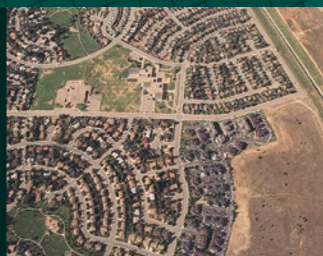
Monica G. Turner
Robert H. Gardner






Landscape Ecology in Theory and Practice

Pattern and Process

Second Edition

Springer

CHAPTER 2

Causes of Landscape Pattern

When we view a landscape, we look at its *composition* and *spatial configuration*—that is, what elements are present and in what relative amount, and how these elements are arranged. In an agricultural landscape, we may observe forests occurring along streams and on steep ridges, whereas croplands and pastures occupy upland areas of gentler slope. In a fire-dominated boreal forest landscape, we may see expanses of old forest, young forest, and early successional vegetation. In a deciduous forest, we may observe small gaps in an otherwise continuous canopy of trees, and we may detect boundaries between forests dominated by different species of trees. In landscapes of small extent (e.g., 100 m by 100 m), we may observe complex patterns of vegetated and unvegetated surfaces. Observations of landscape patterns can trigger a number of general questions: How do all these different patterns develop? What is the relative importance of different causes? Do similar patterns emerge from similar processes? How do landscape patterns change through time? What conditions produce gradual vs. abrupt changes in landscape patterns? Can future patterns be predicted? For how long are patterns discernible after the processes creating the patterns have ceased?

M.G. Turner, R.H. Gardner, *Landscape Ecology in Theory and Practice*,
DOI 10.1007/978-1-4939-2794-4_2

Contemporary landscapes result from many causes, including variability in *abiotic conditions*, such as climate, topography, and soils; *biotic interactions*, such as competition, mutualism, herbivory, and predation, that can generate spatial pattern even when environmental conditions are homogenous; *natural disturbances and succession*; and past and present patterns of *human land use*. Broad-scale variability in the abiotic environment sets the constraints within which biotic interactions and disturbances act. The environmental template sets the stage, but landscape patterns result from multivariate causes that operate and interact over many scales in time and space.

Long-term changes have been profound in many landscapes (Fig. 2.1), yet such changes are often underappreciated. Landscapes are constantly changing, each with a unique history. Many historical studies have provided data that lead to reinterpretations of the contemporary landscape (Foster 2002). Landscape ecologists must account for these long-term changes, and reconstructed landscape histories are an invaluable resource for clearer interpretation of contemporary patterns and dynamics. Determining how and why these histories developed is also critical for anticipating the future (Jackson 2006).

FIGURE 2.1.

This aerial view of Dubai illustrates a profound change in a desert landscape. *Source*: http://flagvruki.com/pictures/design-pic/dubay-s-vysoty-ptichego-poleta/

Exploring the causes of landscape pattern is not so easy as it may seem. Every landscape is unique because the observed spatial patterns result from multiple drivers and include both deterministic and stochastic processes. In a thought-provoking essay, Phillips (2007) developed an analogy between the "perfect storm," which refers to the improbable coincidence of several different factors or forces that produces an unusual outcome, and the "perfect landscape." The perfect landscape results from the combined, interacting effects of multiple environmental controls and drivers that generate a landscape unlikely to be duplicated at any other place or time. In other words, any particular landscape is a singular outcome from a range of plausible outcomes that depended on the occurrence or timing of different driving factors. This view of *multiple and contingent causation* supports an understanding of landscape pattern that allows for multiple outcomes rather than a single, deterministic result from a given set of conditions (Phillips 2007). Landscape patterns are idiosyncratic because of contingent factors that are particular in time and space. The critical observation that "it depends" complicates the task of explaining and predicting landscape patterns: similar landscapes may develop from contrasting trajectories, and different landscapes may have originated from similar initial conditions (Ernoult et al. 2006).

Contingencies that affect landscape patterns may be manifest in several ways. *Historical contingencies* exist when the current state of a landscape is clearly dependent on a specific past event or sequence of events. The term *landscape legacy* is often used to denote a persistent effect of past events or patterns on the contemporary landscape. *Spatial contingencies* exist when the state of a landscape depends on local conditions as well as the surrounding area. That is, characteristics at a given place also depend on characteristics at other locations, and thus changes at a particular location may be propagated spatially through the landscape (Phillips 2007). In practice, the reality of multiple interacting drivers and plausible outcomes means that elucidating the causes of landscape pattern remains surprisingly difficult (i.e., explained variance may be low), and predicting future patterns is not a trivial challenge.

Important information about the causes and changes in landscape patterns comes from the field of *paleoecology*, the study of individuals, populations, and communities of plants and animals that lived in the past and their interactions with changing environments. Paleoecology offers a wealth of insight into the long-term development of today's landscapes and has reestablished its ties with *biogeography*, which seeks to explain patterns of species distribution. One of the most important reasons for understanding landscape history is that we are in a period of rapid global change, and the past can provide us with important insights. We do not attempt a comprehensive review of this rich field, but we draw upon paleoecological studies to discuss the role of climate in the spatial structuring of the biota and the role of prehistoric humans in influencing landscapes. The *Holocene Epoch* (approximately the past 10,000 years) is of particular importance for understanding long-term landscape dynamics because it spans the current interglacial period. Studies in *environmental history* have also produced tremendous insights into how landscapes develop and change.

In this chapter, we discuss the general classes of factor that give rise to landscape patterns, provide a deeper temporal context for understanding present-day patterns, and elaborate the importance of landscape legacies. We then summarize some of the persistent challenges to explaining and predicting landscape change.

FOUR KEY DRIVERS OF LANDSCAPE PATTERN

The Abiotic Template

Landscape patterns develop on the template established by climate, landform, and soils. *Climate* refers to the composite, long term, or generally prevailing weather of a region (Bailey 2009), and climate acts as a strong control on biogeographic patterns through the distribution of energy and water. Climate effects are modified by *landform*—the characteristic geomorphic features of the landscape, which result from geologic process producing patterns of physical relief and soil development. Together, climate and landform establish the template upon which the soils and biota of a region develop.

Climate

General climatic patterns will be familiar to all ecologists from introductory classes in biology or geography (readers might also consult Ruddiman 2008). At the broadest scale, climate varies with latitude, which influences temperature and the distribution of moisture, and with continental position. Because of differential heating of land and water, coastal regions at any given latitude differ from inland regions. The distributions of biomes on Earth result from these broad-scale climate patterns. However, the effects of both latitude and continental position are modified locally by topography, leading to finer scale heterogeneity in climate patterns (Bailey 2009). Temperatures generally decrease with increasing elevation, and north- and south-facing slopes experience different levels of solar radiation and hence different temperatures and evaporation rates.

Landscape ecologists must appreciate the importance of climate (and climate variability) as a driver of pattern. If the currently estimated magnitude of climate change is realized, climate-induced effects will profoundly alter landscape patterns and processes. Even in the absence of intensive human influences, the distribution of plant and animal communities and of entire biomes have varied tremendously with past changes in climate (Jackson 2006). The spatial distribution of today's life forms as a function of latitude/longitude looks quite different than those of 5000 or 10,000 years before present (BP). Furthermore, present assemblages of plants and animals represent only a portion of the ecosystem types that have existed during Earth's history, and future rates of change suggest that *"no-analog"* *communities* (i.e., communities that differ in composition from any that currently exist) will develop in the future (Williams and Jackson 2007). The Earth is warming rapidly in response to human-caused increases in greenhouse gases in the atmosphere, and this warming will continue into the foreseeable future (IPCC 2013). The rate and magnitude of expected climate change means that understanding climate as a driver will remain an active and critically important area for study, and we treat this topic in greater depth in Chap. 9. Already, studies have shown that organisms are rapidly shifting their distributions to higher latitudes and elevations (Chen et al. 2011); disturbance regimes are changing (Westerling et al. 2006); and permafrost, glaciers, and sea ice are melting (e.g., Perovich 2011). Thus, it is important for landscape ecologists to have a general understanding of climate variability and its potential effect on landscapes. We return to this topic in Chap. 9.

Earth's climate is dynamic. Glaciers have advanced and retreated several times during the past 500,000 years. Each glacial–interglacial cycle was about 100,000 years in duration, with 90,000 years of gradual climatic cooling followed by a period of rapid warming and 10,000 years of interglacial warmth. The peak of the last glacial period, or ice age, was about 18,000 years BP and ended approximately 10,000 years BP. These long climate cycles may be produced by cyclic changes in solar irradiance resulting from long-term and complex variation in Earth's orbital pattern (the Milankovitch Cycle) as the earth wobbles on its rotational axis (Crowley and Kim 1994; Overpeck et al. 2003). This orbital eccentricity results in approximately 3.5 % variation in the total amount of solar radiation received by earth and changes its latitudinal distribution.

During the past 150,000 years, the difference between the glacial and interglacial periods was described by a 5 °C shift in mean global temperature. To detect trends in the global climate system, climatologists remove spatial variability in climate by using mean global temperature, which is the only reliable expression of global surface air temperature. Thus, what may seem like small changes in mean global temperature can indicate very large fluctuations in temperature at many locations on Earth. For example, the *Medieval Warm Period* and the *Little Ice Age*, which lasted for >500 years, had large impacts on human populations and were only a 1 °C fluctuation in mean global temperature. Similarly, peak warming (about 1–2°C warmer than today) occurred between 9000 and 4000 years ago. This seemingly small increase led to a 70-km shift eastward in the prairie–forest boundary in the Upper Midwest (USA) compared to its present location. Recent studies suggest that direct and indirect effects of warming climate will result in "savannification" of the forest and once again shift this ecotone northward within the next 50–100 years (Frelich and Reich 2010).

An improvement in understanding the variability in Earth's climate and the ecological consequences of climate fluctuations has been documentation of global-scale climate anomalies, including the El Niño–Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), and Atlantic Multidecadal Oscillation (AMO).

ENSO and the PDO represent variation in sea-surface temperatures and sea-level atmospheric pressure in the equatorial and northern Pacific Ocean that, in turn, affect climate—especially drought—in western North America through midlatitude teleconnections (e.g., Diaz and Markgraf 2000). The AMO reflects slowly varying temperature patterns in the Atlantic Ocean. Drought and wetter-than-usual conditions in different regions are often associated with different phases of these climate anomalies. The La Niña phase of ENSO and warm phase of the AMO both contributed to the extreme 2010–2011 drought in Texas, USA (Nielsen-Gammon 2011). The combined cool phases of the PDO and ENSO (negative PDO during La Niña) are associated with drought and promote large fires in the southern Rocky Mountains, whereas the combined warm phases (positive PDO during El Niño) have such associations in the central and northern Rocky Mountains (Schoennagel et al. 2005). Future warming in the region is expected to increase the frequency of large fires and produce substantial increases in the area burned each year (Fig. 2.2).

The Earth's biota obviously must respond to climate fluctuations. Each species has a unique, multidimensional *fundamental niche*, defined as the environmental envelope within which viable populations can be maintained (Araújo and Guisan 2006). As climate fluctuates, the geographic distribution of environmental conditions that are suitable for any given species to survive and reproduce also shifts. In general, organisms may respond to climate change in three ways (Cronin and Schneider 1990), all of which contribute to long-term changes in their distribution: (1) organisms may evolve and speciate in response to changing patterns of selective forces; (2)

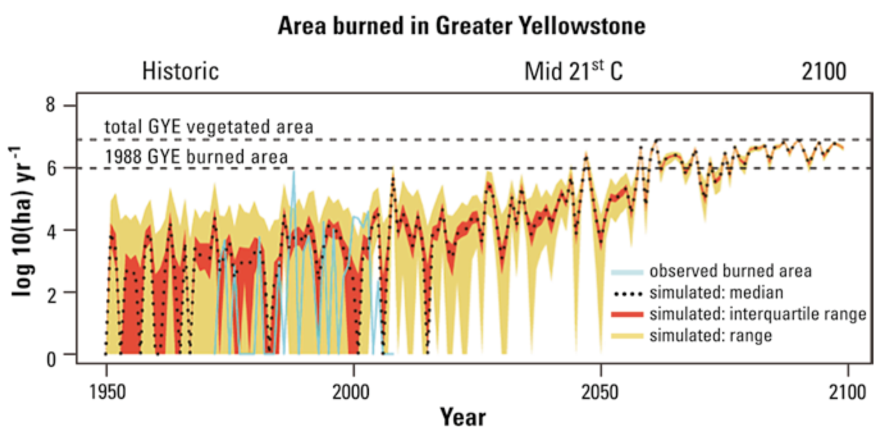


Figure 2.2.

Increased area burned associated with climate warming is projected for the Greater Yellowstone region of Wyoming, USA. Projected annual area burned (median, interquartile range, and full range) is shown here based on 1000 simulations using one global climate model through 2100. Area burned increases and years without fire decline substantially by midcentury.

Adapted from Westerling et al. (2011)

organisms may disperse and migrate to track suitable habitat, each according to its limits of tolerance and movement capability; or (3) species may become extinct if they neither adapt or move. Paleoecological research offers windows to the past by describing the vegetation patterns and shifts that accompanied past changes in climate. For example, classic research by Margaret Davis revealed that range limits of tree species in eastern North America changed dramatically during the past 13,000 years (Fig. 2.3) (Davis 1983). Species have varied not only in their ranges (i.e., the geographic area over which they occur), but also their local abundances—and thus relative dominance. For example, the range of oak (*Quercus*) in eastern North America expanded northward during the past 20,000 years, and the population centers where

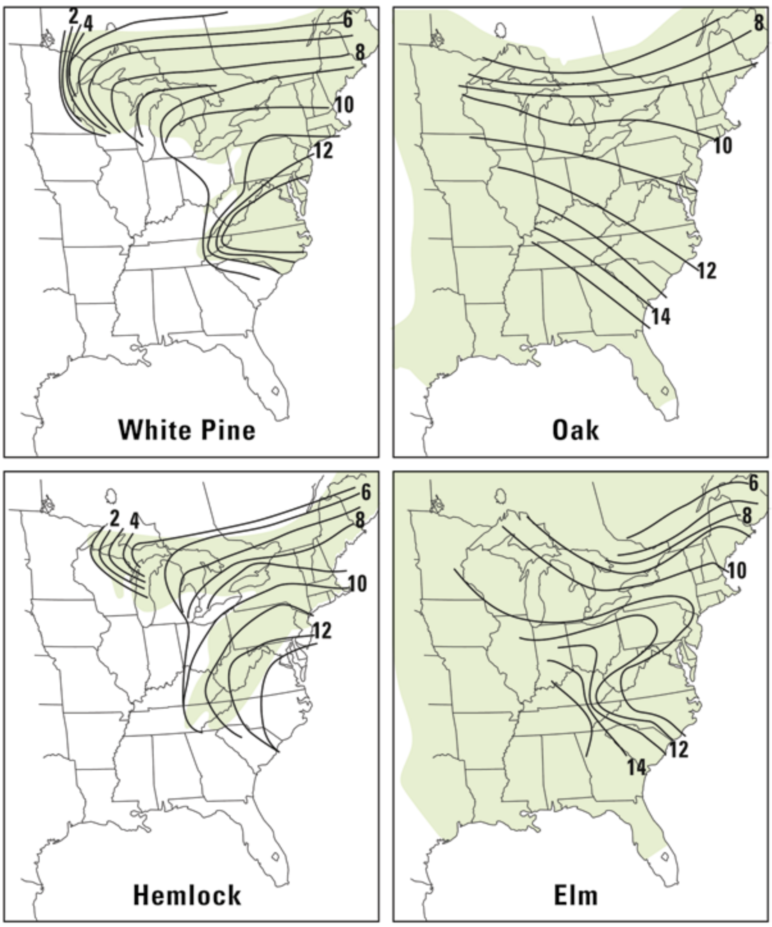


FIGURE 2.3.

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

ADAPTED FROM DAVIS (1983)

oak dominated the plant community also varied spatially (Delcourt and Delcourt 1987). More recent studies also provide examples from the paleoecological record of species assemblages that occurred in the Quaternary but are not observed today, and these co-occuring groups of species were often associated with no-analog climate conditions (Williams and Jackson 2007). The implication is that biotic assemblages of the future may be different from those observed in the past or present.

Although changes in mean climate through time are important, the influence of changes in climate variability is increasingly recognized (e.g., Thornton et al. 2014). Changes in the extreme values, such as maximum or minimum temperature or precipitation, may have large ecological effects, even if the mean value does not change. Increased variability could produce more record hot weather and more record cold weather with no change in mean temperature (Thornton et al. 2014). Extreme values may constrain where a particular species can survive or successfully reproduce. For example, in the Great Lakes region of the Upper Midwestern USA, declines in beech (*Fagus grandifolia*) populations occurred during times and locations of severe drought (Booth et al. 2012). Similarly, weather conditions at the tails of the distribution are often associated with infrequent severe disturbances, such as the very hot, dry conditions that are associated with large forest fires (Westerling et al. 2006). Recent decades have seen many records of maximum daily temperatures exceeded, especially during spring and summer. Such changes in climate variability are likely to have substantial impacts on food security, water supply, and other aspects of human well-being.

Climate is a driver of many natural disturbances (e.g., fire, floods, hurricanes, and landslides), and past changes in climate have altered disturbance regimes. For example, fire-return intervals in the Greater Yellowstone region (Wyoming, USA) varied between 100 and 300 years throughout the Holocene (roughly the past 10,000 years) in response to variability in climate (Millspaugh et al. 2000; Higuera et al. 2010). Similarly, the fire regime in northwestern Minnesota, USA, shifted from a 44-year fire cycle during the warm, dry fifteenth and sixteenth centuries to an 88-year fire cycle after the onset of cooler, moister conditions after 1700 AD and throughout the Little Ice Age (Clark 1990). At finer temporal scales, fire activity is also related to ENSO and PDO cycles (Schoennagel et al. 2005, 2007).

Several points that provide context for interpreting contemporary landscape patterns emerge from the many studies of past vegetation responses to climate. First, glacial–interglacial cycles have triggered the disassembly of communities followed by reassembly that is unpredictable in terms of either species composition or abundance. Compared to present-day communities, the past communities at many sites feature mixtures of species that are absent or very rare on the modern landscape (e.g., Barnosky et al. 1987; Williams and Jackson 2007). Second, the characterization of past plant communities indicates that the displacement of entire vegetation zones or communities is the exception rather than the rule. Species respond individualistically to climatic change, each according to its limits of tolerance, dispersal capability, and interactions with the surrounding biota. Third, disturbance regimes (discussed in detail in Chap. 6) have been very sensitive to past changes in climate. It is critically important for the landscape ecologist to appreciate the dynamic responses of the biota to variability in climate in space and time.

An important lesson from paleoecological studies is that climate has varied at nearly all ecologically relevant time scales, from among years to among millennia (Jackson 2004). The future implications of ongoing climate change for the distribution of Earth's biota and the patterns observed across landscapes are profound. The past decade has seen an exponential increase in the number and variety of studies that document changes that are already underway, with many species shifting northward and upward (e.g., Parmesan and Yohe 2003; Chen et al. 2011). Early evidence of recent climate change effects on tree distributions was detected in tree seedling distributions (Lenoir et al. 2009). For 13 of 17 tree species in French mountain forests, the elevation limit for seedlings was, on average, 29 m higher than the limit for adults (Lenoir et al. 2009). Many studies also forecast the potential ecological consequences of climate change (e.g., Coops and Waring 2011). The outputs from the suite of general circulation models and emissions scenario developed by the IPCC (e.g., IPCC 2013) form the basis for the vast majority of the forward-looking studies.

Landform

Landforms range from nearly flat plains to rolling, irregular plains, to hills, to low mountains, to high mountains (Bailey 2009) and are identified on the basis of three major characteristics: (1) relative amount of gently sloping (<8 %) land, (2) local topographic relief, and (3) generalized profile, i.e., where and how much of the gently sloping land is located in valley bottoms or in uplands (Bailey 2009). Landforms may be described further by considering the topographic sequence of variation, or *soil catena,* of soils and associated vegetation types within each landform. For example, a mountainous landform may have a toposequence that includes ridgetops, steep slopes, shallow slopes, toe slopes, and protected coves. If different areas are composed of similar landforms with similar geology, then soil catenas and vegetation types may also be expected to be similar.

Four general effects of landform on ecosystem patterns and processes (Fig. 2.4) were categorized by Swanson et al. (1988) and still provide a useful classification:

1. *The elevation, aspect, parent materials, and slope of landforms affect air and ground temperature and the quantities of moisture, nutrients, and other materials available at sites within a landscape.* For example, south-facing slopes receive more solar radiation than northward slopes, resulting in warmer, drier conditions. These topographic patterns are strongly related to the distribution of vegetation across a landscape (e.g., Whittaker 1956). Locally, the degree of concavity or convexity may also be important in

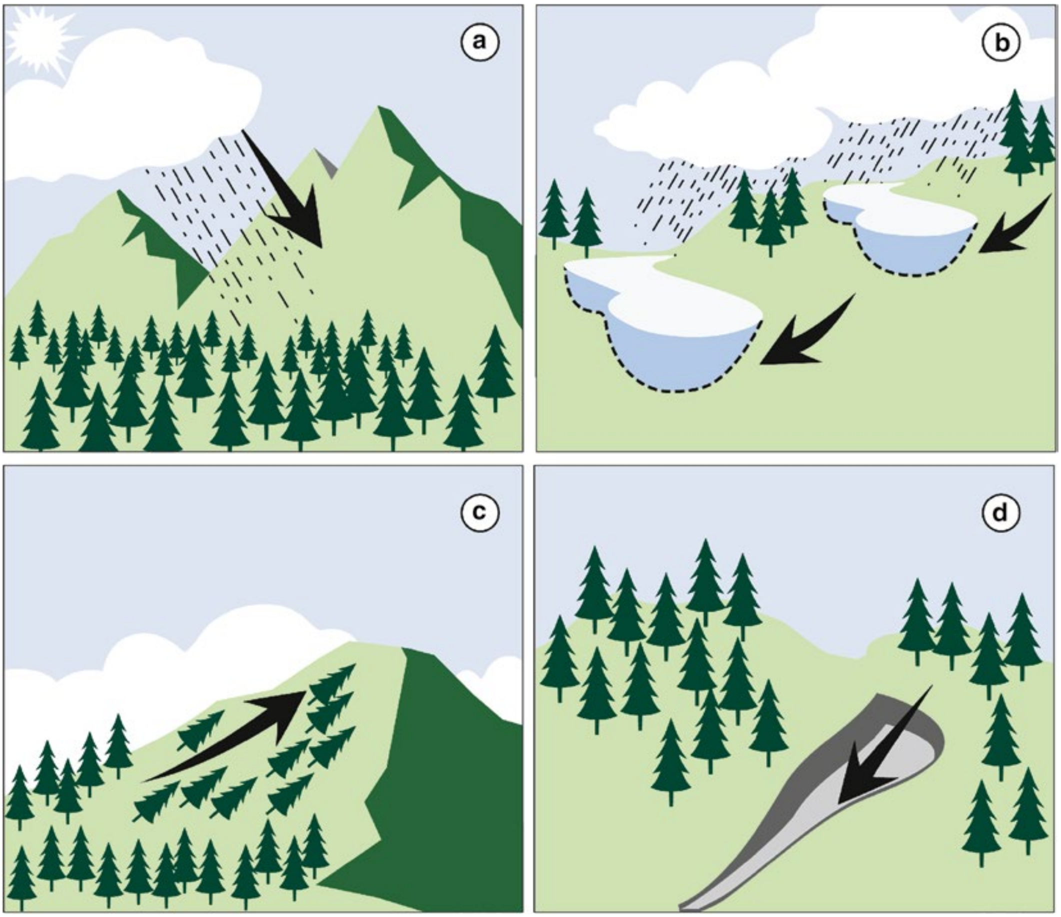


FIGURE 2.4.

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

MODIFIED FROM SWANSON ET AL. (1988)

determining microclimate or the rates of organic matter accumulation, and a landform index (also called a terrain shape index) is often used to characterize such local topographic variation (e.g., McNab 1993; Abella 2007). Methods also exist for estimating temperature variability in areas of complex terrain, such as mountainous environments, by explicitly accounting for topography (e.g., Lookingbill and Urban 2003). These methods are very useful because measurements at a single location (e.g., a weather station) cannot represent all locations in a topographically complex landscape with accuracy, and models that distribute such measurements at finer scales within a landscape are needed.

2. *Landforms affect the flow of many quantities, including organisms, propagules, energy, and matter through a landscape.* The funneling of winds, for example, may lead to dispersal pathways for wind-blown seeds. Many animal species have been observed to travel along riparian corridors (e.g., forest birds in tropical forests, Gillies and St. Clair 2008; wildlife along rivers, Naiman and Rogers 1997), and such corridors are also important for hydrochorous seed dispersal (e.g., Dixon et al. 2002). The position of lakes relative to groundwater flow pathways can strongly influence the chemical and biological characteristics of those lakes (Martin and Soranno 2006; Lottig et al. 2011). Fires are known to burn more rapidly in the upslope rather than downslope direction (e.g., Johnson and Miyanishi 2001).
3. *Landforms affect the frequency and spatial pattern of natural disturbances such as fire, wind, or grazing*. Across a New England landscape, susceptibility to damage from hurricanes varied with landscape position, with greater damage observed in more exposed topographic positions (Foster and Boose 1992; Boose et al. 1994). In coastal forests in Alaska, patterns of windthrow were also strongly influenced by topographic position (Kramer et al. 2001).
4. *Landforms constrain the spatial pattern and rate or frequency of geomorphic processes—the mechanical transport of organic and inorganic material—that alter biotic characteristics and processes.* Many different kinds of transport processes (e.g., by wind or water) move materials around landscapes (Reiners and Driese 2004) and are influenced by landform. Portions of a landscape may be more or less susceptible to landslides or to shifts in river channels.

Taken together, landforms significantly contribute to the development and maintenance of spatial heterogeneity across a landscape through their multiple effects on soils, vegetation, and animals (Swanson et al. 1988). Even in areas of relatively little topographic relief, such as the glacial landforms of the Upper Midwest of the US or riparian floodplains, physiography contributes to spatial variability in vegetation patterns (e.g., Turner et al. 2004a).

Soils

In terrestrial environments, soils provide the mineral nutrients, water, and support medium required by the vegetation. The substrate and soils of the surrounding landscape also affect the chemical qualities of the water in aquatic systems. Although it may be associated with particular landforms, there is tremendous spatial variability in *parent material* (i.e., the unweathered geologic material from which soil develops) across the surface of the Earth. Soils form, in part, through the process of weathering, in which chemical dissolution and physical abrasion break down parent materials. Microbial activity is also important, and plant roots play an important role in soil formation. Soils are important in explaining landscape patterns because they differ substantially in many physical and chemical characteristics (e.g., texture, depth, pH, mineral composition) that influence the species that can be supported. For example, soils have different water-holding capacities, nutrient concentrations, and organic matter content, and such differences can lead to dominance by different plant species. In his classic plant ecology studies, Curtis (1959) described variation in plant communities or Southern Wisconsin that were associated with a soil-moisture gradient—mixed hardwoods on moist soils; *Acer* and *Tilia* on well-drained mesic sites, and a series of *Quercus* species on progressively drier sites.

Studies of ecosystem development on Hawaii have provided convincing evidence for the role of substrate age on landscape patterns. Volcanic lava flows have occurred at varying times in the past, providing a unique opportunity to study ecosystem development on substrates of different age. Nutrient availability changes with long-term soil development (Vitousek and Farrington 1997). Young substrates (300 years BP) are relativity rich in available phosphorus, but plant growth is limited by relatively low nitrogen availability. Mineral phosphorus declines with substrate age, with nitrogen and phosphorus equilibrating in substrates of intermediate age. Eventually, plant growth becomes limited on old substrates (>150,000 years BP) by declining levels of phosphorus (Vitousek and Farrington 1997). These differences in soil development are, in turn, associated with substantial variation in forest structure and disturbance dynamics (Kellner et al. 2011). Although Hawaii offers a somewhat unique set of conditions, the general point is that substrate and soils have strong influences on vegetation and thus landscape structure. It is very important to understand these influences.

Biotic Interactions

Interactions among organisms—both positive and negative, such as competition, predation, and facilitation—can lead to spatial structuring of populations even when environmental resources are homogeneous in space. Theoretical population ecology focuses much attention on these dynamics (Tilman and Kareiva 1997; Ives et al. 1998), with an emphasis on how biotic interactions within and among populations can generate spatial patterns, and how these patterns, in turn, influence the outcome of further interactions. The product of these theoretical approaches often is a map of species distributions, or a time series of how these distributions may change in time and space.

Competition

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

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

Gradients in resources, combined with competitive actions between species, can result in sudden shifts in vegetation types, or ecotones, even when the environmental resource gradients are small (Fig. 2.5). Along a north–south transect, for example, temperature and moisture may change gradually and continuously, with no sharp discontinuities. Conditions to the south may favor one species, while conditions to the north favor another. Somewhere along the transect, conditions will be suitable for the growth of both species. Competition for space may form a sharp ecotone between them, rather than a gradation or intermingling. Resource gradients may also influence mutualisms, such as plant–pollinator interactions, in ways that can produce spatial patterns. For example, the relative abundance of different flower morphologies varies along gradients of elevation and climate in response to variation in pollinator availability (Pellissier et al. 2010).

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

FIGURE 2.5.
Very slight differences in topography in the glaciated landscape of northern Wisconsin, USA, lead to substantial differences in soil water, creating a distinct ecotone between bog vegetation and upland forest.
PHOTO BY M. G. TURNER

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

Influence of Dominant Organisms

In many respects, it is the dominant species that define spatial pattern on the landscape. Such organisms have been termed *foundation species*: a single species that defines much of the structure of a community by creating locally stable conditions for other species, by providing habitat, and by modulating and stabilizing fundamental ecosystem processes such as nutrient cycling (Ellison et al. 2005). Within the context of the abiotic template, foundation species alter the abiotic conditions and provide a resource base and substrate for the other populations in the ecosystem. This is not only true in terrestrial ecosystems; for example, kelp is the foundation species in some coastal ecosystems, and corals can be foundation species along tropical shorelines. The coral forms the substrate and resource base for the entire food web and its spatial distribution dictates the spatial pattern for the rest of the ecosystem.

Another source of landscape pattern derives from the activities of *ecosystem engineers*, organisms that physically create or modify habitat structure (Wright and Jones 2006). A notable example of an ecosystem engineer is the beaver (*Castor canadensis*), which alters riparian landscapes in much of North America. The beaver uses sticks and mud to dam a second- to fifth-order stream, impounding water behind the dam (Johnston and Naiman 1990a) and altering riparian vegetation and soils, forming extensive wetland mosaics. Aerial photography shows that as much as 13 % of the landscape can be altered in this way (Johnston and Naiman 1990b). Beaver activity increases landscape heterogeneity and can increase the number of herbaceous species in the riparian zone by over 33 % (Wright et al. 2002). In the northern portions of Yellowstone National Park, a decline in the stature and abundance of willows (*Salix* spp.) during the twentieth century was linked to reduced beaver activity (Wolf et al. 2007). Hydrologic changes, stemming from competitive exclusion of beaver because of overbrowsing by elk (*Cervus elaphus*), may have caused the landscape to transition from a historical beaver-pond and willow-mosaic state to an alternative stable state where active beaver dams and many willow stands are absent (Wolf et al. 2007). Recovery of willow in the landscape thus may depend on recovery of a key ecosystem engineer. A variety of other examples of ecosystem engineers creating landscape pattern include the American bison (Knapp et al. 1999), earthworm (Holdsworth et al. 2007), and white rhinos (Waldram et al. 2008).

Landscape Consequences of Trophic Cascades

The concept of *trophic cascades* emerged from studies of within-lake communities and referred to the control exerted by a predator's influence "cascading" down the food chain (Carpenter et al. 1985). In landscape ecology, trophic cascades have been considered in the context of predators influencing the spatial patterns of herbivore presence or abundance, which can in turn affect vegetation patterns. Predators may affect herbivores directly by consuming them, or indirectly (i.e., nonconsumptive) by creating a *landscape of fear* that causes herbivores to alter their behavior. If herbivores avoid riskier areas of the landscape and use safer locations, the distribution and/or abundance of forage plants may also change. Thus, predators can initiate spatial trophic cascades by consuming and/or scaring their prey. Such dynamics were hypothesized in northern Yellowstone National Park, USA, following the 1995 reintroduction of wolves (*Canis lupus*) (e.g., Laundre et al. 2001), a landscape in which large populations of elk have been implicated in constraining the distribution of preferred browse species including aspen (*Populus tremuloides*) and willow (*Salix* spp.). After considerable study, some authors concluded that wolf reintroduction restored behaviorally meditated trophic cascades that allowed woody vegetation to grow taller and canopy cover or stem growth to increase in some locations (Beyer et al. 2007; Ripple and Beschta 2012). Other authors, however, found no evidence for recovery of aspen or willow, even where wolf populations were high (e.g., Creel and Christianson 2009; Kauffman et al. 2010; Kimball et al. 2011). The spirited scientific discussions surrounding this topic reflect the excitement associated with integrating behavioral ecology and trophic cascades as they may jointly affect landscape patterns.

Human Land Use

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

Prehistoric Influences

Prehistoric humans had a major role in influencing landscapes (Fig. 2.6), and their past effects contribute to present-day landscape patterns. Using the pollen record, indications of human activities can be traced back thousands of years, and discrete episodes of human disturbance can be correlated with archeological data. Consider, for example, the historical expansion of human influences in Europe (Delcourt and Delcourt 1991). In the early Holocene, there was broad-based foraging throughout the Mediterranean region. The switch from a nomadic to a more sedentary way of life was just beginning ~10,000 BP, and by ~800 BP, when permanent settlements were established in Greece. These settlements included cultivation of crops and maintenance of livestock, and food production became more

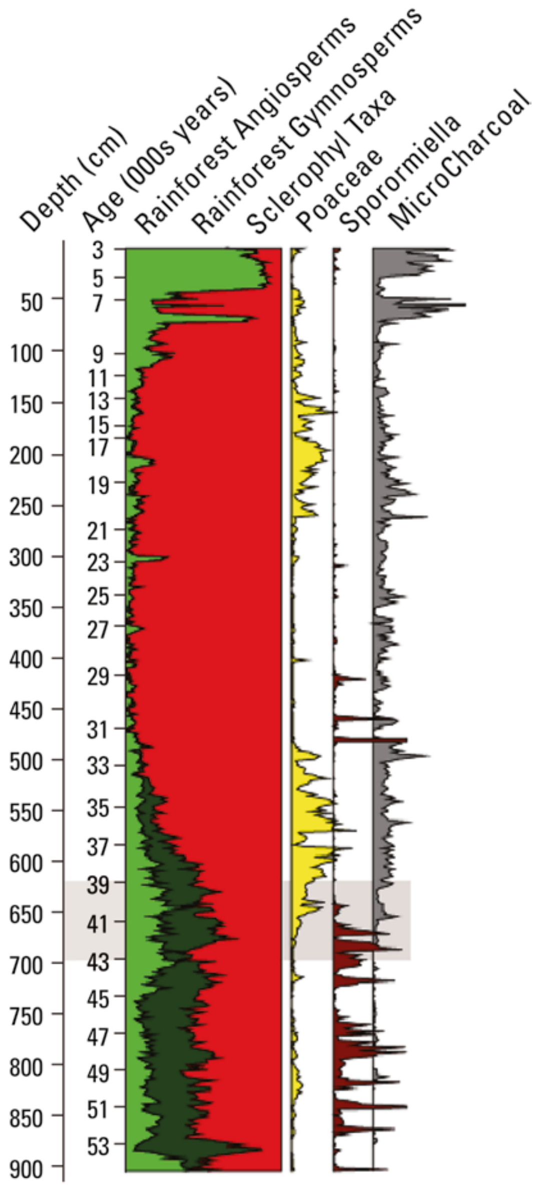


Figure 2.6.
Using a high-resolution 130,000-year environmental record, Rule et al. (2012) helped to resolve the cause of extinction of Australia's megafauna. Results suggest that human arrival rather than climate caused megafaunal extinction, which then triggered replacement of mixed rainforest by sclerophyll vegetation through a combination of direct effects on vegetation of relaxed herbivore pressure and increased fire in the landscape. This ecosystem shift was as large as any effect of climate change over the last glacial cycle and indicates the magnitude of changes that may have followed megafaunal extinction elsewhere in the world.
Modified from Rule et al. (2012)

labor intensive. Cereal cultivation caused a major shift in patterns of land use because the permanent fields needed weeding and required nutrient replenishment, both of which were activities requiring considerable human labor. By about 6500 BP, farming expanded north of Greece as winters became warmer and precipitation increased. Development of more efficient technologies also contributed to the continued expansion of agriculture in Europe. Use of the "ard," a tool that used the angle between the trunk and roots of a tree to break through the soil and which was pulled by an oxen, became prevalent ~5000 BP. Further human expansion became based on the maintenance of work animals because oxen-drawn plows that could both furrow and turn over the soil were developed and used by ~3000 BP. More efficient bronze sickles also replaced wooden sickles.

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

The influences of prehistoric humans on landscapes were characterized by Delcourt (1987) into five main types. (1) Humans changed the relative abundances of plants, especially the dominance structure in forest communities. In the pollen record from Crawford Lake, Ontario, land clearance and maize cultivation by the Iroquois is documented by pollen sequences spanning the fourteenth to seventeenth centuries. During this time, the dominance of tree species in the surrounding forest changed from late-successional species such as beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) to forest of oak (primarily *Quercus rubra*) and white pine (*Pinus strobus*). (2) Humans extended or truncated the distributional ranges of plant species (woody and herbaceous). In Europe, for example, the range of olives (*Olea europaea*) after 3000 years BP was extended through cultivation from the Mediterranean coast throughout southern Europe. Truncation of the range of a native tree species by prehistoric humans has been documented for bald cyprus (*Taxodium distichum*) in the central Mississippi and lower Illinois valleys in eastern North America. Charcoal evidence suggests a preference for cyprus wood during the period from 2000 years BP to 1450 AD, with the species becoming locally extinct as human populations increased (Delcourt 1987). (3) Opportunities were created for the invasion of weedy species into disturbed areas. In many places, weedy species assemblages associated with cultivated fields increase in abundance in the pollen record, and these increases are correlated with archeological evidence of human occupation (Delcourt 1987). (4) The nutrient status of soils was altered through both depletion and fertilization. (5) The landscape mosaic was altered, especially the distribution of forest and nonforest. This last change is also easiest to detect in the paleoecological record by examining ratios of tree to herbaceous pollen.

A key point from this brief discussion of long-term development of the cultural landscape is that what we perceive to be "natural" today may be, in fact, the product of human alterations that date back over several centuries. For instance, one can still see the imprint of Roman roads when fields lie fallow in Belgium. A wide range of ecosystem effects due to human activities may be found, from harvests of resources, agricultural development, and urban construction. Because humans have long been present in many landscapes, their role in creating landscape pattern should not be discounted.

Historical and Present-Day Effects

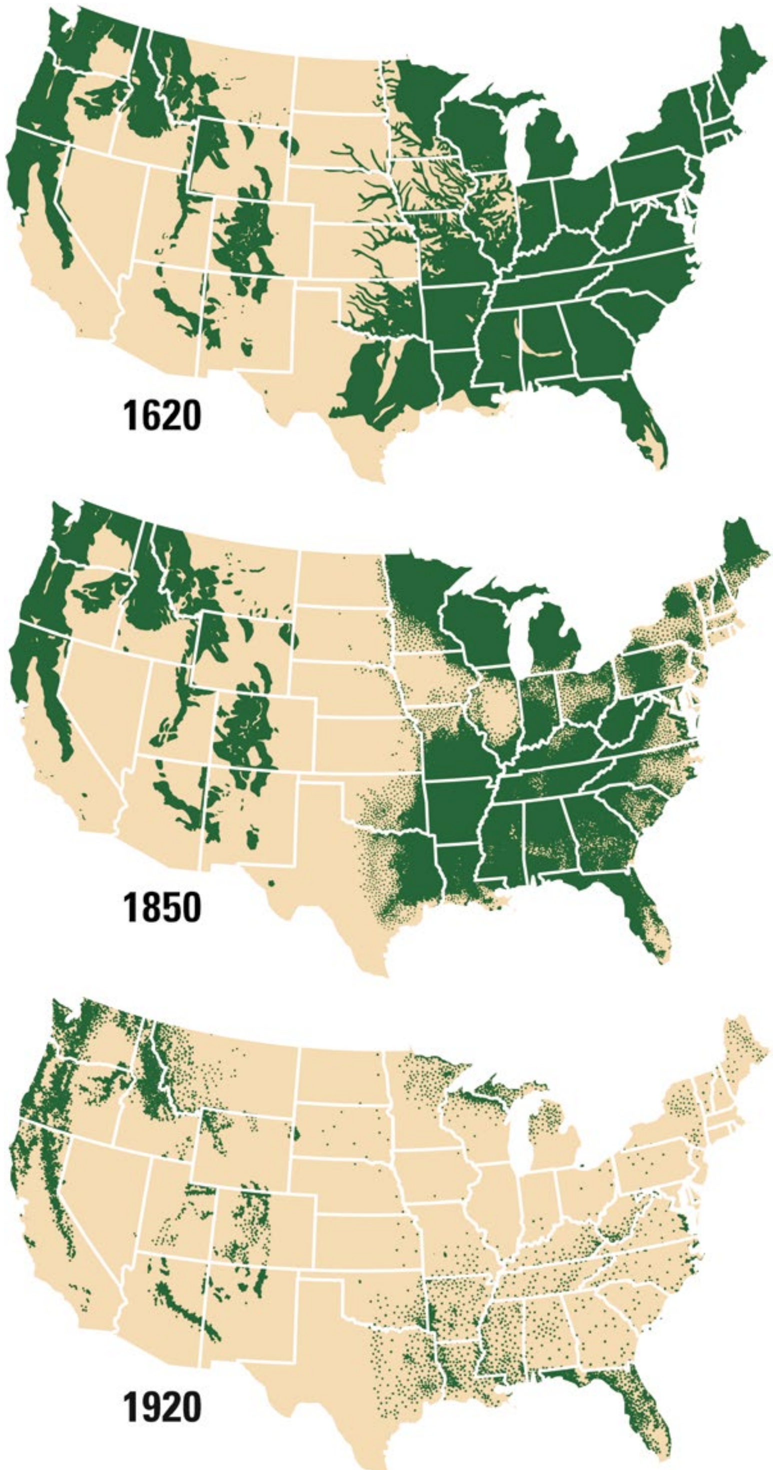
Both worldwide and in the United States, land-cover patterns today are altered principally by direct human use: by agriculture, raising of livestock, forest harvesting, and construction (Meyer 1995). Human society relies on natural habitats for a variety of services, including productivity; recycling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

Land-use changes in the United States serve as a handy example. At the time of European settlement, forest covered about half the present lower 48 states. Most of the forestland was in the moister east and northwest regions, and it had already been altered by Native American land-use practices (Williams 1989). Clearing of forests for fuel, timber, and other wood products, and to open the land for crops led to a widespread loss of forest cover that lasted through the early 1900s. So extensive was this loss that by 1920 the area of virgin forest remaining in the conterminous United States was but a tiny fraction of that present in 1620 (Fig. 2.7). Some originally cleared areas, for example, New England, the Southeast and the Upper Midwest, have become reforested due to lack of cultivation. In other regions, clearing for agriculture has been more permanent (e.g., the Lower Midwest), or harvest of primary forest has continued until recent times (e.g., Pacific Northwest).

Through their activities, modern humans have often been shown to simplify landscape patterns, creating straighter and more regular spatial arrangements (Krummel et al. 1987). Roads, transportation corridors, and other linear features impose new spatial patterns in landscapes (e.g., Laurance et al. 2009; Forman et al. 2003). Urbanization results in profound changes to aquatic systems, burying first-order streams (Elmore and Kaushal 2008), replacing vegetation that shades stream corridors and prevents erosion (Baron et al. 1998) with hardened surfaces producing high-intensity flows that transport greater levels of sediment and nutrients (Lookingbill et al. 2009).

Developed land in the United States has expanded as the population has grown in number, with most of the population now living in cities, towns, and suburbs rather than on farms. Americans spread out more across the land as transportation technologies improved, especially as the automobile became the primary mode of

Figure 2.7.
Approximate area of virgin old-growth forest in the contiguous United States in 1620, 1850 and 1920. Note that this does not depict total forest area because many forests, especially in the eastern United States, have regrown following clearing and the abandonment of agriculture.
Adapted from Meyer (1995)



transportation. Present-day patterns of settlement take up more land per person than in the past, and homes and subdivisions are more dispersed across the landscape. Exurban development has increased in many North American landscapes as environmental amenities attract residents to more rural areas. The resulting increase in the *wildland–urban interface* (WUI) has received considerable attention (e.g., Radeloff et al. 2005; Theobald and Romme 2007). The consequences of increased residential development in forested regions (i.e., houses under the canopy) are not well understood but are receiving considerable study. Expansion of the WUI is associated with increasing conflicts between human values and ecological processes, such as natural disturbance and activities of large predators.

Urbanization is a strong trend globally, and a frontier of rapid and sometimes chaotic land-use change surrounds urban areas (Meyer 1995; Mcdonald et al. 2009). For example, changes in landscape pattern around Beijing, China, show increased fragmentation associated with the concentric rings of expanding urbanization (Shi et al. 2012). Trends in urban land are unique because they typically run in only one direction—that is, urban lands do not revert readily to other categories in the short term. Thus, the distribution of developed lands will leave a long-lasting footprint on the landscape (Turner et al. 1998a), and proximity to urban lands is strongly associated globally with increased threats to conservation lands (Mcdonald et al. 2009).

Emergence of the Anthropocene

The pervasive influence of humans on landscapes throughout the world is widely recognized, and there is growing consensus that humans have transformed ecosystem patterns and processes across most of the terrestrial biosphere (e.g., Foley et al. 2005). This recognition has led some researchers to suggest that the traditional depiction of global biomes based on climate and physiography is insufficient to depict the patterns of terrestrial ecosystems. Ellis and Ramanukutty (2008) introduced the concept of anthropogenic biomes, or *anthromes*, to assess the human-caused changes in the classic biomes. Globally, anthropogenic transformations of biomes between 1700 and 2000 resulted about equally from land-use expansion into wildlands and from intensification of land use (Fig. 2.8; Ellis et al. 2010a, b) See following note in figure legend. These authors report that the terrestrial biosphere made a critical transition from mostly wild to mostly anthropogenic early in the twentieth century (Ellis et al. 2010a, b). For landscape ecologists, it is clear that human activities and land use must be considered a key driver of landscape pattern.

Disturbance and Succession

Disturbance and the subsequent development of vegetation are key contributors to pattern on the landscape. By *disturbance*, we mean any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource availability, substrate, or the physical environment (White and Pickett

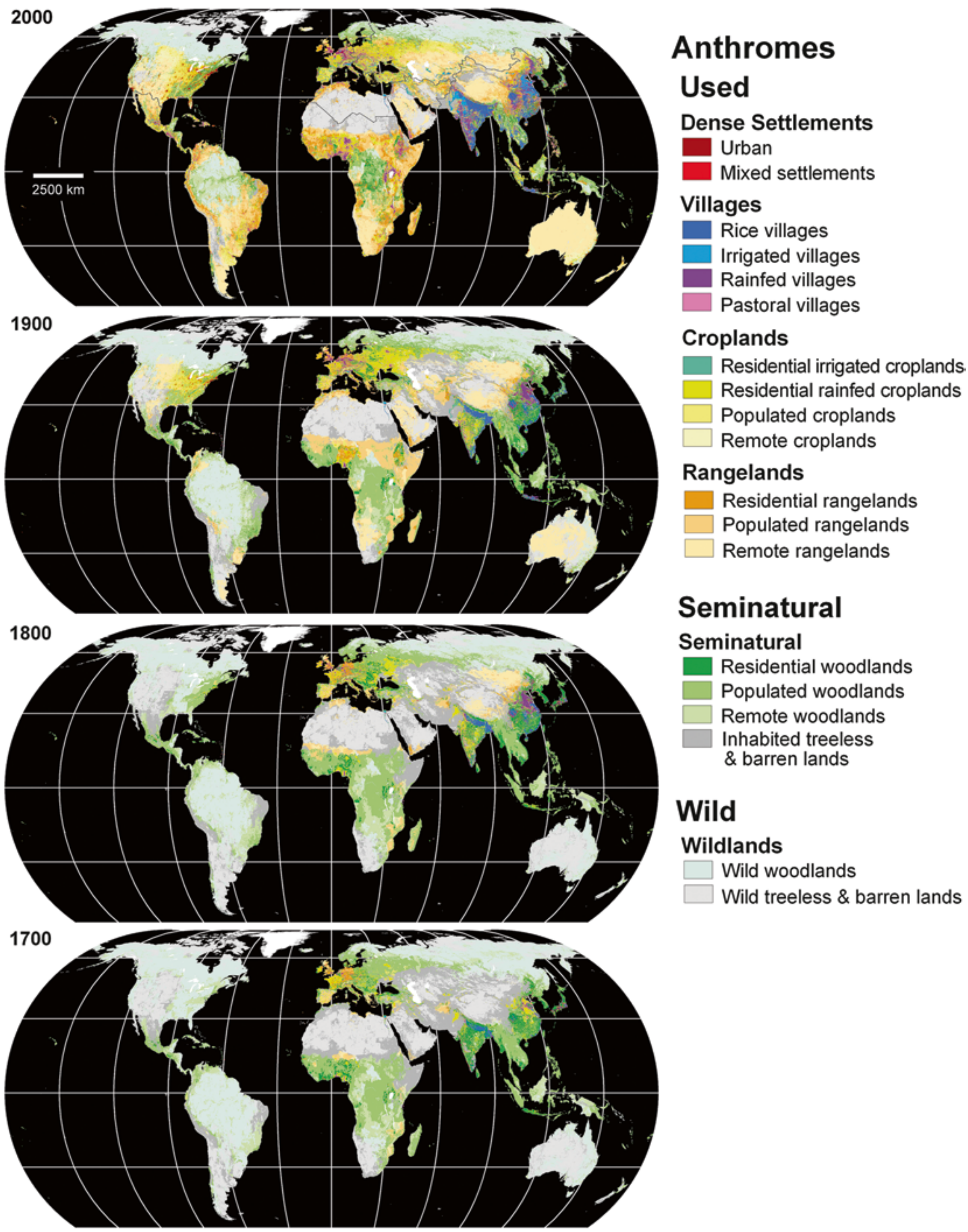


FIGURE 2.8.

Anthropogenic biomes and changes in their global distribution between 1700 and 2000.

From Ellis et al. (2010b) and available at http://ecotope.org/anthromes/maps/

1985). Examples include fires, volcanic eruptions, floods, and storms. Disturbances are often described by a variety of attributes including their spatial distribution, frequency, spatial extent, and magnitude. The spread of disturbance and spatial patterns of recovery have received considerable attention in landscape ecology, and we devote a chapter to exploring these dynamics (see Chap. 6). Here, we briefly recognize disturbance as an important agent of pattern creation at a variety of spatial and temporal scales. As with the other factors discussed in this chapter, disturbances leave a heterogeneous imprint on terrestrial landscapes (e.g., Foster et al. 1998; Turner 2010) as well as within aquatic systems, such as riverine landscapes (e.g., Parsons et al. 2005).

LANDSCAPE LEGACIES AND THE ROLE OF HISTORY

A major development in contemporary landscape ecology has been confirmation of the role of history in today's landscapes and the widespread importance of landscape legacies. Since the 1980s, this recognition has grown along with the rise of environmental history (e.g., Cronon 1982) and an early recognition in ecology that history might explain contemporary patterns. Many scientists thought that the distant past had little effect on modern ecosystem patterns and processes (Foster et al. 2003). However, when ecological studies expanded to regional scales, it became difficult to avoid consideration of current and historical human activities—the role of people could no longer be ignored. There was also growing evidence that most "natural areas" had more cultural history than had been assumed previously, and there was acknowledgement that the legacies of historic land use were remarkably persistent. Finally, there was appreciation that history adds explanatory power to understanding the structure and function of contemporary landscapes. Numerous empirical studies have now documented effects of historical events on a wide range of attributes (e.g., species presence and abundance, forest stand structure, nutrient pools and fluxes, and vulnerability to nonnative invasive species). Vegetation and soils seem to be particularly sensitive indicators of historic land use. Although historic timber harvesting and agriculture [i.e., "the *ghost of land use past*" (Harding et al. 1998)] have received most attention, natural disturbances can also leave their mark on landscape patterns for decades or even centuries.

In well-developed forests of the northeastern US, David Foster and colleagues found that variation in soil characteristics and the plant community reflected land use that occurred over 100 years ago (Foster 1992). Although the regional distribution of forests was similar to that of presettlement, some tree species (e.g., birch, red maple) had increased over time while others (e.g., sugar maple, beech) had declined. Their analyses showed that the variety and abundance of trees varied with past land use. Indeed, despite environmental variation in the region, studies have shown that the extensive nineteenth-century forest clearance and land use resulted in severe reductions or local extinction of forest plant populations and remains an overriding factor influencing modern vegetation composition and structure (Bellemare et al. 2002). In northern US Great Lakes forests, historical land use was associated with homogenization of forest communities across the landscape, and current forests that have lower species diversity, functional diversity, and structural complexity compared to pre-Euro-American forests (Schulte et al. 2007). In forests of the southern Appalachians, the legacies of historic land use also affected the likelihood that forest understories might be invaded by nonnative species (Kuhman et al. 2010).

Effects of historical land use were especially pronounced on forest herbs that have limited dispersal capability, a trend also reported in other regions (e.g., Southern Appalachians, Pearson et al. 1996; Mitchell et al. 2002; Ontario, Canada, Brown and Boutin 2009). While effects of historical agriculture on forest understory plants are partly mediated by establishment limitation (Flinn and Vellend 2005), mortality of seedlings and juveniles may also be higher in more recent forests (Jacquemyn and Brys 2008). Biomass allocation patterns also can differ with historical land use (Fraterrigo et al. 2006a). Soil nutrient concentrations sometime vary with land-use history (e.g., Bellemare et al. 2002), and Fraterrigo et al. (2005) found that historical land use altered the variance and spatial structure of soil nutrients. Soil microbial communities also showed a persistent legacy of land use history (Fraterrigo et al. 2006b). Geostatistical analyses (which are covered in Chap. 5) suggested that the spatial patterns of soil carbon, potassium, and phosphorus were homogenized in former pastures (Fraterrigo et al. 2005). Carbon storage can also be affected by land-use history. In Wisconsin, USA, total aboveground live forest carbon declined by nearly 75 % between presettlement times and the peak of agricultural clearing in the 1930s (Rhemtulla et al. 2009). Carbon stocks recovered subsequently to about 60 % of the presettlement value, but the landscape distribution of carbon storage shifted. Former savanna ecosystems in the south store more carbon, and forest ecosystems in the north store less (Rhemtulla et al. 2009).

In addition to the actual use land in the past, the spatial pattern of historic land use can influence contemporary patterns. In seminatural grasslands in Sweden, the spatial configuration of habitats in the landscape influenced plant species diversity for 50–100 years (Lindborg and Eriksson 2004). Species diversity was not related to current connectivity of the grasslands, and strong relationships were found with the historic patterns of the grasslands. Historic connectivity was positively related to estimates of species diversity, the total species richness, and species density, and the model with the highest explanatory power included the configuration from 100 years ago (Lindborg and Eriksson 2004). This study demonstrated that present-day species composition was related to historic landscape structure and suggested time-lagged influences of historical habitat patterns. Other studies have demonstrated similar consequences of historical habitat connectivity on contemporary species assemblages, including butterflies in European grasslands (Sang et al. 2010) and understory plants in pine woodlands on the coastal plain of the southeastern US (Brudvig and Damschen 2011).

For how long do land-use legacies persist? The answer varies among landscapes, of course, but studies in western Europe have revealed exceptionally long land-use legacies. In northeastern France, large areas were cleared of forest during Roman occupation, farmed, and then abandoned to forest. Using archeological evidence to reconstruct land-use patterns, Dupouey et al. (2002) tested the hypothesis that legacies of the ancient agriculture may last for millennia. The data supported this hypothesis: plant community composition was closely related to the intensity of ancient land use (Dupouey et al. 2002). These authors concluded that 200 years of farming during Roman times induced gradients in soil nutrients and plant assemblages that were still measurable almost 2000 years later! Further, the effects of Gallo-Roman occupation 1600 years ago were observed not only on current-day soils and plant communities but also in the seed bank (Plue et al. 2008). Historic land use was associated with persistent ruderal species in the seed bank, co-occuring with several ancient forest species that were at high abundance in the occupied sites. Clearly, the impact of ancient land use on forest vegetation in Europe must not be underestimated (Plue et al. 2008).

We have emphasized land-use legacies, but natural disturbances can also produce persistent legacies through their influence on spatial patterns of postdisturbance succession. Disturbances themselves produce patterns (e.g., Foster et al. 1998), and a stand-age mosaic is often observed across a landscape that has been subjected to disturbances at different times in the past. However, a single disturbance event can also create a long-lasting imprint on landscape pattern. Following the 1988 fires in Yellowstone National Park, WY, studies reported enormous variation in postfire stand density (0 to >500,000 stems ha^{-1}) within the burned landscape (Turner et al. 2004b). Chronosequence studies used to reconstruct the spatial variability of tree density in the past revealed that postfire variation in stand structure and function persists for nearly 200 years (Kashian et al. 2005a, b).

In sum, landscape legacies are ubiquitous and important. Current studies continue to explore the role of history, and many questions remain to be explored. For example, variation in agricultural practices (e.g., tillage, crop rotations, fertilizer applications) often is not well resolved in space or time, and arid lands can be more difficult to study. How do historical legacies constrain restoration alternatives? Under what conditions can reintroduction of historically natural processes (e.g., fire) restore historic landscape conditions? What will be the future legacies of today's patterns of land use?

WHY IS IT STILL DIFFICULT TO EXPLAIN AND PREDICT LANDSCAPE CHANGE?

At the beginning of this chapter, we claimed that predicting landscape change remains very challenging. It is much easier to explain patterns by looking back in time than it is to anticipate future rates, directions, and spatial patterns on a given landscape. Why does this remain so difficult? What approaches are useful? Returning to the notion of the perfect landscape, Phillips (2007) summarized three take-home points that we paraphrase here for landscape ecologists:

1. A landscape at a given place and time is a particular, contingent outcome of deterministic, global laws operating in a specific environmental and historical context. Historical and spatial contingencies are very important, and landscape patterns may converge or diverge over time.
2. A given landscape is only one possible outcome of a given set of processes and boundary conditions, which is determined by a specific, perhaps irreproducible set of contingencies. However, the possible outcomes are constrained by deterministic controls that set boundaries on what outcomes are feasible.
3. Explaining landscape patterns requires the integration of global approaches that consider the deterministic controls and local approaches that account for the contingencies.

From this, it follows that predicting future landscape patterns is difficult because contingencies may be unanticipated or even unpredictable. When similar locations can arise from different histories, and similar histories can produce different outcomes (e.g., Ernoult et al. 2006), it is not easy to infer causation. Here, we highlight four key factors that make prediction landscape patterns difficult.

Multivariate Interacting Drivers

Landscape patterns are clearly not the result of single drivers. Multiple drivers are often operating across a wide range of spatial and temporal scales, and they may interact in unpredictable ways.

Statistical methods are increasingly employed to detect multivariate correlates of changing patterns (e.g., Turner et al. 1996; Black et al. 2003; Crk et al. 2009). One comprehensive analysis focused on changing spatial patterns in forest landscapes of the interior Columbia Basin, located in the northwestern US (Black et al. 2003). This study considered a wide range of social and biophysical correlates, including demographic, cultural, climatic, topographic, and geologic factors. The authors hypothesized that patterns of change would be explained by social and biophysical variables operating at a similar scale, but changes were not necessarily correlated to factors at the same scale. Broad-scale social variables, including land ownership, economic market structure, and cultural values, were important covariates in all models. Biophysical parameters related to local growing conditions modified these influences (Black et al. 2003). Results confirmed the strong influence of humans on landscape patterns and identified interactions with biophysical variables that were difficult to predict; in the authors' words, "The story is overwhelmingly that of social system factors imposed on biophysical factors" (Black et al. 2003).

Interacting drivers are also key in wildland landscapes, and recent studies in the Serengeti ecosystem nicely illustrate this point while also demonstrating the use of simulation modeling to study pattern–process interactions. The Serengeti is a well-studied savanna-grassland landscape in east Africa that is especially famous for its native wildlife. The spatial patterns of tree cover in the Serengeti landscape change over time and are difficult to predict. Using a spatial simulation model that included vegetation, fire and dominant herbivore dynamics, Holdo et al. (2009) detected interactions among multiple drivers of pattern. For examples, elephants and fire had synergistic negative effects on woody cover; fire increases the heterogeneity of tree cover when grazers are present, but decreases that heterogeneity when grazers are absent; the steep rainfall gradient in this landscape directly affects the pattern of tree cover in the absence of fire, but with fire, the woody cover is determined by the grazing patterns of migratory wildebeest (Holdo et al. 2009). Thus, as mobile consumers, grazers could greatly affect the spatial patterns of tree cover in the Serengeti via their effects on fire.

Thresholds and Nonlinearities

Another challenge to predicting landscape patterns involves nonlinear dynamics and thresholds. An *ecological threshold* is the point at which there is an abrupt change in an ecosystem quality, property, or phenomenon, or where small changes in an environmental driver produce large responses in the ecosystem (Groffman et al. 2006b). If a landscape is characterized by thresholds that have not been resolved, future changes are likely to be surprising. As we discuss in detail in Chap. 3, the connectivity (or fragmentation) of habitat patterns change nonlinearly with the proportion of the landscape occupied by the habitat.

Social–Ecological Systems

The past decade has seen a tremendous increase in the number of studies trying to integrate social and ecological drivers of landscape patterns and changes in meaningful ways. Given the dominant influence of human activities on global ecosystems, the importance of this is apparent. However, such interdisciplinary studies are difficult, in part because of the need to integrate quantitative and qualitative approaches, and in part because disciplinary traditions can be hard to bridge. Early approaches used quantitative proxies for social drivers, including land ownership, population density, distances to nearest road or market centers (e.g., Spies et al. 1994; Turner et al. 1996; Wear et al. 1996). Contemporary studies attempt to integrate institutions, governance structures, and cultural attitudes (e.g., see Turner and Robbins 2008). Successful studies usually require multi-investigator teams that include natural and social scientists. Furthermore, it remains important to continue development of methods that allow qualitative and quantitative data to be combined for analysis (Bürgi et al. 2004).

Limited Ability to Perform Experiments

Experimentation is often considered the "gold standard" for demonstrating mechanism and causality. In landscape studies, experimentation at broad spatial scales is often logistically impossible, and one is often limited to studying correlations (Bürgi et al. 2004). Hypothesized causalities between drivers and landscape patterns or changes can be evaluated statistically (e.g., Bürgi and Turner 2002; Crk et al. 2009). Another approach borrows from historical methods and reconstructs landscape history in narrative form using methods such as oral histories to augment archival data sources. For example, a case study of landscape history in a Peruvian Amazon landscape from 1948 to 2005 identified key socioeconomic drivers (e.g., boom and bust in demand for barbasco, a native plant that contains rotenone in its roots; commercialization of DDT; introduction of agricultural credit programs) that were related to observed landscape changes (Arce-Nazario 2007). Such place-based studies probe the complexity of landscape dynamics and are rich in detail and understanding, although they may not be general. To understand landscape pattern and change, landscape ecologists generally use a multipronged approach that includes comparative study of landscapes that differ in putative drivers, simulation models in which the consequences of different drivers can be explored, and "natural experiments" that may include disturbances or human land-use patterns.

In conclusion, landscape patterns are generated by complex relationships among multiple factors. Every landscape has resulted from multiple and contingent causation. History both shapes current conditions and constrains future responses, and current landscape patterns are creating legacies for the future. Landscape ecologists need a healthy appreciation for multiple causality, a lengthy temporal perspective, and an awareness of legacies.

SUMMARY

Today's landscapes result from many causes, including variability in abiotic conditions such as climate, landform, and soils; biotic interactions that generate spatial patterning even under homogeneous conditions; past and present patterns of human settlement and land use; and the dynamics of natural disturbance and succession. All landscapes have a history, and determining the conditions that gave rise to different landscapes in the past is critical for anticipating the future. Every landscape is unique because the combined, interacting effects of multiple environmental controls and drivers generate a landscape that is unlikely to be duplicated exactly at any other place or time. Any particular landscape is a singular outcome from a range of plausible outcomes. Historical and spatial contingencies play a big role.

Variability in climate and landform is observed over broad scales, and these abiotic drivers constrain other causes of landscape change. Climate effects are modified by landform—which includes both geology and topography, or physical relief. The distribution of plant and animal communities and indeed of entire biomes has varied tremendously with past changes in climate, even in the absence of human activities. Not only have species varied in their ranges, but also the local abundances—and thus relative dominance—of taxa have changed. Landforms are important influences on landscape pattern because they influence moisture, nutrients, and materials at sites within a landscape; they affect flows of many quantities; they may influence the disturbance regime; and they constrain the pattern and rate of geomorphic processes. Landscape ecologists must understand the influence of climate and landform on the biota and recognize the dynamic responses of the biota to variability in climate in space and time.

Interactions among organisms, such as competition, facilitation, and predation, may lead to spatial structure, even in the absence of abiotic variation. Keystone species or dominant organisms may define spatial pattern on a landscape. Disturbance and succession are key contributors to landscape pattern. Humans are also a strong driver of landscape patterns, as land-use patterns interact with the abiotic template to create the environment in which organisms must live, reproduce, and disperse. Nearly all landscapes, even those we perceive as “natural” today, probably have a history of human influence that dates back a long time. Many landscapes today have become mosaics of natural and human-influenced patches, and once-continuous natural habitats have become increasingly influenced by human activities. Effects of past land use (i.e., land-use legacies) are increasingly recognized as important determinants of the present-day biota that inhabit our landscapes. Studies in Europe have demonstrated legacies of land use that have persisted for over 1000 years. The future legacies of contemporary land-use patterns may shape landscapes for decades and centuries to come. Explaining and predicting landscape change remains challenging because of multiple interacting drivers, thresholds and nonlinearities, complex interactions with social drivers, and the limited ability to experiment at landscape scales.

DISCUSSION QUESTIONS

1. What is meant by the concept of the "perfect landscape," and how does this concept influence the way we explain contemporary landscape patterns or project future patterns?
2. Consider the variety of factors that create landscape pattern. How would you rank their relative importance? Do you think this ranking has changed through time? Explain your answers.
3. Why is it important to understand the history of a landscape? What types of effects of events from the past may remain in a present-day landscape patterns?
4. As human influences intensify and climate change continues, how do you think landscape ecology should evolve so that it can help address key questions of the twenty-first century?

FURTHER READING

Black AE, Morgan P, Hessburg PF (2003) Social and biophysical correlates of change in forest landscapes of the interior Columbia Basin, USA. Ecol Appl 13:51–67

Jackson ST (2006) Vegetation, environment and time: the origination and termination of ecosystems. J Veg Sci 17:547–557

Kramer MG, Hansen AJ, Taper ML, Kissinger EJ (2001) Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. Ecology 82:2749–2768

Lindborg R, Eriksson O (2004) Historical landscape connectivity affects present plant species diversity. Ecology 85:1840–1845

Phillips JD (2007) The perfect landscape. Geomorphology 84:159–169

Plue J, Hermy M, Verheyen K, Thuiller P, Saguez R, Decocq G (2008) Persistent changes in forest vegetation and seed bank 1,600 years after human occupation. Landsc Ecol 23:673–688

Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96–101