12 Temporal Dynamics

Ecosystem processes constantly adjust to temporal variation in environment over all time scales. This chapter describes the major patterns and controls over the temporal dynamics of ecosystems.

Introduction

Ecosystems are always changing in response to past **changes as well as responding to current environment** (Holling 1973, Wu and Loucks 1995, Turner 2010). In earlier chapters, we emphasized ecosystem responses to the *current* environment. *Past* changes that influence current dynamics include relatively predictable daily and seasonal variations, less predictable or longer-term changes in environment (e.g., passage of weather fronts, el Niño events, and glacial cycles), and disturbances (e.g., treefalls, herbivore outbreaks, logging, and volcanic eruptions). Consequently, the behavior of an ecosystem is always influenced by both the current environment and many previous environmental fluctuations and disturbances. This chapter addresses these temporal dynamics of ecosystems.

A Focal Issue

People have altered ecosystems more rapidly and extensively in the last 50 years than in any comparable time period in human history. These changes have resulted from an exponentially rising human population, our consumption of resources, and our ever-increasing technological capacity to alter Earth's environment and ecosystems. Perhaps the most urgent need in ecosystem ecology is to improve our understanding of factors governing resilience and change in ecological systems. How do we prepare for changes in the types and severity of disturbances that are occurring? Warming temperatures, for example, are expected to increase sea-surface temperatures and therefore the intensity of hurricanes that impact coastal cities, such as occurred with Hurricane Katrina (see Fig. 2.1). Warmer, drier conditions in dry regions of the world are expected to cause drought and associated wildfires and insect outbreaks, as have occurred in Australia, southern Europe, and the western United States (Fig. 12.1). Flooding is expected to occur more often in wet and low-lying coastal regions. How do ecosystems respond to disturbances that they often encounter? To novel disturbances? What properties of ecosystems enhance their capacity to sustain their structure and functioning in response to changing disturbance regimes? As disturbance regimes move outside their historical patterns due to human-caused climate change, ecosystem ecologists will play a key role in understanding the causes and consequences of altered patterns of disturbance, both for the protection of life and property and to sustain the diversity and other ecological attributes of ecosystems.

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Fig. 12.1 Climate-induced warming has increased the extent of wildfire in many dry areas, often directly threatening life and property in the wildland–urban interface, as in this 2010 fire in Gold Hill, Colorado. Photograph courtesy of Greg Cortopassi @ Cortoimages.com

Ecosystem Resilience and Change

Alternative Stable States

A given environment can often support more than one potential state of an ecosystem. The ecosystems we observe today depend not only on their capacity to thrive under current conditions but also on historical **legacies**, that is, things that happened to them in the past. Legacies such as the past history of land use are important because ecosystems are **complex adaptive systems**. This means the system changes its properties ("adapts") in complex ways in response to changes imposed on it (Levin 1999, Chapin et al. 2009). Large areas of northeastern North America, for example, were deforested for agriculture and since 1850 have reverted to forests (Fig. 12.2). A plow layer is still evident in 150-year-old forests that developed on former agricultural fields. This sharp vertical discontinuity in soil properties and nutrient supply does not occur, however, in forests that developed from previous woodlots (Motzkin et al. 1996, Foster et al. 2010). These alternative histories give rise to forests with different species composition, drought sensitivity, and services provided to society. A more recent trajectory, which is also sensitive to its historical roots, is toward extensive areas of pavement and other hard surfaces in cities and towns. These hard surfaces also influence species composition, runoff to aquatic ecosystems, and the likely trajectories of future ecosystem change.

The frequent occurrence of **alternative stable states** that can occur in the same current environment is familiar to anyone who has walked through a landscape and observed the bewildering fine-scale variation in ecosystem composition and structure that has no obvious explanation based on spatial variation in the current environment – for example, forest patches dominated by different species due to (often unknown) legacies of past disturbance, colonization by particular species, grazing history, etc. At larger scales, landscape patterns in a watershed may be substantially structured by past fire or land-use history. At continental scales, the historical absence of mammals in New Zealand strongly influenced ecosystem responses to the relatively recent arrival of people and the plants and animals they brought with

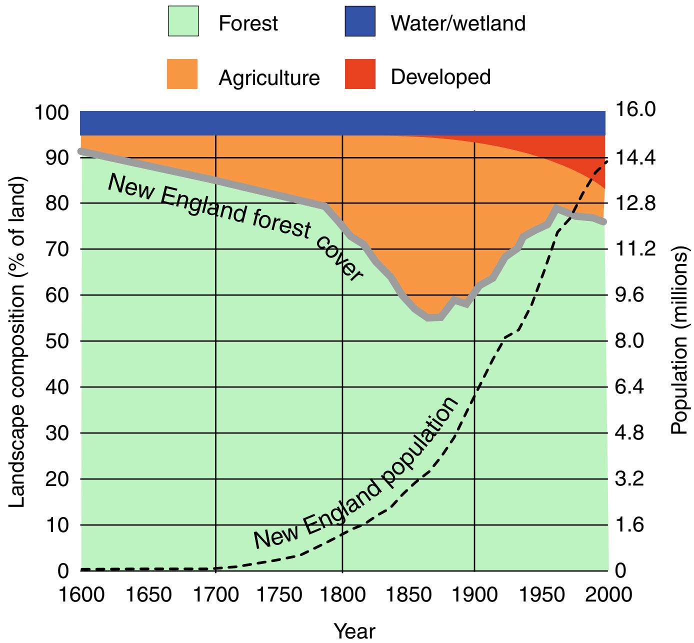

Fig. 12.2 Changes in landscape composition and population of New England (Northeastern U.S.) since European colonization. Most land that was cleared for agriculture by 1850 has regrown as forest or more recently been developed as cities and suburbs. Data from Foster et al. (2010)

them (Kelly and Sullivan 2010). Extinction of Pleistocene megafauna as a result of climate change and human hunting contributed substantially to the ecosystem changes that occurred 10,000 years ago and are legacies that still structure today's biomes (Flannery 1994, Zimov et al. 1995, Gill et al. 2009). The important role of historical legacies and **path dependence** in explaining current dynamics of ecosystems provides a clear motivation for ecosystem stewardship. Management actions taken today can make a difference in determining the future state of ecosystems (see Chap. 15).

Resilience and Thresholds

Sources of Resilience

Resilience constrains ecosystem responses to perturbations. Although many alternative states of an ecosystem are plausible, ecosystems often maintain relatively stable functional properties for long time periods. Ecosystem **resilience** is the capacity of an ecosystem to sustain its fundamental function, structure, and feedbacks in the face of a spectrum of shocks and perturbations (Holling 1973, Chapin et al. 2009).

Ecosystems are particularly resilient to those fluctuations to which organisms are well-adapted, including day-night or seasonal cycles of light and temperature, El Niño oscillations in weather that recur every 2–10 years, and droughts, fires, or other extreme events that have occurred repeatedly during the evolutionary history of organisms that occupy the ecosystem.

Internal dynamics of ecosystems also generate fluctuations in ecosystem processes. The population density of herbivores, for example, can vary more than 100-fold over a few years, causing large fluctuations in plant biomass, nutrient cycling, and other processes (Fig. 12.3). Fluctuations, outbreaks, or cycles of grasshoppers, gypsy moths, snowshoe hares, and lemmings, for example, are typical of internal dynamics that characterize many ecosystems. These fluctuations and cycles reflect interactions between positive and negative feedbacks among plants, herbivores, predators, and parasites (Hanski et al. 2001). Herbivore populations, for example, often decline after a depletion of their food supply, due to insufficient food or buildup of predators. These feedbacks constrain potential population changes in both predator and prey, conferring resilience to the trophic dynamics of the system (see Chaps. 1 and 10).

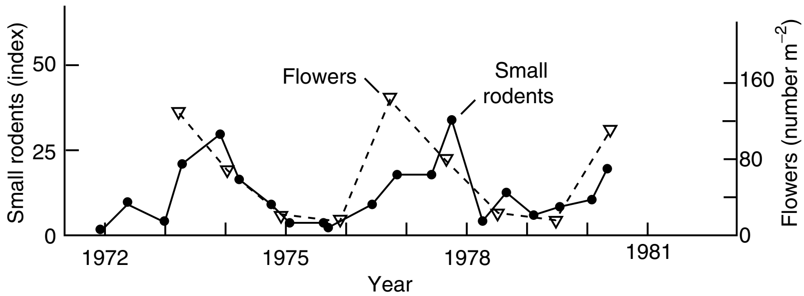

Fig. 12.3 Interannual variation in flowering density of an understory shrub (*Vaccinium myrtillus*) and of small rodents in northern Finland. These herbivores and their food plants show approximately 4-year cycles of abundance. Data from Laine and Henttonen (1983)

Maintenance of slowly changing biogeochemical pools, long-lived organisms, and biodiversity are particularly critical to long-term resilience because these variables structure so many of the interactions in ecosystems (Carpenter and Folke 2006). For example, ecosystems with a high response diversity (see Chap. 11), due to either high plasticity or high genetic or species diversity also exhibit high resilience because of the wide range of environmental or biotic conditions under which particular functions are sustained (Elmqvist et al. 2003). A grassland with both cool-season and warm-season grasses (C_3 and C_4 grasses, respectively), for example, can sustain productivity across a broader range of temperature and moisture conditions than a grassland that contains only one of these grass types. Stabilizing (negative) feedbacks that constrain changes in key slow variables at large temporal and spatial scales confer resilience to the system.

Limits to Resilience

Biological and physical limits to ecosystem resilience make ecosystems vulnerable to large or directional changes. When biotic or environmental changes exceed ecosystem resilience, some trigger for change (e.g., pest outbreak, species invasion, or change in internal dynamics) is increasingly likely to cause path-dependent change to some alternative state. Warmer temperatures that stress trees and increase winter survivorship of mountain pine beetle at high elevations, for example, can cause widespread tree mortality and restrict pine regeneration (Raffa et al. 2008). This increases the likelihood of a shift to a non-forested state. Saturation of the phosphorus-binding capacity of lake sediments can also exceed the resilience of clearwater lakes (Carpenter 2003), as described earlier.

Many of the recent changes in the global environment, including species introductions and extinctions, environmental changes, land-use changes, and introductions of novel chemicals, are likely to exceed the resilience of many ecosystems (Rockström et al. 2009). This can occur if a directional change in environment eventually exceeds the **adaptive range** of the system, that is, the difference between the upper and lower tolerance limits of the system (Fig. 12.4a) or if the environment becomes more variable and exceeds the adaptive range of the system more often (Fig. 12.4b; Smit and Wandel 2006). Alternatively, the adaptive range of the ecosystem may contract (Fig. 12.4c) due to factors such as loss of biotic diversity (e.g., when genetic diversity of crops is reduced), loss of buffering capacity of ecosystems (e.g., due to cation leaching from acid rain), or interactions with other stresses (e.g., exotic pests or high-ozone urban pollution) that constrain the limits to productivity and survivorship of species. These patterns suggest that ecosystem resilience can be enhanced by reducing environmental stresses, fostering biotic response diversity, and minimizing the complexity of interacting stresses that impact ecosystems.

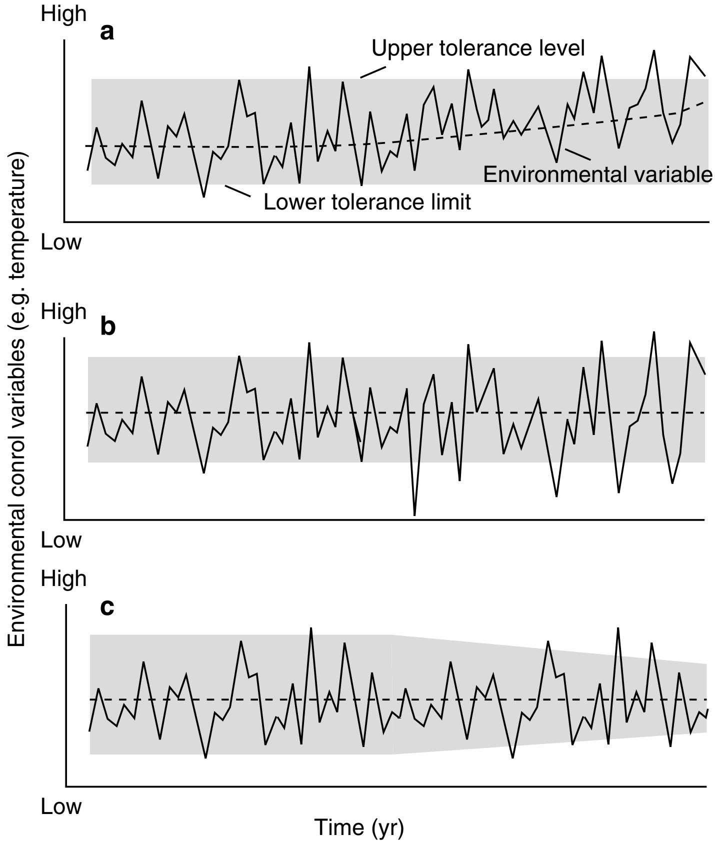

Fig. 12.4 The adaptive range of an ecosystem (difference between upper and lower tolerance limits) relative to temporal variations in an important environmental control (e.g., temperature), when (**a**) the environmental control changes directionally or (**b**) becomes more variable, or (**c**) when the adaptive range declines. Based on Smit and Wandel (2006)

Thresholds and Regime Shifts

When ecosystem resilience is exceeded, regime shifts can occur rapidly and unexpectedly. Most ecosystems exhibit an impressive degree of resilience to natural environmental variability, as a result of their evolutionary and developmental history. They are also often remarkably resilient to the insults imposed by many human-caused changes in environment, structure, and diversity. Consequently, over a broad range of conditions, ecosystems appear to "take care of themselves" through the feedbacks described in earlier chapters. It therefore often comes as quite a surprise when resilience is exceeded, and ecosystems undergo an abrupt (threshold) change to an alternative state. Due to the path-dependent nature of changes in complex adaptive systems, the new state of the system is likely to exhibit different environmental responses and may not readily return to the original system, even when external stresses are removed and the environment returns to its previous state (Box 12.1). In response to this **regime shift**, a new set of feedbacks and environmental responses emerge, generating resilience of the altered state. In the western U.S., for example, introduction of cheatgrass combined with overgrazing caused widespread replacement of native bunchgrasses by this unpalatable grass. The combination of reduced grazing and increased fire frequency that resulted from cheatgrass invasion maintains this grassland in its new state, which has become quite resilient to a wide variety of management efforts to restore the original grasslands (Brooks et al. 2004). Similarly, once clearwater lakes shift to a turbid state because of phosphorus saturation of sediments, the public becomes concerned and wants to fix the problem. However, it is often extremely difficult to return to the clearwater state, even when phosphorus inputs from

Box 12.1 Resilience and Regime Shifts

The response of an ecosystem to perturbation depends on its resilience and the strength and directionality of perturbations that push it toward alternative states. The behavior of a ball on a surface provides a useful analogy (Fig. 12.5; Holling and Gunderson 2002). The location of the ball represents the state of a system in relationship to some ecological variable (e.g., water availability, as represented by the position along the horizontal axis). Resilience is the tendency for the system to remain in the same state, despite temporal fluctuations in environment. This can be represented by a cup-shaped depression in the surface. If the ecosystem is highly resilient because of adaptations and stabilizing (negative) feedbacks that sustain its properties over a wide range of available moisture conditions, the cup will be broad and deep, and the system will persist in its original state despite substantial moisture perturbations (e.g., floods or droughts; Fig. 12.5a).

If droughts become more frequent or severe, it becomes increasingly likely that some drought, perhaps interacting with another event such as an insect outbreak, may push the system into a different stability domain (a regime shift), where new feedbacks maintain it in the new state (Fig. 12.5b). If ecosystem resilience to drought is eroded, for example by loss of soil organic matter (SOM) or drought-resistant species (shown by the resilience cup becoming less deep), even a modest perturbation may cause a regime shift (Fig. 12.5c).

In practice, stability landscapes are highly dynamic with constant changes in the depth and locations of stability domains (i.e., cups on the landscape that represent alternative stable states of the system). In a directionally changing world, some new stability domains become increasingly likely and current states become increasingly vulnerable (Fig. 12.5d). The challenge for ecosystem ecologists is to enhance the resilience of those stability domains that provide ecosystem integrity and benefits to society and to reduce the resilience of undesirable states. In some cases, the historical ecosystem may be feasible to maintain, but increasingly it may become necessary to choose among alternative novel states, if the current system cannot be sustained in the new environment (Hobbs et al. 2009).

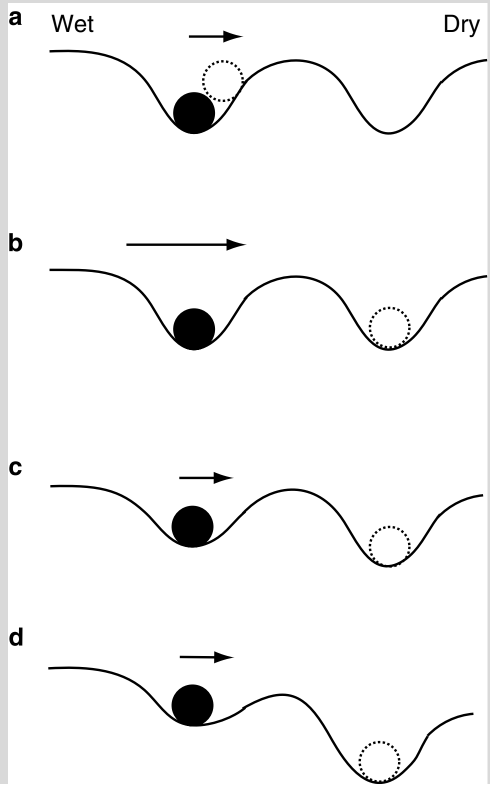

Fig. 12.5 The location of the ball represents the state of an ecosystem in relationship to some ecological variable (e.g., water availability, as represented by the position along the horizontal "water" axis). The depth of each cup defines the resilience of the ecosystem; the breadth of each cup is the range of environmental variation over which the ecosystem tends to remain in the same domain (i.e., is resilient); and the length of the arrow represents the strength of the perturbation (e.g., drought) to which the ecosystem is exposed. The solid ball is the original state of the system and the open ball is the most likely final state. (**a**) Response of a resilient system to a mild drought at steady state; (**b**) response of a resilient system to an extreme drought; (**c**) response of a less resilient system to a mild drought; and (**d**) response of a system to mild drought during a trajectory of declining moisture availability

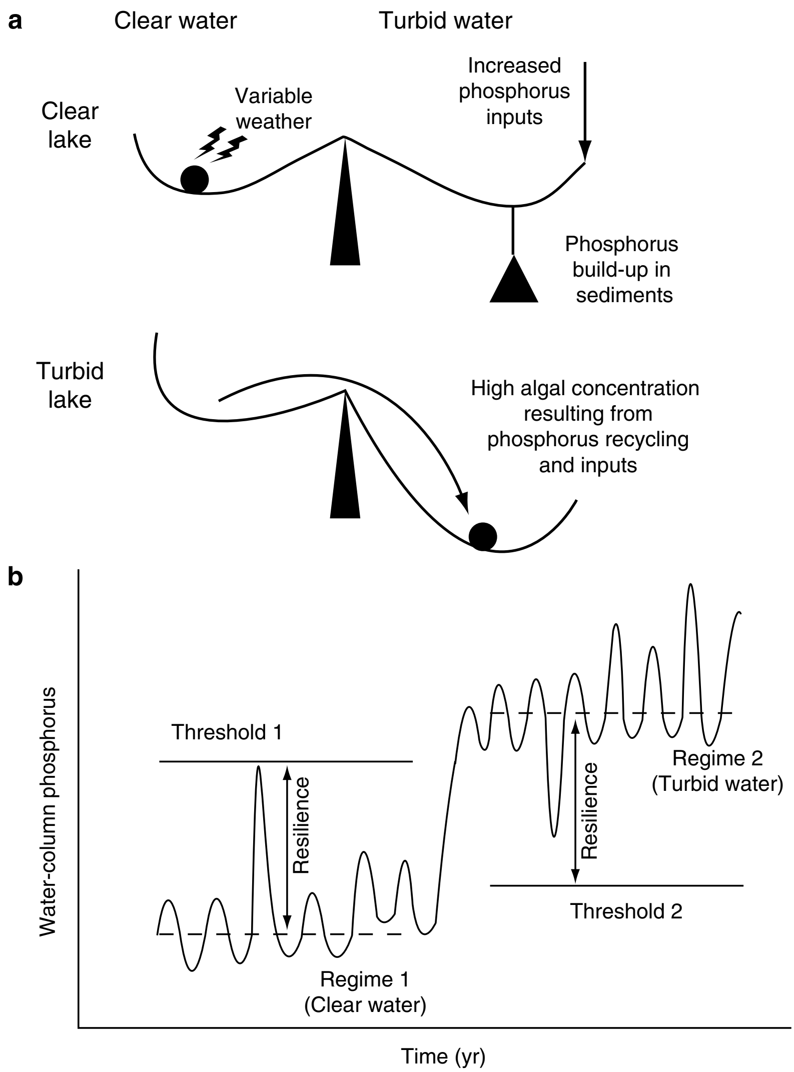

Fig. 12.6 Pan balance model (**a**) and time course (**b**) of changes in lakes in response to increases in phosphorus inputs. In the pan model, the clear lake loses resilience as phosphorus inputs increase. At some point, a stochastic shock such as a wind-driven mixing event shifts the lake from a clearwater to a turbid state. The time course of this change involves fluctuations in water-column phosphorus, initially around concentrations typical of clearwater lakes. When a fluctuation exceeds the resilience of the system, it shifts to a turbid-water regime that has a different average value of water-column phosphorus and a different threshold for return to the clearwater state. Redrawn from Carpenter (2003)

the watershed are greatly reduced (Fig. 12.6; Carpenter 2003).

Disturbances are often the trigger for regime shifts in communities facing gradual changes in conditions (Turner 2010). These shifts are seen in storms that resuspend sediment phosphorus (Carpenter 2003), severe wildfires that alter seedbed characteristics (Johnstone et al. 2010), and windthrow and fires in a warming climate that shift forests to savannas (Frelich and Reich 2009). These regime changes sometimes lead to communities with novel species composition and properties (Williams and Jackson 2007).

Ecologists often understand some of the ecosystem consequences of environmental stresses such as drought, pollution, and warming, but there is currently a very poor ability to predict how much change or stress an ecosystem can withstand before a regime shift occurs or what interacting stresses or events (e.g., insect outbreak) might trigger the shift. Sometimes key parameters like water-column phosphorus become temporally or spatially more variable as the limits of resilience are approached (Scheffer and Carpenter 2003, Carpenter and Brock 2006). A precautionary approach to reducing the risk of regime shifts is to foster resilience and reduce vulnerability by minimizing known stresses (e.g., pollution), maintaining diversity (capacity to deal with a broader range of conditions), and providing conditions where the ecosystem can adjust naturally to persistent environmental changes (Walker et al. 2004).

How can the adaptive range of ecosystems be broadened or shifted to accommodate expected changes in environment? The natural rate of ecosystem response to a changing environment through evolution or migration of genotypes and species may be too slow to keep pace with current rapid rates of change. One approach is to manage migration corridors to maximize opportunities for migration of non-weedy and noninvasive species. A second more controversial approach is **assisted migration**, in which genotypes or species are moved from a region where climate is becoming unfavorable to new places where climate is, or is expected to become, more favorable. Australia, for example, is encouraging the establishment of vineyards in areas where climate is projected to be favorable for grapes 30 years from now, a time when vines reach peak production (NRC 2010). Given the checkered history of efforts to solve management problems by introducing species to new locations, assisted migration raises concerns among many conservation biologists (McLachlan et al. 2007). This approach has received most attention among foresters, who recognize that climate may shift significantly during the lifetimes of individual trees. One approach may be to reforest logged or burned forests with seeds from a wide range of climates and allow whatever climate emerges to select among the tree seedlings that establish (Millar et al. 2007). This contrasts strikingly with current "best practices" of reseeding with locally adapted genotypes. Assisted migration becomes a publicly attractive alternative in areas where insect outbreaks (e.g., mountain pine beetle) or species shifts (e.g., cheatgrass or junipers) have radically modified the composition of unmanaged ecosystems. Highly flammable invasive grasses have invaded Saguaro National Park, for example, threatening the slow-growing, long-lived species that the park was established to protect (see Fig. 11.1). Should saguaro cactuses be planted beyond their current range in places where grasses have not yet invaded? Ecosystem ecologists can play a constructive role in these debates by exploring the ecosystem consequences of proposed species manipulations (see Chap. 11).

Restoration ecology seeks to trigger regime shifts to alternative, potentially more favorable states. Many terrestrial and aquatic ecosystems that have been degraded by mining, industrial development, stream channelization, or overgrazing are extremely resilient and can remain in a degraded state for a long time due to unfavorable soil or site-moisture conditions. The explicit goal of restoration ecology is to transform these systems to an alternative state that would then generate its own feedbacks to sustain the restored state. For example, nitrogen-fixing trees have been used to speed soil development on mine tailings in the U.K. to generate nutrient cycles similar to those of nearby forested ecosystems (Bradshaw 1983). A valuable new wrinkle in restoration ecology is the goal of transforming degraded ecosystems to a state that is compatible with the projected *future* climate rather than to some historical reference point (Choi 2007, Hobbs and Cramer 2008).

Disturbance

Conceptual Framework

Disturbance is a major cause of long-term fluctuations in the structure and functioning of ecosystems. We define **disturbance** as a relatively discrete event in time that removes plant biomass (Grime 2001). Disturbance has also been described as a relatively discrete event in time and space that alters the structure of populations, communities, and ecosystems and causes changes in resource availability or the physical environment (White and Pickett 1985). Disturbances include herbivore outbreaks, treefalls, fires, hurricanes, floods, glacial advances, and volcanic eruptions. The dividing line between disturbance and normal function is somewhat arbitrary. Herbivory, for example, is often treated as part of the steady-state dynamics of ecosystems, whereas stand-killing insect outbreaks are treated as disturbances. Drought also ranges from minor moisture stress to severe moisture limitation that kills plants and triggers wind erosion. There is a continuum in size, severity, and frequency between normal function and extreme disturbance. Disturbance is not an external event that "happens" to an ecosystem. Like other interactive controls (see Chap. 1), disturbance is an integral part of the functioning of all ecosystems, which responds to and affects most ecosystem processes. Naturally occurring disturbances such as fires and hurricanes are therefore not "bad"; they are normal properties of ecosystems. They are appropriately viewed as disasters when they negatively impact society, often as a result of changes in human interactions with ecosystems.

Human activities have altered the frequency and size of many natural disturbances, such as fires and floods, and have produced new types of disturbance such as large-scale logging, mining, and wars. Many human disturbances have ecological effects that are similar to those of natural disturbances, so the study of either natural or human disturbances provides insights into the regulation of ecosystem processes and human impacts on these processes. Natural and human disturbances interact with environmental gradients to create much of the spatial patterning in landscapes (see Chap. 13; Turner 2010).

After disturbance, ecosystems undergo **succession**, a directional change in ecosystem composition, structure, and functioning. Disturbances that remove live or dead organic matter, for example, are colonized by plants that gradually reduce the availability of light at the soil surface and alter the availability of water and nutrients (Tilman 1985). If there were no further disturbance, succession would proceed toward a steady state. Because of the path-dependent nature of succession, this steady state might be similar to the pre-disturbance ecosystem or it might move toward some alternative endpoint. Stands of lodgepole pine that burned in the 1988 Yellowstone fires, for example, moved along trajectories of very different stand density, nutrient availability, and productivity, depending on initial seed availability (which depended on seed retention in cones and fire severity) and seedling establishment (Turner et al. 1997, Turner 2010). In practice, however, new disturbances or environmental changes usually occur before succession reaches a steady state. Nonetheless, the concept of directional changes in vegetation after disturbance provides a useful framework for analyzing the role of disturbance in ecosystem processes.

Impact of a Disturbance Event

The impact of a disturbance event depends on three attributes of the disturbance: (1) the type of disturbance, (2) ecosystem sensitivity, and (3) disturbance severity or intensity.

Different **disturbance types** have radically different effects on ecosystems. Fire removes live and dead organic matter and raises environmental temperatures to lethal levels. An unseasonable freeze may also produce lethal temperatures. Floods and landslides remove or add soils and deplete soil oxygen. Hurricanes, storm surges, and logging remove or damage organisms. Species are often adapted to withstand disturbances that occur relatively frequently in their evolutionary history but may be vulnerable to novel disturbances. Benthic communities, for example, may recover slowly from bottom trawling that scrapes surface sediments, although they recover rapidly from severe storms that dislodge individuals. Many upland species are intolerant of flooding, whereas trees from wet environments generally tolerate periodic flooding, but have thin bark and are killed by fire.

Sensitivity to a particular disturbance type depends on system properties at the time of disturbance. Species traits, such as rooting depth

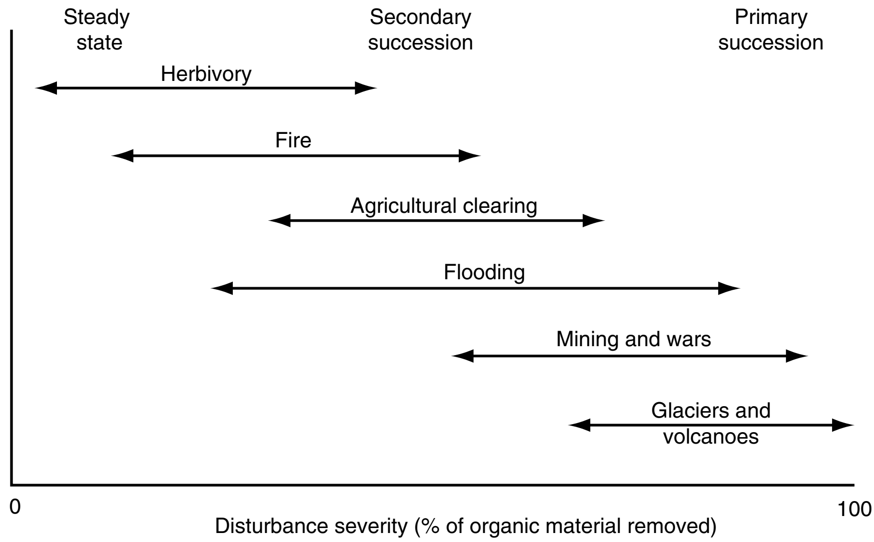

Fig. 12.7 Spectrum of disturbance severity associated with major types of disturbance, ranging from normal steady-state functioning of ecosystems to primary succession

or tolerance to frost, fire, or drought influence sensitivity of individual organisms. In addition, system properties such as density or configuration of plants can influence spread of fire, pathogens, or insect pests and therefore landscape sensitivity to disturbance.

Disturbance severity is magnitude of loss of biomass, soil resources, and species caused by a disturbance. **Intensity** is the energy released per unit area and time. **Primary succession** occurs after severe disturbances that remove or bury most products of ecosystem processes, leaving little or no organic matter or organisms. Disturbances leading to primary succession include volcanic eruptions, glacial retreat, landslides, mining, flooding, coastal dune formation, and lake drainage.

Secondary succession occurs on previously vegetated sites after disturbances such as fires, hurricanes, logging, and agricultural plowing. These disturbances remove or kill substantial live aboveground biomass but leave some soil organic matter and plants or plant propagules in place. Disturbance severity is probably *the* major factor determining the rate and trajectory of vegetation development after disturbance. A severe fire that kills all plants, for example, has a different effect on vegetation recovery than does a fire that burns only surface litter, allowing surviving vegetation to resprout (Johnstone et al. 2010). There is also a continuum in disturbance severity between large-scale defoliation events and the removal of a single leaf by a caterpillar or between landslides and the burial of surface litter by an earthworm. In other words, there is a continuum in disturbance severity between the day-to-day functioning of ecosystems and events that initiate primary succession (Fig. 12.7).

Recovery and Renewal after Disturbance

Resilience to disturbance and subsequent successional trajectory depend not only on initial disturbance impact but also on disturbance size, pattern, and landscape matrix, which influence post-disturbance recruitment.

The traits and abundance of organisms that survive disturbance are critical to post-disturbance succession. Depending on the type and severity of disturbance and ecosystem sensitivity to the disturbance event, a variable number of individuals and species will survive, grow, and reproduce. Recruitment of new individuals is also important. Some traits, such as heat-induced germination of chaparral post-fire annuals, enable species to respond to specific types of disturbance. Other traits enable species to colonize many types of disturbances. Weedy species, for example, produce abundant small seeds that disperse long distances or remain dormant in the soil from one disturbance to the next. Their germination is often triggered by fluctuations in temperature and nutrients that characterize most disturbed sites (Fenner 1985, Baskin and Baskin 1998), so they are relatively insensitive to disturbance type. Novel disturbances are more likely to lead to slow recovery or trigger a new successional trajectory than are disturbances to which organisms are well adapted.

Disturbance size is highly variable. **Gap-phase succession**, for example, occurs in small gaps created by the death of one or a few plants. Many tropical wet forests or intertidal communities, for example, are mosaics of gaps of different ages. Similarly, gophers create patchy disturbances in grasslands (Yoo et al. 2005). Other ecosystems develop after **stand-replacing disturbances** that can be hundreds of square kilometers in area. Disturbance size influences ecosystems primarily through effects on landscape structure, which influences lateral flow of materials, organisms, and disturbance among patches in the landscape (see Chap. 13). Disturbance size, for example, affects the rate of seed input after fire. Small fires are readily colonized by seeds that blow in from surrounding unburned patches or are carried by mammals and birds. In contrast, regeneration in the middle of large fires, fields, or clearcuts may be limited by seed availability and be colonized primarily by light-seeded species that disperse long distances. Disturbance size also influences the spread of herbivores and pathogens that colonize early successional sites.

Disturbance pattern on the landscape influences the effective size of a disturbance event. Disturbances often leave islands of undisturbed vegetation or create highly irregular shapes with variable distances to propagule sources, causing the effective size of the disturbance to be much smaller than its areal extent would suggest (Turner 2010).

Resilience to disturbance also depends on the properties of the landscape in which the disturbed ecosystem is embedded, particularly its diversity of types and ages of ecosystems that serve as potential propagule sources for post-disturbance colonization. A nature reserve or forest stand that is isolated within an agricultural or urban matrix, for example, has less access to propagules and is less resilient than a similar stand embedded in a matrix of forest stands of varying ages (Fig. 12.8). Similarly, a diverse landscape is more resilient to a broad spectrum of disturbance types than is a uniform landscape, as described in the next section. This suggests that management for harvest efficiency by planting uniform ages of single-species stands reduces landscape resilience (Peterson et al. 1998).

Disturbance Regime

The overall role of disturbance in an ecosystem depends on the frequency and interaction of multiple disturbance types, the nature of individual disturbance events, and the landscape patterns that govern resilience and renewal. Over time, most ecosystems experience a diverse array of disturbance types that occur with differing frequencies and severities. Together these constitute the **disturbance regime** of the ecosystem.

Disturbance frequency varies dramatically among ecosystems and among disturbance types. Herbivory occurs continuously in most ecosystems. At the opposite extreme, volcanic eruptions or floods may never have occurred in some locations. Average fire frequency ranges from once per year in some grasslands to once every several thousand years in some mesic forests. Ecosystems are usually most resilient to disturbances that occur frequently. Ecosystems that experience frequent fire, for example, support fire-adapted species that recover biomass more quickly than in ecosystems in which fire occurs infrequently. Human activities often modify disturbance frequency through initiation or suppression of disturbance. Damming of streams can eliminate spring floods that scour sediments and detritus

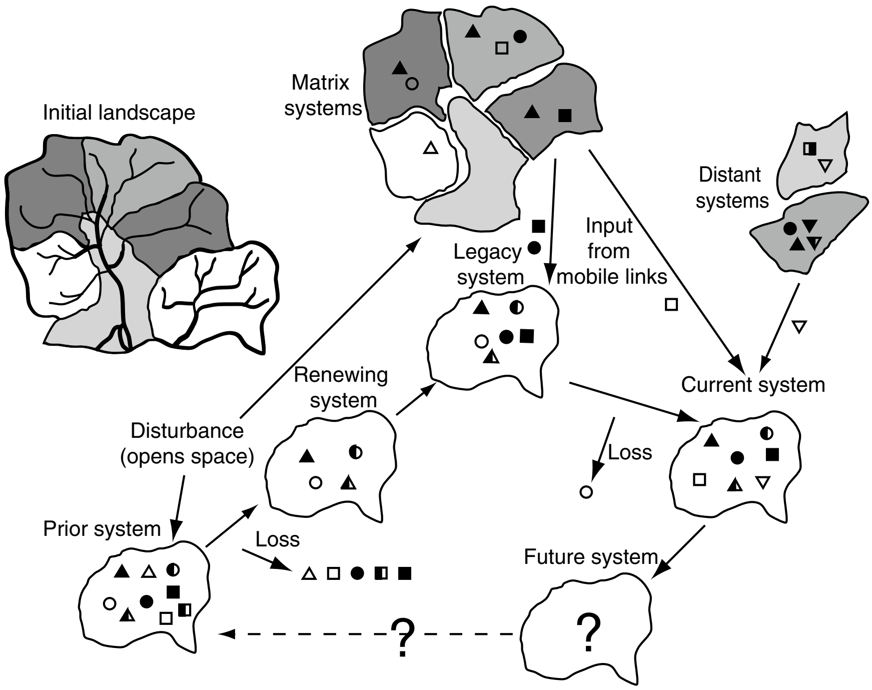

Fig. 12.8 Roles of stand and landscape diversity in ecosystem renewal after disturbance. A disturbance such as a fire, hurricane, volcanic eruption, or war opens space in an ecosystem. In this diagram, each shape represents a different functional group such as algal-grazing herbivores in a coral reef, and the different patterns of shading represent species within a functional group. After disturbance, some species are lost, but an on-site legacy of surviving species serves as the starting point for ecosystem renewal. For example, after boreal fire, about half of the vascular plant species are lost (Bernhardt et al. 2011). The larger the *species diversity* of the pre-disturbance ecosystem, the more species and functional groups are likely to survive the disturbance; the more severe the disturbance the larger the proportion of species lost. (In this figure, all functional groups except "squares" survived the disturbance.) *Landscape diversity* of the matrix surrounding the patch is also important to ecosystem renewal because it provides a reservoir of diversity that can recolonize the disturbed patch. In this figure, the "square" function was renewed by colonization from the matrix surrounding the ecosystem. Through time, some additional species may be gained or lost, and new functional groups (inverted triangles in this diagram) may invade from a distance. Reprinted from Chapin et al. (2009)

from channels, resulting in large changes in stream food webs and capacity to support fish (Power 1992a). Fire suppression in the giant sequoias (*Sequoiadendron gigantea*) of the Sierra Nevada mountains of California made this ecosystem more vulnerable to fire, as a result of the growth of understory trees that formed a ladder for fire to reach from the ground to the canopy. Although the thick-barked sequoias are resistant to ground fires, they are vulnerable to fires that extend into the canopy. In this way, fire suppression increased the risk of catastrophic fires that could eliminate giant sequoias.

The **timing of disturbance** often influences its impact. A strong freeze or fire that occurs during budbreak has greater impact than one that occurs 2 weeks earlier. Similarly, anaerobic conditions associated with flooding of the Mississippi River during the 1993 growing season caused more root and tree mortality than if the flood had occurred when roots were inactive. Hydroelectric dams may eliminate seasonal flooding associated with rain or snowmelt and regulate flow based on electricity demand, often causing a mismatch between disturbance timing and the disturbance regime to which organisms are adapted.

Disturbance is a key interactive control that governs ecosystem processes (see Chap. 1) through its effects on other interactive controls (microenvironment, soil resource supply, and functional types of organisms). Post-fire stands, for example, often have warm, moist soils because of the low albedo of the charred surface and the decrease in leaf area that transpires water and shades the soil. Fire both volatilizes nitrogen, which is lost from the site, and returns inorganic nitrogen and other nutrients to the soil in ash, thus altering soil resource supply. The net effect of fire is usually to enhance nutrient availability, although the magnitude of this effect depends on the nutrient and on fire severity and intensity (Wan et al. 2001, Smithwick et al. 2005). Fire affects the functional types of plants in an ecosystem through its effects on differential survival and competitive balance in the post-fire environment. Because of its sensitivity to, and effect on, other interactive controls, changes in disturbance regime alter the structure and functioning of ecosystems.

Succession

Successional changes occurring over decades to centuries explain much of the local variation among ecosystems. Although climate, soils, and topography explain most of the broad global and regional patterns in ecosystem processes, disturbance regime and post-disturbance succession account for many of the local patterns of spatial variability (see Chap. 13). In this section, we describe common patterns of successional change in major ecosystem processes. These successional changes are most clearly delineated in primary succession, so we begin with a description of primary successional processes and then describe how the patterns differ between primary and secondary succession.

Ecosystem Structure and Composition

Primary Succession

Primary succession occurs after severe disturbances that remove or bury most products of ecosystem processes. Initial species composition on these sites depends on the capacity of plants to deal with the environmental stresses associated with low nitrogen availability and the generally low water-holding capacity of organic-poor soils. Vascular plant species capable of symbiotic nitrogen fixation occur most often (about 75% of sites studied) in early primary succession, although they dominate the vegetation only about 25% of the time (Walker 1993). These species are most common on glacial moraines and mudflows, intermediate on mine tailings, landslides, floodplains, and dunes, and least abundant on volcanoes and rock outcrops. When early successional colonizers fix abundant nitrogen, their net effect is generally to **facilitate** (enhance) the establishment and growth of later successional species (Fig. 12.9; Walker 1993).

Due to their lack of plants and plant propagules, primary successional sites must be colonized by species that disperse to the site. Most initial colonizers have small wind-dispersed seeds. Fresh lava or glacial moraines, for example, are first colonized by wind-dispersed spores of algae, cyanobacteria, and lichens that form soil-stabilizing crusts (Walker and del Moral 2003). These are followed by small-seeded wind-dispersed vascular plants (primarily woody species), whose arrival rates depend largely on distance to seed source (Shiro and del Moral 1995). Late successional species with heavier seeds generally arrive more slowly (Fig. 12.10).

The identity of initial colonizers strongly influences the long-term successional trajectory. After volcanic eruption in Hawai'i, for example, succession usually proceeds slowly from short-statured vegetation dominated by algal crusts, herbaceous plants, and small shrubs to forests dominated by slowly growing tree ferns and trees. An exotic bird-dispersed nitrogen-fixing tree, *Morella faya*, can, however, add enough nitrogen to alter substantially the nitrogen supply, production, species composition, and therefore the successional trajectory of vegetation (Vitousek et al. 1987).

A similar change in successional trajectory occurred after glacial retreat at Glacier Bay, Alaska, but for different reasons. When the glacier first began to retreat in 1800, *Populus* (poplar) and *Picea* (spruce) were the major initial colonizers. Further retreat of the glacier, however, brought early successional habitat within

Stage	Pioneer	*Dryas*	Alder	Spruce
Life history patterns	Dominance by light-seeded species	Dominance by rapidly growing species	Dominance by tall shrubs of intermediate longevity	Dominance by long-lived trees
Facilitative effects	↑ Survivorship	↑ N (weak) ↑ Growth (weak)	↑ SOM ↑ N ↑ Mycorrhizae ↑ Growth	↑ Germination
Inhibitory effects	↓ Germination (weak)	↓ Germination ↓ Survivorship ↑ Seed predation and mortality	↓ Germination ↓ Survivorship ↑ Seed predation and mortality Root competition Light competition	↓ Growth ↓ Survivorship ↑ Seed predation and mortality Root competition Light competition ↓ N
Impacts of herbivory	Minimal	Reduce growth of early successional species	Eliminate early successional species	Minimal

Fig. 12.9 Interaction of life-history traits, competition, facilitation, and herbivory in causing successional change after glacial retreat at Glacier Bay, Alaska. Life-history traits determine the pattern of dominance at each successional stage. The rate at which this dominance changes is determined by facilitative or inhibitory effects of the dominant species and by patterns of herbivory. In general, all four of these processes contribute simultaneously to successional change, with the most important processes being life-history traits in the pioneer stage, herbivory in mid-successional stages, facilitation in the alder stage, and competition in late succession. Modified from Chapin et al. (1994)

dispersal distance of nitrogen-fixing alders, which then became an important early successional species (Fastie 1995). Alders increased the nitrogen inputs and long-term productivity of later successional stages (Bormann and Sidle 1990). The late-successional forests on older sites at Glacier Bay therefore followed a different (less productive) successional trajectory than alder-supported forests on younger sites. Human activities strongly affect both the post-disturbance environment and availability of propagules, so future trajectories of succession will likely differ from those that currently predominate.

Secondary Succession

Secondary succession begins on soils that developed beneath vegetation. There is usually a pulse in nutrient availability after disturbance because of the absence of vegetation to absorb nutrients released by mineralization.

Secondary succession also differs from primary succession in having colonizers that are already present on site immediately after disturbance. They may resprout from roots or stems that survived the disturbance or germinate from a soil **seed bank** – seeds produced after previous disturbance events that remain dormant in the

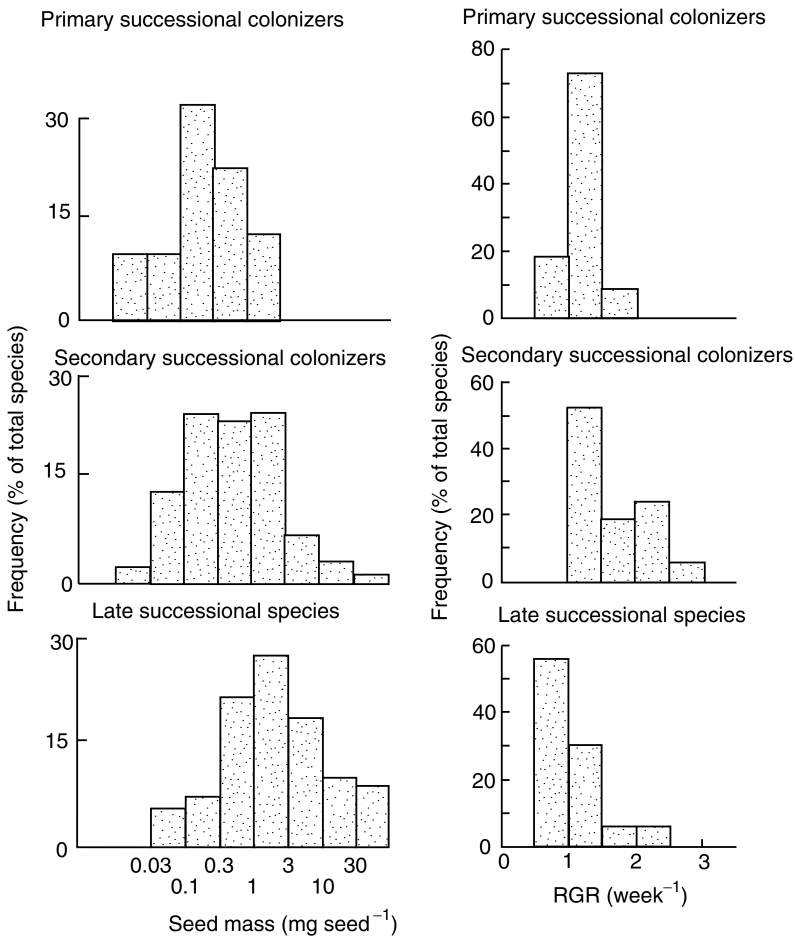

Fig. 12.10 Frequency distribution of log (seed mass) and relative growth rate (RGR) for British species that are primary successional colonizers, secondary successional colonizers, and late-successional species. Data from Grime and Hunt (1975) and Grime et al. (1981). Redrawn from Chapin (1993a)

soil until post-disturbance conditions (light, wide temperature fluctuations, or high soil nitrate) trigger germination (Fenner 1985, Baskin and Baskin 1998). Many forests also have a **seedling bank** (advanced regeneration) of large-seeded species that show negligible growth beneath the dense shade of a forest canopy but grow rapidly when treefall gaps occur. Other colonizers of secondary succession disperse into the disturbed site from adjacent areas. Dispersing species include both small-seeded, wind-dispersed species and large-seeded, animal-dispersed species (Fig. 12.10). Initial colonizers grow rapidly to exploit the resources made available by disturbance. Gap-phase succession is seldom limited by propagule availability, whereas the successional trajectory of large disturbed sites may depend on the species that disperse to the site (Fastie 1995). Even large disturbances may not be dispersal-limited if the disturbances are so patchy that undisturbed seed sources are well distributed within the disturbed area (Turner 2010).

The changes in species composition that occur after the initial colonization of a site result from a combination of (1) the inherent life-history traits of colonizers, (2) facilitation, (3) competitive interactions, (4) herbivory, and (5) stochastic variation in environment (Connell and Slatyer

Table 12.1 Successional changes in life-history traits after glacial retreat in Glacier Bay, Alaska[a]

Genus	Successional stage	Seed mass (g seed^{-1})	Maximum height (m)	Age at first reproduction (year)	Maximum longevity (year)
Epilobium	Pioneer	72	0.3	1	20
Dryas	*Dryas*	97	0.1	7	50
Alnus	Alder	494	4	8	100
Picea	Spruce	2,694	40	40	700

[a] Data from Chapin et al. (1994)

1977, Pickett et al. 1987, Walker 1999). **Life-history traits** include seed size and number, potential growth rate, maximum size, and longevity. These traits determine how quickly a species can get to a site, how quickly it grows, how tall it gets, and how long it survives. Most early secondary successional species arrive soon after a disturbance, grow quickly, are relatively short statured, and have a low maximum longevity, compared to late-successional species (Fig. 12.10, Table 12.1; Noble and Slatyer 1980). Even if no species interactions occurred during succession, life-history traits alone would cause a shift in dominance from early to late successional species because of differences in arrival rate, size, and longevity.

Facilitation involves processes in which early successional species make the environment more favorable for the growth of later successional species. Facilitation is particularly important in severe physical environments, such as primary succession, where nitrogen fixation and addition of soil organic matter by early successional species ameliorates the environment and increases the probability that seedlings of other species will establish and grow (Callaway 1995, Brooker and Callaghan 1998). **Competition** is an interaction among two organisms or species that use the same limiting resources (resource competition) or that harm one another in the process of seeking a resource (interference competition). Both competitive and facilitative interactions are widespread in plant communities (Callaway 1995, Bazzaz 1996); their relative importance in causing changes in species composition during succession probably depends on environmental severity (Fig. 12.9; Connell and Slatyer 1977, Callaway 1995). **Herbivores and pathogens** account for much of the plant mortality during succession. Selective browsing by mammals generally targets early successional species, reducing their competition with later successional species and therefore speeding the rate of successional change (Paine 2000, Walker and del Moral 2003). In intertidal communities, grazing by fish and invertebrates such as limpets exerts a similar effect. Insects exert their greatest impacts during outbreaks that reduce growth or increase mortality of ecologically important plant species. During mid and late succession, for example, when plant demands for water and nutrient are high, periodic drought stress can reduce plant resistance to insects and trigger an outbreak, as in the mountain pine beetle outbreak in western North America (Raffa et al. 2008).

In general, life-history traits determine the *pattern* of species change through succession, and facilitation, competition, and herbivory determine the rate at which this occurs (Chapin et al. 1994). These processes interact with other disturbances to create a diversity of successional pathways in natural ecosystems (Pickett et al. 1987, Walker and del Moral 2003, Turner 2010).

Opportunities for seedling establishment often decline through succession. In many forests, for example, all tree species colonize in early succession, and the successional changes in dominance reflect a gradual transition from small rapidly growing plants to taller, more slowly growing species (Egler 1954, Walker et al. 1986). In other cases, late successional species may establish more gradually. As succession proceeds, the soil becomes covered by leaf litter, creating a less favorable seedbed, and competition increases for light and nutrients among established seedlings.

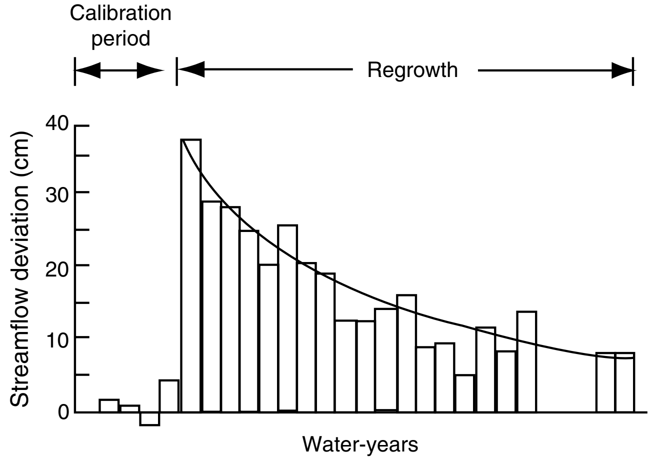

Fig. 12.11 Runoff from a watershed in a North Carolina forest in the Southeastern U.S. under natural conditions (the calibration period) and after forest harvest. Water yield from the watershed greatly increased in the absence of vegetation and approached pre-harvest levels within 20 years. Redrawn from Hibbert (1967)

Water and Energy Exchange

Disturbances that eliminate plant biomass increase runoff through a reduction in evapotranspiration. One of the most dramatic consequences of forest cutting or overgrazing is increased runoff to streams and rivers during times of both low flows and flooding (NRC 2008). This has led some resource managers to suggest forest cutting as a way to increase water yields to meet societal demands for water. These increases in discharge are, however, often short lived. As vegetation regrows during succession, runoff declines to pre-harvest levels (or even lower; see Chap. 4), often within 5 years or less (Fig. 12.11; Jones and Post 2004). The rate and pattern of change in runoff after forest harvest depends on patterns of vegetation recovery, relative to the vegetation that was present before harvest (Jones and Post 2004, Brown et al. 2005, NRC 2008). The high nitrogen availability, high photosynthetic rate, and high leaf area early in secondary succession can lead to even higher evapotranspiration and lower runoff than in undisturbed stands (Jones and Post 2004). The short-term gains in discharge after forest harvest are generally smallest in dry ecosystems and dry seasons, that is, the situations where human demands for water are highest (NRC 2008), suggesting that forest harvest is not an effective strategy to increase water yield for human use. As roots proliferate during succession, more water is absorbed by plants, and less water moves to groundwater and streams. As the canopy increases in height and complexity, a larger proportion of solar energy is trapped, reducing albedo and increasing the energy available to drive evapotranspiration. The high surface roughness of tall complex canopies increases mechanical turbulence and mixing within the canopy. All of these factors contribute to rapid recovery of evapotranspiration during succession.

Successional changes in albedo differ among ecosystems because of the wide range among ecosystems in albedo of bare soil (see Table 4.1). Many recently disturbed sites have a low albedo because of the dark color of moist exposed soils or of charcoal. Albedo increases when vegetation, with its generally higher albedo, begins to cover the soil surface (Fig. 12.12). Albedo probably declines again in late succession due to increased canopy complexity (see Chap. 4). In ecosystems that succeed from deciduous to conifer forest, this species shift causes a further reduction in albedo. The winter energy exchange of northern forests is influenced by snow, which has an albedo three to fivefold higher than vegetation (Betts and Ball 1997). Winter albedo of these forests declines through succession, first as vegetation grows above the snow, then as the canopy becomes denser, and finally when (if) vegetation switches from deciduous to evergreen. All of these changes increase the

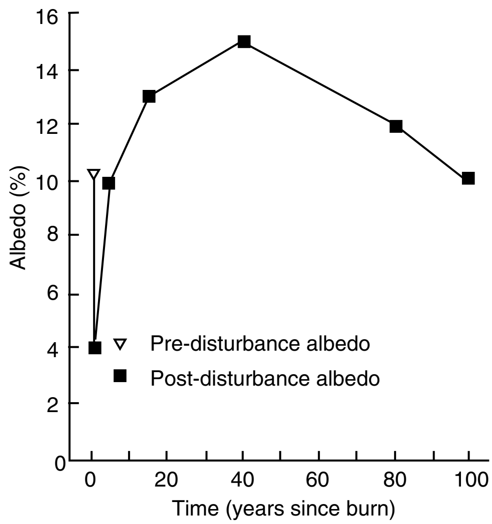

Fig. 12.12 Successional changes in albedo after fire in Alaskan boreal forests. The black post-fire surface causes a decline in albedo. Albedo increases during the herbaceous and deciduous forest phases of succession and declines in late succession due to a switch to conifer vegetation. This successional change occurs more rapidly after moderate fires because of the more rapid replacement of deciduous species by conifers. Data from Chambers and Chapin (2002)

extent to which vegetation masks the snow from incoming solar radiation (Euskirchen et al. 2009).

High surface temperatures that contribute to high emission of longwave radiation dominate energy budgets of early successional sites. Early successional sites often have a high surface temperature for several reasons: (1) The low albedo of recently disturbed sites maximizes radiation absorption and therefore the quantity of energy available at the surface. (2) The low leaf area, small root biomass, and low hydraulic conductance of dry surface soils limits the proportion of energy dissipated by evapotranspiration. (3) The relatively smooth surface of unvegetated or early successional sites minimizes mechanical turbulence that would otherwise transport the heat away from the surface. The resulting high surface temperature promotes both emission of longwave radiation and a high Bowen ratio (ratio of sensible to latent heat flux; see Chap. 4).

The large longwave emission dissipates much of the absorbed radiation after disturbance, so *net* radiation (the net energy absorbed by the surface) is not as great as we might expect from the low albedo of these sites. For example, net radiation actually declines after fire in the boreal forest despite a reduction in albedo because of the large emission of longwave radiation (Chambers et al. 2005). The soil surface of unvegetated sites is prone to drying between rain events due to the combination of high surface temperatures and the low resupply of water from depth, due to the low hydraulic conductance of dry soils (see Chap. 4). Dry surface soils provide little moisture for surface evaporation and are good thermal insulators, so both evapotranspiration and average ground heat flux are often relatively low on unvegetated surfaces (Oke 1987). Consequently, sensible heat flux accounts for the largest proportion of energy that is dissipated from these sites to the atmosphere. The absolute magnitude of sensible heat flux from early successional sites differs among ecosystems and climate zones and depends on both net radiation (the energy available to be dissipated) and the energy partitioning among sensible, latent, and ground heat fluxes. As succession proceeds, latent heat fluxes become a more prominent component of energy transfer from land to the atmosphere.

Carbon Balance

Primary Succession

In primary succession, productivity and heterotrophic respiration are often greatest in mid-succession. Primary succession begins with little live or dead organic matter, so net primary production (NPP) and heterotrophic respiration are initially close to zero. NPP increases slowly at first because of low plant density, small plant size, and strong nitrogen limitation of growth. NPP and biomass generally increase most dramatically after nitrogen fixers colonize the site. The planting of nitrogen-fixing lupines on English mine wastes (Bradshaw 1983) and the natural establishment of nitrogen-fixing alders after retreat of Alaskan glaciers (Bormann and Sidle 1990), for example, cause sharp increases in plant biomass and NPP. In primary successional sequences that lack a strong nitrogen fixer, successional increases in biomass and NPP depend on other forms of nitrogen input, including atmospheric deposition, plant and animal detritus, and lateral delivery from flowing groundwater.

Long-term successional trajectories of biomass and NPP differ among ecosystems. A common pattern in forests is that NPP increases from early to mid-succession, then declines after the forest reaches its maximum leaf area index (LAI) (Fig. 12.13; Ryan et al. 1997). Several processes may contribute to these patterns. In some forests, hydraulic conductance declines in late succession, causing water to limit the leaf area that can be supported and therefore gross primary production (GPP) and NPP (see Chap. 6). In other forests, nutrient supply declines in late succession, leading to a corresponding reduction in GPP and NPP (Van Cleve et al. 1991). It is less likely that late-successional declines in NPP reflect increased maintenance respiration to support the increasing biomass, as had been suggested earlier (Odum 1969), because much of forest biomass increase consists of dead cells that do not respire. The mortality of branches and trees often increases in late succession, as trees age. The combination of reduced NPP and increased mortality of plants and plant parts in late succession slows the rate of biomass accumulation, so biomass approaches a relatively constant value (steady state; Fig. 12.14) or declines due to stand thinning. The rate and patterns with which carbon pools and fluxes change through succession depend on both initial conditions and events and climatic fluctuations that occur during succession and are therefore variable within and among ecosystem types (Fig. 12.14; Turner 2010). The long-term endpoints of successional trajectories in biomass and NPP are also uncertain because disturbance usually resets the successional clock before the ecosystem reaches steady state.

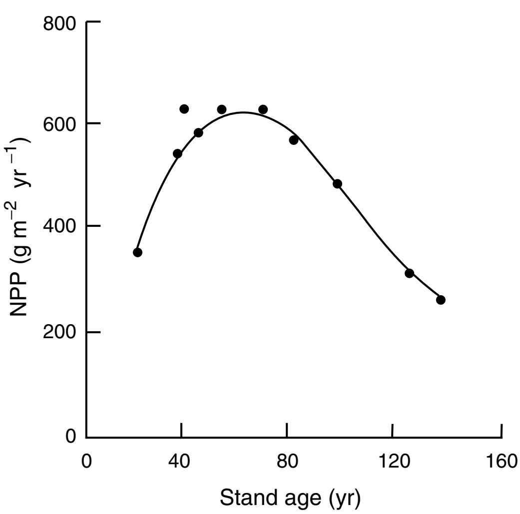

Fig. 12.13 Successional changes in aboveground spruce production in Eastern Russia. NPP declines after the forest reaches maximum LAI at about 60 years of age. Redrawn from Ryan et al. (1997)

Over extremely long time scales, changes in rates of weathering and soil development lead to further changes in biomass and other ecosystem properties (see Chap. 3). Redwoods in California coastal forests, for example, are replaced by a pygmy forest of evergreen trees and shrubs after hundreds of thousands of years due to the formation of a hard pan that prevents drainage and creates anaerobic conditions that retard decomposition and root growth (Westman 1978). The slow-growing plants capable of surviving under these low-nutrient conditions produce litter with high concentrations of phenolics, which further reduce decomposition rate, resulting in an amplifying (positive) feedback that leads to progressively lower biomass, productivity, and nutrient turnover (Northup et al. 1995).

Heterotrophic respiration rate at the start of primary succession is near zero because there is little or no soil organic matter. The low organic content of these soils contributes to their low moisture-holding capacity and CEC (Fig. 12.15; see Chap. 3). The *pattern* of change in heterotrophic respiration through primary succession is similar to the pattern described for NPP. Heterotrophic respiration, however, lags behind the changes in NPP, causing soil organic matter to accumulate (Fig. 12.16). Initially, heterotrophic respiration is low in primary succession because it is limited by the quantity of soil organic matter.

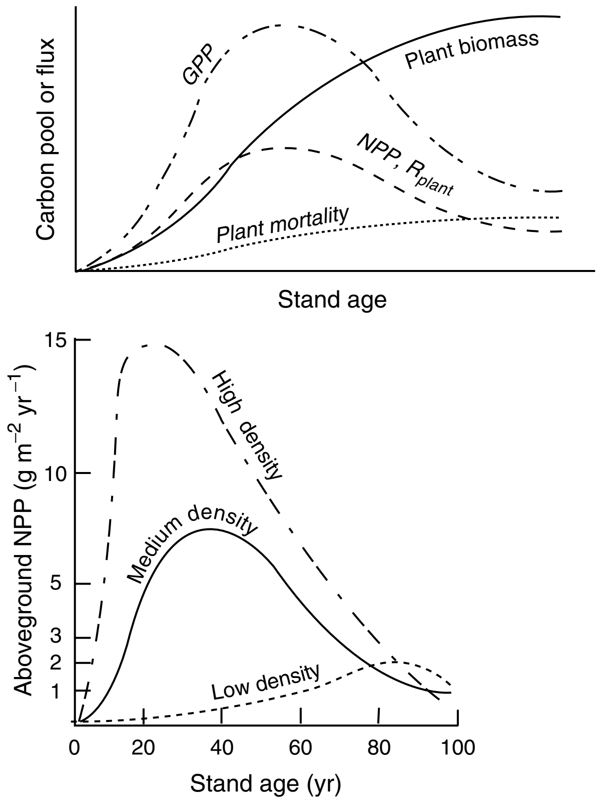

Fig. 12.14 Idealized patterns of primary successional changes in plant biomass, *GPP*, *NPP*, plant respiration (R_{plant}), and plant mortality of a forest (*top*). GPP, NPP, and plant respiration often reach a peak in mid-succession and decline in late succession. The actual patterns vary considerably among ecosystems, as illustrated by patterns of aboveground NPP hypothesized for lodgepole pine stands of different initial seedling density in Yellowstone National Park (*bottom*). Redrawn from Turner (2010)

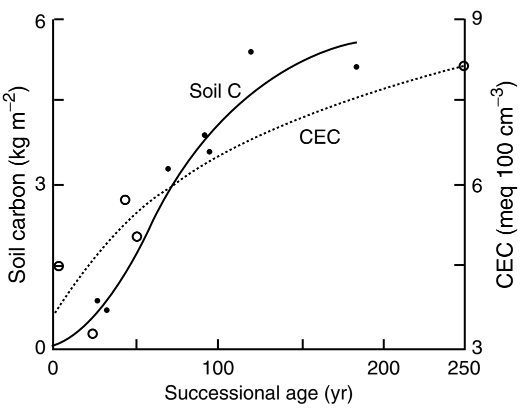

Fig. 12.15 Accumulation during succession of soil organic carbon (Crocker and Major 1955) and associated change in cation exchange capacity (CEC) of mineral soil (Ugolini 1968) after deglaciation at Glacier Bay Alaska. Measurements were made to a depth of 45 cm in mineral soil. The accumulation of soil carbon contributes to the increased CEC, which retains nutrients to support plant growth

Heterotrophic respiration increases substantially in mid-succession in response to increases in the quantity and quality of litter. In forests, the late-successional decline in NPP reduces litter inputs to soils, causing heterotrophic respiration to decline. In those ecosystems where nutrient availability declines in late succession, this reduces litter quality and quantity, further reducing decomposition rate and heterotrophic respiration (Van Cleve et al. 1993).

NEP is the balance between carbon inputs in NPP and carbon losses from heterotrophic respiration. NEP usually increases from early and mid-succession, due to the lag of heterotrophic respiration behind NPP (Figs. 12.16, 12.17). This contributes to the carbon accumulation of mid-latitude north temperate forests that established in abandoned agricultural lands one to two centuries earlier (Goulden et al. 1996, Valentini et al. 2000). NEP typically declines in late succession but generally remains positive, even after many centuries (see Fig. 7.20; Luyssaert et al. 2007, Xiao et al. 2008).

Net ecosystem carbon balance (NECB) reflects not only photosynthesis and heterotrophic respiration (i.e., NEP) but also other carbon transfers, including losses by combustion and leaching and

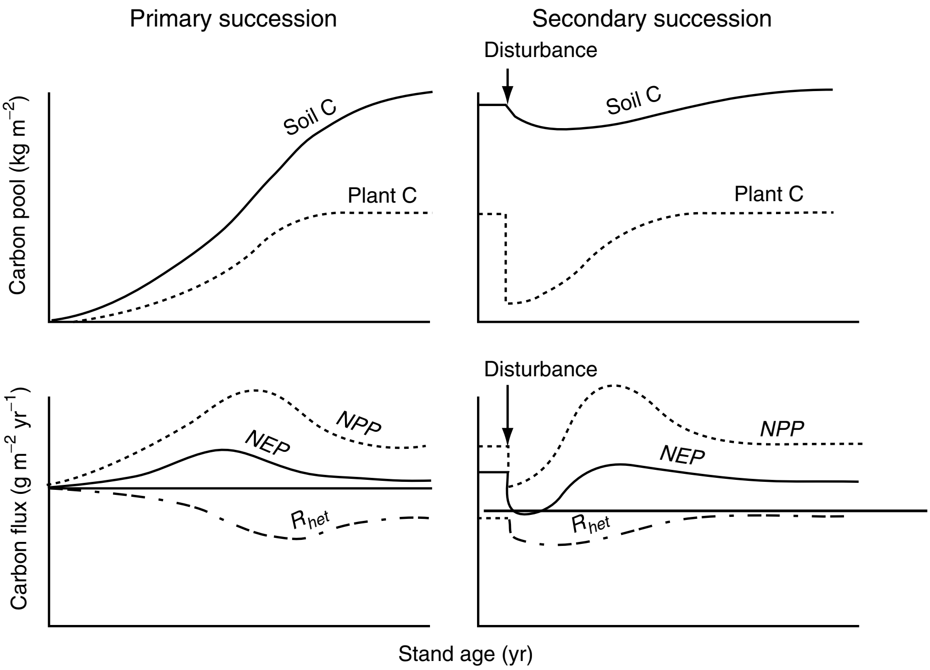

Fig. 12.16 Idealized patterns of change in carbon pools (plants and soils) and fluxes (*NPP*, R_{het}, and *NEP*) in primary and secondary succession. In early primary succession, plant and soil carbon accumulates slowly because NPP is greater than heterotrophic respiration, that is, there is a positive NEP. In early secondary succession, soil carbon declines after disturbance because carbon losses from heterotrophic respiration exceed carbon gain from NPP, leading to a negative NEP. In late succession, plant and soil carbon approach steady state (in this idealized diagram), and NEP approaches zero. In both primary and secondary succession, NPP and NEP are maximal in mid-succession. Net carbon accumulation in the ecosystem (NECB) would differ from the patterns shown, if leaching losses and other carbon fluxes are substantial

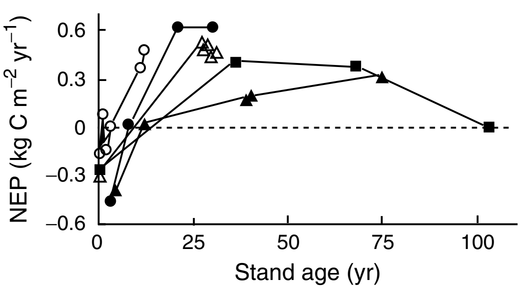

Fig. 12.17 Successional changes in NEP of European forests measured by CO_2 exchange. *Black circles*, *Picea sitkensis*; *white triangles*, *Pinus pinaster*; *gray squares*, *Pinus sylvestris*; *black triangles*, *Pinus sylvestris*; *white circles*, *Quercus cerris*. Redrawn from Magnani et al. (2007)

lateral transfers among ecosystems (e.g., animal movements, forest harvest, and food or waste transfers). Like NEP, NECB typically remains positive in mid to late succession (Magnani et al. 2007, Luyssaert et al. 2008), indicating that ecosystem carbon balance seldom reaches steady state before disturbance recurs. Alternatively, late-successional ecosystems may be responding to recent environmental changes (rising temperature, atmospheric CO_2, and nitrogen deposition) that support continued carbon accumulation (Magnani et al. 2007, Luyssaert et al. 2008) or loss (Oechel et al. 2000). In the boreal forest, climate warming governs NECB more strongly through effects on fire regime than through its effects on NEP (Bond-Lamberty et al. 2007).

Secondary Succession

The initial carbon pools and fluxes are much larger in secondary than in primary succession. Carbon dynamics are dramatically different between secondary and primary succession because secondary succession begins with an initial stock of soil organic matter. Immediately after disturbance, NPP is low in secondary succession because of low plant biomass, just as in primary succession (Fig. 12.16). NPP recovers more quickly in secondary than in primary succession, however, due to the generally rapid colonization and high growth rate of herbs, grasses, and resprouting perennial species. High availability of light, water, and nutrients supports the high growth potential of early successional vegetation in many secondary successional sequences. The herbaceous species that dominate most early secondary successional sites return most of their biomass to the soil each year. Perennial plants, particularly woody species, increase in abundance, biomass, and NPP more rapidly because they retain a larger proportion of their biomass. Changes in biomass and NPP in mid- and late secondary succession are similar to patterns described for primary succession (Figs. 12.13, 12.16) because they are controlled by the same factors and processes – largely the soil resources available to support production and the growth potential of the species typical of the ecosystem.

In contrast to primary succession, heterotrophic respiration in mesic ecosystems is often quite high early in secondary succession (Fig. 12.16) because many disturbances transfer large amounts of labile carbon to soils and create a warm, moist environment that is favorable for decomposition. The size of the initial input to the soil carbon pool depends on the type and severity of the disturbance. After a treefall, hurricane, or insect outbreak, there are large inputs of new labile carbon from leaf and root death. Fire consumes some of the surface SOM but also adds new carbon to the soil through death of roots and unburned aboveground plant material. The large quantity and high quality of litter of early secondary successional plants also promotes heterotrophic respiration. In mid-succession, the regrowing vegetation uses an increasing proportion of the available water and nutrients and reduces soil temperature by shading the soil surface. These changes in environment cause a decline in decomposition. Heterotrophic respiration declines in late succession because the decline in NPP reduces litter input; litter quality often declines; and the environment becomes less favorable than in early succession.

How do these contrasting patterns of NPP and heterotrophic respiration affect NEP? In early secondary succession, NEP is negative because heterotrophic respiration causes large carbon losses, and there is little NPP (Figs. 12.16, 12.17). In early succession before the peak in NPP, ecosystems begin accumulating carbon again, as soon as NPP outpaces heterotrophic respiration. In late succession, ecosystems typically accumulate carbon at a slow rate that depends on the environmental limitations to NPP and heterotrophic respiration (Magnani et al. 2007, Luyssaert et al. 2008). Other avenues of carbon loss from ecosystems such as leaching of dissolved organic carbon may influence NECB in ways that are not readily predicted from successional dynamics.

Although the successional patterns of NPP, heterotrophic respiration, and carbon stocks in plants and soils that we have described are often observed, the details, timing, and long-term trajectory of these patterns differ substantially within and among ecosystems, depending on factors such as initial ecosystem carbon stocks, resource availability, disturbance severity, and successional pathway (Turner 2010).

Nutrient Cycling

Primary Succession

Nutrient dynamics during succession are both a cause and a consequence of the dynamic interplay between NPP and decomposition. The most dramatic change in nutrient cycling during early primary succession is the accumulation of nitrogen in vegetation and soils. Most parent materials have extremely low nitrogen contents in the absence of biotic influences, so the initial nitrogen pools in the ecosystem are small and depend on atmospheric inputs. At this initial stage of primary succession, nitrogen is the element that most strongly limits plant growth and therefore the rates of accumulation of plant biomass and SOM (Crocker and Major 1955, Vitousek 2004). The rate of nitrogen input, which is often associated with the establishment of nitrogen-fixing plants (both free-living cyanobacteria and symbiotic nitrogen fixers), therefore governs the initial dynamics of nutrient cycling in primary succession. As leaves and roots of nitrogen-fixing plants senesce and are eaten by herbivores, the nitrogen is transferred from plants to the soil, where it is mineralized and absorbed by both nitrogen-fixing and non-fixing plants. Litter from non-nitrogen-fixing plants becomes an increasingly important source for nitrogen mineralization as primary succession proceeds. This causes the ecosystem to shift from an open nitrogen cycle, with substantial input from nitrogen fixation (see Chap. 9), to a more closed nitrogen cycle in which plant growth depends on the mineralization of soil organic nitrogen. During mid-succession, plants and soil microbes are so efficient at accumulating nutrients that losses of nitrogen and other essential elements from ecosystems are often negligible (Fig. 12.18; Vitousek and Reiners 1975). In late-successional ecosystems that approach steady state (NECB approximately zero), nitrogen inputs to the ecosystem may be largely balanced by nitrogen losses from leaching (especially as dissolved organic nitrogen) and denitrification, causing ecosystem nitrogen pools to approach a relatively stable size. In those ecosystems where NECB remains positive, nitrogen will also likely continue to accumulate.

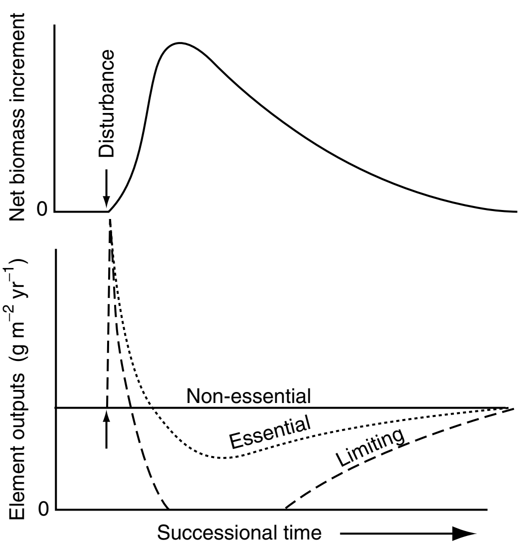

Fig. 12.18 Changes through succession in net biomass increment in vegetation and in the losses of limiting, essential, and nonessential elements. In early succession, when biomass accumulates rapidly, elements that are required for this production (especially growth-limiting elements) accumulate in new plant and microbial biomass, so they are not lost from the ecosystem by leaching. In late succession, when the element requirements for new plant and microbial biomass are balanced by element release from the breakdown of dead organic matter, nutrient inputs to the ecosystem are approximately balanced by nutrient outputs, regardless of whether nutrients are required by vegetation or not. Modified from Vitousek and Reiners (1975)

The accumulation of other essential elements during primary succession depends on accumulation in biotic pools and the formation of secondary minerals. Early in primary succession, biological storage pools in vegetation and soils are small, and so they can retain only a small fraction of the elements mobilized by weathering. Abiotic processes, especially the formation of secondary clay minerals (see Chap. 3), are more important in retaining many elements, both through the incorporation of some elements (e.g., magnesium) into clay lattices and through cation-exchange processes. The formation of secondary clay minerals and the elements they retain vary depending on climate (with a larger fraction of elements retained by the clays that form in dry sites) and parent material (with the formation of highly reactive allophone in volcanic areas). Organic matter is more important as a source of, and sink for, elements later in primary succession and throughout secondary succession.

Later in soil development, additional changes in nutrient cycling occur as the supply of weatherable minerals is depleted or becomes bound in unavailable forms. Availability of phosphorus and cations, for example, typically declines in old, highly weathered sites as they leach or become bound in unavailable forms (see Chaps. 3 and 9). Under these circumstances, phosphorus or other elements may limit plant production (Chadwick et al. 1999), and cycling rates of these limiting elements regulate cycling rates of nitrogen and other minerals.

Secondary Succession

Secondary succession after natural disturbances differs from primary succession because it generally begins with higher nitrogen availability. Natural disturbances that initiate secondary succession produce a pulse of nutrient availability because disturbance-induced changes in environment and litter inputs increase mineralization of dead organic matter and reduce plant biomass and nutrient absorption. Fires, which may volatilize large amounts of nitrogen, also return nutrients in ash, as described earlier, leading to increased nutrient availability after fire (Wan et al. 2001). Plant growth is therefore generally less strongly nutrient-limited early in secondary succession compared to primary succession, nitrogen is usually adequate to support high rates of photosynthesis and growth (Scatena et al. 1996, Smithwick et al. 2005). The pulse of nutrient availability and the reduction in plant biomass and capacity for plant absorption after disturbance also increase the vulnerability of ecosystems to nutrient loss. High rates of nitrogen mineralization and nitrification stimulate the production of nitrate that can be denitrified or leached below the rooting zone. The occurrence or extent of nitrogen loss depends on the balance between nitrogen mineralization and absorption by plants and microbes. Rains that occur immediately after a fire (Minshall et al. 1997, Betts and Jones 2009) or hurricane (Schaefer et al. 2000) often leach nitrate into groundwater and streams. These nutrient losses to streams decline as nutrients are immobilized by microbes and absorbed by regrowing vegetation (Turner 2010).

The vulnerability of ecosystems to nutrient losses after disturbance has been illustrated in many forest-harvest experiments, such as those at Hubbard Brook in the U.S. After stream discharge and chemistry had been monitored for several years, the forest was cut on an entire watershed and regenerating vegetation was killed with herbicides (Bormann and Likens 1979). The combination of high decomposition and mineralization rates and absence of plant absorption after disturbance caused large losses of essential plant nutrients in stream water (see Fig. 9.14). When vegetation was allowed to regrow, the increased plant absorption caused nutrient losses in stream water to decline to pre-harvest levels. These studies show clearly that the dynamics of nutrient loss after disturbance are highly variable, with the extent of nutrient loss often depending on nutrient availability at the time of disturbance and the capacity of regenerating vegetation to absorb nutrients.

Human disturbances create a wide range of initial nutrient availabilities. Some disturbances, such as mining, can produce an initial environment that is even less favorable than most natural primary successional habitats for initiation of succession. These habitats may have toxic by-products of mining or mineral material with a low capacity for water and nutrient retention. Some agricultural lands are abandoned to secondary succession after erosion or (in the tropics) formation of plinthite (iron- and aluminum-rich) soil horizons (see Chap. 3), reducing the nutrient-supplying power of soils. Secondary succession in degraded lands may therefore be quite slow. At the opposite extreme, abandonment of rich agricultural lands or the logging of productive forests may create conditions of high nutrient availability, leading to the potential loss of nutrients through leaching and denitrification. These nutrient losses are particularly dramatic in the tropics, where rapid mineralization and biomass burning associated with forest clearing release large amounts of nitrogen as trace gases (NO_x and N_2O) and as nitrate in groundwater (Matson et al. 1987). The impact of agricultural nutrient additions is particularly long-lived for phosphorus because of its effective retention by soils. An understanding of the successional controls over nutrient cycling provides the basis for management strategies that minimize undesirable environmental impacts (see Chap. 15). The return of topsoil or planting of nitrogen-fixing plants on mine wastes, for example, greatly speeds successional development on these sites (Bradshaw 1983). Retention of some organic debris after logging may support microbial immobilization of nutrients that would otherwise be lost.

Trophic Dynamics

The proportion of primary production consumed by herbivores is maximal in early to mid-succession. In early primary and secondary succession, rates of herbivory may be low because of low food density, insufficient cover to hide vertebrate herbivores from their predators, and insufficient canopy to create a humid, non-desiccating environment for invertebrate herbivores. Herbivory is often greatest in early to mid-secondary succession because the rapidly growing herbaceous and shrub species that dominate this stage have high nitrogen concentrations and a relatively low allocation to carbon-based plant defenses (see Chap. 10). This explains why abandoned agricultural fields, recent burn scars, or riparian areas are focal points for browsing mammals, insect herbivores, and their predators. In early successional boreal floodplains, for example, moose consume about 30% of aboveground NPP and account for a similar proportion of the nitrogen inputs to soil (Kielland and Bryant 1998). The abundant insect herbivores on these sites support a high diversity of neotropical migrant birds. Similarly, in temperate and tropical regions, early successional forests support large populations of deer and other browsers. In ecosystems in which nutrient availability declines from early to late succession, plants shift allocation from growth to defense (see Chap. 10). The resulting decline in forage quality reduces levels of consumption by most herbivores and higher trophic levels. Some insect outbreak species are an important exception to this successional pattern. They often attack late-successional trees that are weakened by environmental stress (Raffa et al. 2008).

Vertebrate herbivores can either promote or retard succession, depending on their relative impact on early vs. late-successional species. Vertebrate herbivores both respond to (see Chap. 10) and contribute to successional change. The effects of herbivores on succession differ among ecosystems, depending on the nature and specificity of plant–herbivore interactions. However, several common patterns emerge.

In forested regions, birds, rodents, and other vertebrates often enhance the dispersal of early successional species such as blackberries, junipers, and grasses into abandoned agricultural fields and other disturbed sites. Birds and squirrels also disperse the large seeds of late-successional species such as oak and hickory into early successional sites. These animal-mediated dispersal events are particularly important in secondary succession, where the rapid development of herbaceous vegetation makes it difficult for small-seeded woody species to compete and establish successfully.

The relatively low levels of carbon-based plant defenses in species that typically characterize early secondary forest succession make these plants a nutritious target for generalist insect and vertebrate herbivores. Preferential feeding on these species reduces their height growth and reproductive output. Browsed plants respond to aboveground herbivory by reducing root allocation, making them less competitive for water and nutrients (Ruess et al. 1998). Many late-successional species produce chemical defenses that deter generalist herbivores. Selective herbivory contributes to the **competitive release** of late successional species, enabling them to overtop and shade their early successional competitors. In this way, selective browsing by mammals often speeds successional change in forests (Pastor et al. 1988, Kielland and Bryant 1998, Paine 2000). In tropical rainforests, mammalian herbivores maintain the diversity of understory seedlings that become the next generation of canopy dominants because they feed preferentially on the "weedy" tree seedlings that are most common in the understory (Dirzo and Miranda 1991).

In contrast to forests, many grasslands and savannas are maintained by mammalian herbivores that prevent succession to forests. Elephants, for example, browse and uproot trees in African savannas. These savannas succeed to closed forests in areas where elephant populations have been reduced by overhunting. In North American prairies, browsers and fire restrict the invasion of trees. When these sources of disturbance are reduced, trees often invade and convert the grassland to forest. Similarly, at the end of the Pleistocene, the decline in large mammals that occurred on many continents, in part from human hunting, contributed to the vegetation changes that occurred at that time (Flannery 1994, Zimov et al. 1995, Gill et al. 2009).

Herbivores have multiple effects on nutrient cycling in early succession. In the short term, they enhance nutrient availability by returning available nutrients to the soil in feces and urine, which short-circuits the decomposition process (Kielland and Bryant 1998). Herbivory can also alter the temperature and moisture regime for decomposition at the soil surface by reducing leaf and root biomass. The quality of litter that a given plant produces is also enhanced by herbivory (Irons et al. 1991). Over the long term, however, herbivory accelerates plant succession by removing early successional species, which tends to reduce nutrient cycling rates and nutrient losses (see Fig. 10.9; Pastor et al. 1988, Kielland and Bryant 1998).

Temporal Scaling of Ecological Processes

Temporal extrapolation requires an understanding of the typical time scales of important ecological processes. Ecologists generally measure ecological processes for shorter time periods than the time scales over which we would like to make predictions. No studies, for example, provide detailed information about the functioning of ecosystems over time scales of decades to centuries – the time scale over which ecosystems are likely to respond to global environmental change. **Temporal scaling** is the extrapolation of measurements made at one time interval to longer (or occasionally shorter) time intervals. Simply multiplying an instantaneous flux rate by 24 h to get a daily rate or by 365 days to get an annual rate seldom gives a reasonable approximation because this ignores the temporal variation in driving variables and the time lags and thresholds in ecosystem responses to these drivers. Rates of photosynthesis, for example, differ between night and day and between summer and winter.

One approach to temporal scaling is to select measurements that are consistent with the time scale and question of interest. A second approach is to extrapolate results based on models that simulate processes accounting for important sources of variation over the time scale of interest. The key to temporal scaling is therefore to focus clearly on the processes that are important over the time scales of interest. Entire books have been written on temporal scaling based on isotopic measurements (Ehleringer et al. 1993), long-term measurements (Sala et al. 2000), and modeling (Ehleringer and Field 1993, Waring and Running 2007). Here we provide a brief overview of these approaches.

Isotopic tracers are an important tool for estimating long-term rates of net carbon exchange of plants and ecosystems because they integrate the net effect of carbon and some nutrient inputs and losses throughout the time period of carbon exchange (see Box 5.1). ^{13}C content of plants in dry environments, for example, provides an integrated measure of water use efficiency (WUE) during the time interval during which the plant material was produced. ^{13}C content of soils in ecosystems that have changed in dominant vegetation from C_3 to C_4 plants provides an integrated measure of soil carbon turnover since the time that the vegetation change occurred. These measurements are appropriate for estimating long-term rates because they incorporate effects of processes that occur slowly or intermittently that might not be captured in short-term gas-exchange measurements. Seasonally integrated water use efficiency measured with stable isotopes, for example, is affected by dry and wet periods that influence seasonal water and carbon exchange, whereas instantaneous measurements of gas exchange are unlikely to be representative of the entire annual cycle. Similarly, NPP integrates over longer time periods than does photosynthesis or respiration, and successional changes in soil carbon stocks integrate over longer time periods than do measurements of NPP and decomposition.

Process-based models are important tools for temporal scaling because they make projections of the state of the ecosystem over longer time intervals (or at different times or places) than can be measured directly. The challenge in developing models for temporal extrapolation is the selection of the driving variables that account for the most important sources of temporal variation over the time scale of interest. The diurnal pattern of net photosynthesis can often be adequately simulated based on the relationship of net photosynthesis to light and temperature. Annual estimates of photosynthetic flux (GPP), however, also require information on seasonal variation in leaf biomass and photosynthetic capacity. In annual simulations, the diurnal variation in photosynthesis is less important to model explicitly because it is quite predictable, based on the empirical relationship between daily photosynthesis and average daily temperature and light. **Slow variables**, such as successional changes in LAI or nitrogen availability, are often treated as constants in

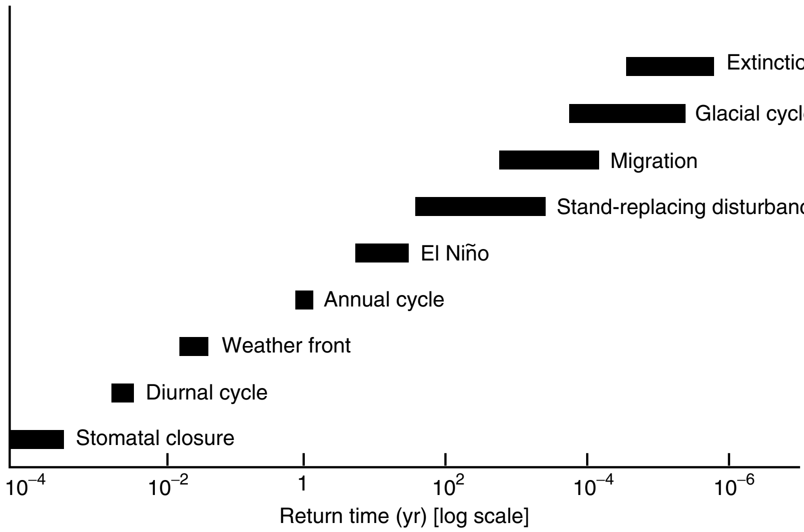

Fig. 12.19 Variation in return time for variables that strongly affect ecosystem processes. For any particular process, such as NPP, fast variables like stomatal closure can be ignored, slow variables like El Niño or stand-replacing disturbance strongly affect the process, and extremely slow variables, such as glacial cycles can be treated as constants

short-term ecological studies, but can become key control variables over longer time scales (Peterson et al. 1998, Carpenter and Turner 2000). We must therefore think carefully about which critical driving variables are likely to change over the time scale of intended predictions and look for evidence of the relationship of ecological processes to these slow variables. Models of carbon flux based on the relationship of GPP and respiration to daily or monthly climate, for example, can be validated by comparing model output to patterns of carbon flux observed over longer time scales (e.g., interannual variation in carbon flux). Ecosystem controls vary over a wide range of temporal scales (Fig. 12.19).

Spatial variation in driving variables sometimes gives hints as to which slow variables are important to include in long-term extrapolations. The spatial relationship between the distribution of biomes or plant functional types and climate, for example, has been used to predict how vegetation might respond to future climatic warming (Prentice et al. 1992, VEMAP-Members 1995, Euskirchen et al. 2009). Spatial relationships with driving variables often reflect quasi-equilibrium relationships. Tropical dry forests, for example, occur where the average climate is warm and has a distinct dry season. Temporal extrapolations should also consider extreme events and time lags that may not be evident from an examination of spatial pattern. Ice-storms, a spring freeze, intense droughts, 100-year floods, and other events with long-lasting effects strongly influence the structure and functioning of ecosystems long after they occur.

Summary

Ecosystem processes are constantly adjusting to past changes that have occurred over all time scales, ranging from sun flecks that last milliseconds to soil development that occurs over millions of years. Ecosystem processes that occur slowly, such as soil organic matter development, deviate most strongly from steady state and are most strongly affected by legacies of past events. Ecosystem processes are highly resilient to predictable changes in environment such as those that occur diurnally and seasonally and in response to disturbances to which organisms are well adapted.

Stand-replacing disturbances greatly reduce evapotranspiration and increase runoff. Evapotranspiration increases through succession more rapidly than might be expected from biomass recovery because early successional vegetation has high transpiration rates. Sensible heat flux tends to show the reverse successional pattern with high sensible heat flux (or longwave radiation) immediately after disturbance and lower sensible heat flux as rapidly growing mid-successional vegetation establishes and transfers energy to the atmosphere as water vapor.

Because disturbance is a natural component of all ecosystems, the successional changes in ecosystem processes after disturbance are important to understanding regional patterns of ecosystem dynamics. Successional changes in ecosystems are particularly sensitive to the severity, frequency, and type of disturbance. Through primary succession, carbon accumulates in vegetation and soils and leads to positive NEP because changes in decomposition lag behind changes in NPP. NPP in forests is often greatest in mid-succession. Secondary succession begins with a large negative NEP due to low NPP and rapid decomposition, but carbon cycling in mid- and late succession is similar to the patterns in primary succession.

Nutrient cycling changes through early primary succession as nitrogen fixers establish and add nitrogen to the ecosystem. Other elements cycle in proportion to the cycling of nitrogen. In secondary succession, however, nitrogen is generally most available in early succession. At this time, nitrogen and other elements are vulnerable to loss until the potential of plants and microbes to absorb nutrients exceeds the rate of net mineralization. This tightens the nitrogen cycle. Recycling within the ecosystem is strongest in mid-succession, when rates of nutrient mineralization constrain the rates of absorption by vegetation.

The role of herbivores in succession differs among ecosystem types and successional stages. Mammals often accelerate the early successional changes in forests by eliminating or reducing the competitive ability of palatable early successional species. In grasslands, however, herbivores prevent the establishment of woody species that might otherwise transform grasslands into shrublands and forests. Some insects have their greatest impact in late succession, particularly in forests, where they can be important agents of mortality.

Review Questions

1. Provide examples of ways in which the carbon and nitrogen cycling of an ecosystem might be influenced by the legacy of events that occurred 1 week ago, 5 years ago, 100 years ago, 2,000 years ago.
2. What properties of disturbance regimes determine the ecological consequences of disturbance? How do these properties differ between treefalls in a tropical wet forest and fire in a dry conifer forest?
3. What are the major processes causing successional change in plant species? How does the relative importance of these processes differ between primary and secondary succession?
4. How do NPP, decomposition, and the carbon pools in plants and soils change through primary succession? At what successional stage does carbon accumulate most rapidly? Why? How do these patterns differ between primary and secondary succession? Why do these differences occur?
5. How does nitrogen cycling differ between primary and secondary succession? At what stages is this difference most pronounced?
6. How do trophic dynamics change through succession? Why?
7. How do water and energy exchange change through succession? What explains these patterns?
8. What are the major issues to consider in extrapolating information from one temporal scale to another? Describe ways in which this temporal extrapolation might be done.

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