you decide to measure, and what variables were excluded? How will the choice of variables affect the generality of your results (i.e., application to other landscapes and situations)?

   (b) *Sampling design*. Stratified sampling often reduces effort and cost. Did you use stratified sampling in your design? Why or why not? If yes, by what variables did you stratify, and why?

   (c) *Spatial autocorrelation*. Many landscape and ecosystem variables are correlated in space and time. Did you consider spatial autocorrelation in your design? How might autocorrelation among variables reduce costs and increase the generality of results?

   (d) *Cost*. Estimate the cost of implementing your design in terms of person-hours and laboratory costs (if any). Could costs be reduced by combining remotely sensed data with field measurements? Why or why not?

2. Describe how the processes associated with the release, uptake, and storage of carbon would change in the following scenarios over a period of 100 years (graphical representations may be helpful): (1) a temperate deciduous forest is affected by small-gap disturbances that affect 1 % of the landscape each year and initiate succession within the gaps; (2) a temperate deciduous forest is cleared for agriculture and farmed continuously for 50 years. Farming is then abandoned, and the land undergoes natural succession for the next 50 years; (3) a mature boreal forest landscape experiences wildfire that burns 60 % of the landscape and initiates forest succession. Ten years later, a second fire burns 50 % of the previously burned area and eliminates the newly established trees, resulting in the area of double-burn being dominated by herbaceous vegetation for the next 80 years.

3. Consider an agricultural watershed in which fertilizers are applied to upland crop fields. A management goal for this watershed is to maintain acceptable water quality while producing agricultural products. Under what conditions might a riparian buffer help to maintain water quality? Under what conditions would reduction in the nutrient source (e.g., fertilizers or manure) be needed to maintain water quality?

4. Ecosystem vectors can move materials rapidly and against a gradient. For instance, wind moves dust from Africa to the South of the USA—something that could hardly happen by diffusion alone. Can you develop a set of principles (or "rules of thumb") to determine for landscape-scale studies of different ecosystem processes when vectors of movement should be considered?

5. Chose an ecosystem function of interest (e.g., carbon loss or accumulation). How do you expect the statistical relationships between a measurement of this ecosystem function and the abiotic variables that control that function to change with spatial scale? Are the changes with scale linear? Why or why not? How does a nonlinear function determine our ability to measure and predict?

FURTHER READING

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