The Importance of Land-Use Legacies to Ecology and Conservation

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Recognition of the importance of land-use history and its legacies in most ecological systems has been a major factor driving the recent focus on human activity as a legitimate and essential subject of environmental science. Ecologists, conservationists, and natural resource policymakers now recognize that the legacies of land-use activities continue to influence ecosystem structure and function for decades or centuries—or even longer—after those activities have ceased. Consequently, recognition of these historical legacies adds explanatory power to our understanding of modern conditions at scales from organisms to the globe and reduces missteps in anticipating or managing for future conditions. As a result, environmental history emerges as an integral part of ecological science and conservation planning. By considering diverse ecological phenomena, ranging from biodiversity and biogeochemical cycles to ecosystem resilience to anthropogenic stress, and by examining terrestrial and aquatic ecosystems in temperate to tropical biomes, this article demonstrates the ubiquity and importance of land-use legacies to environmental science and management.

Keywords: land use, disturbance, conservation, ecosystem process, natural resource management

In the mid-1980s two groups met independently, at the tropical Luquillo Experimental Forest in Puerto Rico and at the temperate Harvard Forest in New England, to draft proposals for a competition to qualify for the National Science Foundation's (NSF) Long Term Ecological Research (LTER) program. Despite the contrasting settings, the groups engaged in remarkably similar, animated exchanges concerning one issue: Should human history and the consequences of past land use be embraced as research themes in the proposal? Ultimately, the research teams decided to focus their studies rather narrowly on natural disturbance processes and ecosystem dynamics and to avoid addressing all but the indirect and unavoidable consequences of human activity, such as acid rain, exotic organisms, and future climate change. The consequences of past land use, which has been lengthy and intense in New England and Puerto Rico, were consciously avoided for pragmatic reasons: (a) Many, though not all, of the scientists believed that modern ecosystem patterns and processes are largely unaffected by the distant past; and (b) consensus emerged among the scientists that the community of peer reviewers and the Division of Environmental Biology at the NSF would be unsympathetic toward such an applied and historical subject (Foster 2000).

Both proposals were successful, the sites joined the LTER Network, and the scientists followed through on their programs of basic research on natural processes (Waide and Lugo 1992, Foster and Aber 2003). Over the past decade, however, researchers at these and other LTER projects, as well as most scientists engaged in ecology, conservation, and natural resource management, have come to recognize that site history is embedded in the structure and function of all ecosystems, that environmental history is an integral part of ecological science, and that historical perspectives inform policy development and the management of systems ranging from organisms to the globe (Motzkin et al. 1996, Casperson et al. 2000, Tilman et al. 2000, Goodale and Aber 2001, Foster 2002). This fundamental shift in outlook was driven by at least four factors: (1) expansion of ecological studies to regional scales where current and historical human activity is unavoidable, (2) realization that most "natural areas" have more cultural history than assumed, (3) recognition that legacies of land use are remarkably persistent, and (4) appreciation that history adds explanatory power to our understanding of modern structure and function and reduces missteps in anticipating or managing for future conditions.

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Table 1. Partial listing of ecosystem types, both singly and in terrestrial–aquatic combination, and ecosystem characteristics, in which land-use legacies are represented and studied within the LTER Network. (For site identification abbreviations, see Hobbie and colleagues [2003]; C = carbon, N = nitrogen.)

	Land-use legacies				
Land-use type	C/N	Soil/ sediment	Woody debris	Flora	Fauna
Wild forest → agriculture → forestry (HFR, CDR, LUQ, CWT)	x	x	x	x	x
Wild forest → managed forest → unmanaged forest					
Forest only (HBR, HFR)	x	x	x	x	
Forest and aquatic (AND, BNZ, CWT, HBR, LUQ, PLM, VCR)	x	x	x	x	x
Forest and lake (NTL, HFR)		x	x	x	x
Wild grassland, shrub → grazing					
Terrestrial only (JRN, SGS, SVT)	x	x		x	x
Terrestrial and stream (KNZ)	x	x		x	x
Wild grassland → modified fire regime					
Terrestrial and stream (KNZ)	x	x		x	x

In this article, we outline some critical aspects of land-use legacies for ecology, conservation biology, and resource management and policy. We draw especially from the LTER experience, because this network is opportunely positioned to apply multiple approaches and comparative studies to investigate the long-term consequences of human history (table 1). In particular, LTER studies have combined retrospective studies from paleoecology, dendrochronology, archaeology, and history to define rates and drivers of past changes in ecosystems and to frame research questions (Foster et al. 1998, Swanson et al. 1998), long-term measurements to complement space-for-time studies (e.g., Tilman et al. 2000), large-scale experiments to identify mechanisms underlying changes in pattern and process (Aber et al. 1998, Knapp et al. 1999), and integrative models that facilitate the testing and synthesis of diverse studies and the projection of future conditions (Parton et al. 1987, Aber and Driscoll 1997). Such pluralistic approaches are not unique to the LTER Network, but they are fostered by the long-term relationships and place-based science that are characteristic of the LTER program. Indeed, our experience is that insights and new challenges continue to emerge at a rapid pace from these studies (Driscoll et al. 2001).

Land-use drivers of ecosystem change and legacies

Human activity and its effects are so varied, ranging from direct physical impacts such as logging to indirect consequences such as global climate change, that a consideration of land-use legacies could be boundless. We concentrate on four activities that have exerted widespread impact on terrestrial and aquatic ecosystems worldwide: forestry, agriculture, modification of natural disturbance regimes (especially fire), and manipulation of animal populations. We examine these processes not so much in terms of their immediate effects (see Turner et al. 2003) but with regard to their enduring consequences on ecosystem structure and function decades or centuries or longer after they have occurred and natural processes have been operative. We look particularly at long-term impacts on terrestrial and aquatic ecosystem structure and composition, soil structure and chemistry, and carbon (C) and nitrogen (N) dynamics, and the persistence of land-use legacies through subsequent episodes of natural disturbance and environmental change. Since such legacies from past human activity are easily overlooked and yet are widespread across broad areas, they are of particular interest to conservationists and land managers as well as to scientists. Consequently, we conclude by considering the importance of a historical perspective and awareness of land-use legacies for the development and implementation of land policy.

Persistent imprints of ancient land use

Surprisingly, in many parts of the globe ancient land-use activity continues to influence modern pattern and process. Nearly 1000 years ago, the Maya civilization, which had converted the southern Yucatán Peninsula to a mosaic of fields, house sites, and temple cities, declined, thereby allowing native biota to dominate the landscape again (Turner 1974). Until the mid-20th century, the region remained largely unpopulated and forested (figure 1). Today regional gradients in precipitation control broad forest patterns, local vegetation varies with soil moisture and past fires and hurricanes, and forest reserves have a deceivingly natural appearance (Turner et al. 2003). Nonetheless, it is impossible to interpret the physical environment, vegetation patterns, or ecosystem

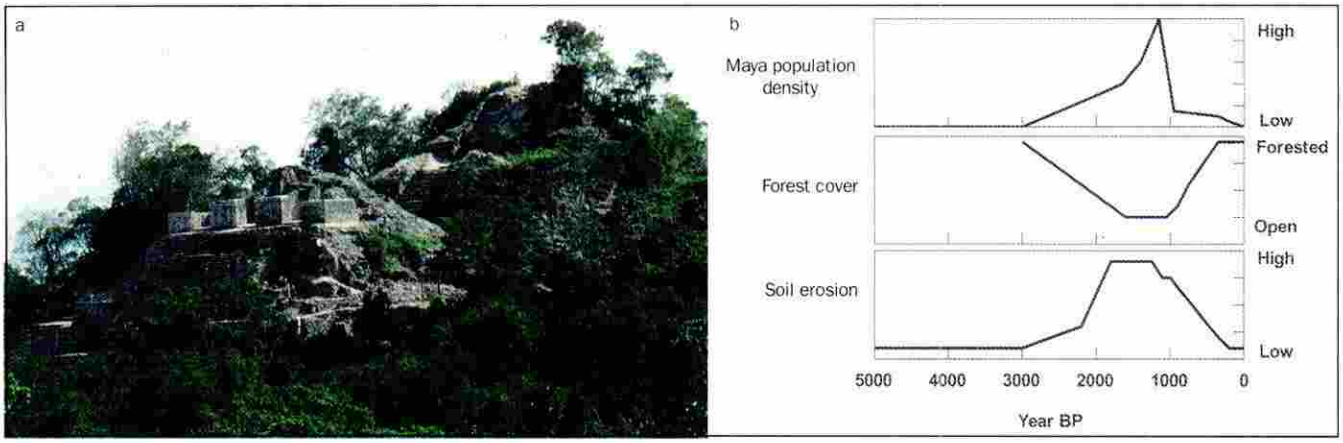

Figure 1. Maya impacts to the tropical forests of the southern Yucatán include (a) temple ruins emerging from a closed canopy forest and (b) a history of population change, deforestation and reforestation, and a lengthy history of soil erosion and sediment accumulation in lakes and lowland basins. Modified and used with permission from Binford and colleagues (1987). BP = before the present. Photograph: David R. Foster.

characteristics without reference to ancient history (Beach 1998, Turner et al. 2003). Forest composition at landscape to regional scales is linked to past human use. Forest microtopography is often defined by the millennia-old relief of house mounds, stonewalls, and terraces, and soil structure is tied to erosion associated with deforestation in AD 700–900. In fact, erosional deposits form a distinct sediment layer ("Maya clay") in many lakes and wetlands. The ancient past shapes modern conditions and raises intriguing issues, such as whether the centuries-old forests should be considered primary or secondary and how the insights from this history should alter our thinking on the resilience and restoration of tropical ecosystems.

The Maya story of profound yet easily overlooked legacies of ancient impact is hardly singular. In Chaco Canyon, New Mexico, the ongoing spread of juniper and pine is creating woodlands in the semidesert environment. This transformation is most likely not a response to recent climate change but just another episode in the lengthy recovery of the landscape from overharvesting by the Anasazi some 800 to 1000 years ago (Swetnam et al. 1999). Similar stories of a decline in land-use intensity yielding apparently natural modern conditions emerge from tropical to boreal regions worldwide (Birks et al. 1988).

Land-use legacies in forest structure and composition

Yucatán and Puerto Rico research is part of a cross-site LTER study in the eastern United States and the Caribbean that is evaluating the duration and underlying mechanisms of land-use legacies initiated by a deforestation–reforestation sequence. Across much of this region, a history of early European settlement, logging, and agriculture has been followed since the mid-19th century by declining land-use intensity and natural reforestation (Trimble 1974, Thomlinson et al. 1996, Foster and O'Keefe 2000). For eight LTER sites (Hubbard Brook, Harvard Forest, Plum Island Ecosystem, Baltimore Ecosystem Study, Virginia Coast Reserve, Cedar Creek, Coweeta Hydrologic Laboratory, and Luquillo Experimental Forest), this history has left persistent imprints on ecosystem structure and function with local, regional, and even global implications (figure 2).

At stand to landscape scales, differences in land-use history strongly control modern vegetation patterns (Zimmerman et al. 1995, Motzkin et al. 1999a, 1999b). Overstory composition in many eastern and midwestern US forests has shifted from long-lived and shade-tolerant late-successional species to more rapidly growing and often shorter-lived species that sprout effectively or invade open sites aggressively. The age and size structures of modern forests are often unimodal and tied to the time since agricultural abandonment or the last episode of logging (Goodale and Aber 2001). An important structural consequence of cutting history is the abundance of multiple-stemmed trees, a condition uncommon in forests that have not experienced human impacts, except on chronically disturbed sites (Del Tredici 2001). Regionally, forests of the eastern United States lack large trees, dead snags, and structures (e.g., coarse woody debris, uproot mounds, and pits) that diversify ecosystems under natural disturbance regimes. Globally, one legacy of intensive logging is a significant reduction in the amount of C stored in coarse woody debris (Harmon et al. 2001).

Studies from Harvard Forest show that another enduring legacy of land use in New England is the homogenization of tree species composition at a regional scale (Foster et al. 1998). Because of the broadly similar history of agriculture, logging, and reforestation, a subset of the regional tree flora with disturbance-adapted life-history traits has been favored. The result is a shift from pre-European patterns of forest variation that correspond to subtle gradients in regional climate to a more homogeneous condition (Fuller et al. 1998).

In contrast, at a landscape scale, striking variation in understory species assemblages corresponds to historical impacts that may date back a century or more. Studies by Harvard

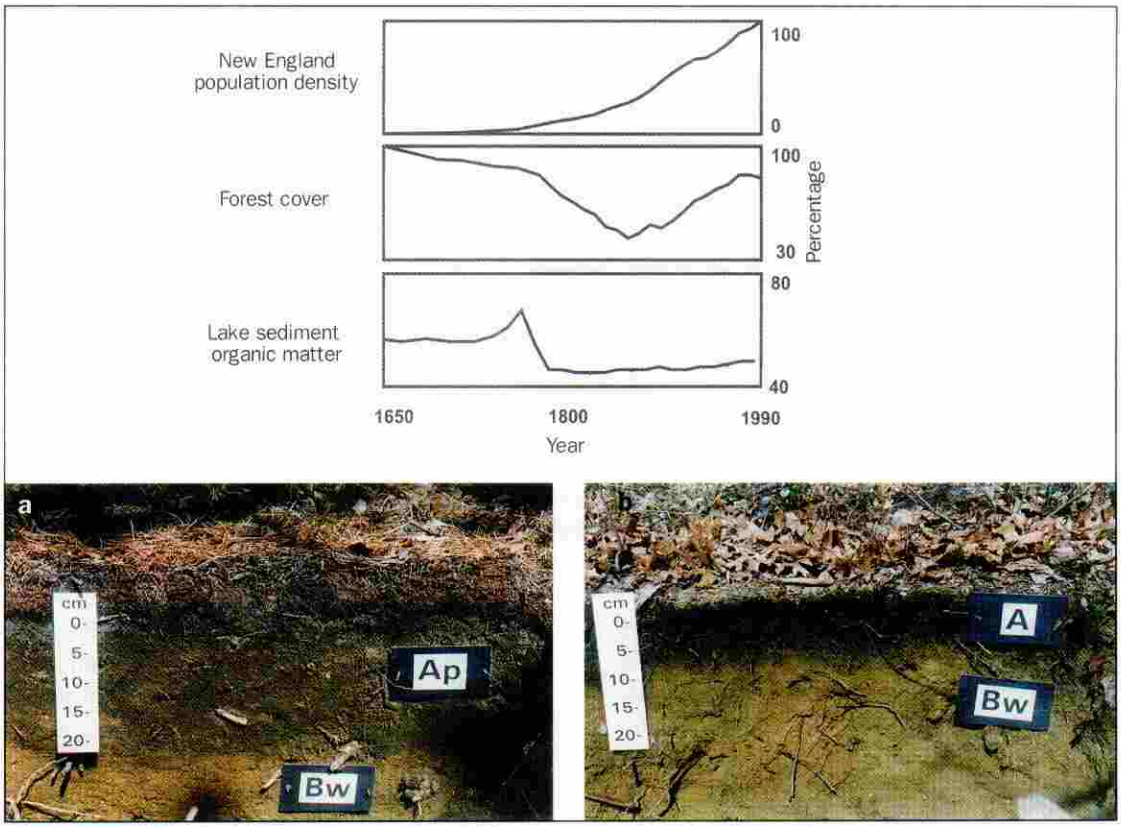

Figure 2. In the New England landscape, a history of deforestation and intensive agriculture was followed by farm abandonment and natural reforestation. These dynamics were driven by changing social and economic conditions, especially a shift of the growing population away from the rural landscape and into urban and suburban settings and employment other than farming and natural resources. Lake sediments reflect increased inorganic matter delivery as a consequence of land clearance and an absence of a return to prior conditions, despite regional reforestation and complete reforestation for more than 75 years in the particular watershed (see the line graphs above). On some sites cultivation has left a persistent legacy of Ap (plow) horizons in soils, despite a subsequent history of forest growth over the past century or more (a), in comparison with undisturbed soils (b). Modified and used with permission from Foster and colleagues (1998) and Francis and Foster (2001).

Forest researchers across coastal to inland sites (Motzkin et al. 1996, 1999a, 1999b, 2002, Eberhardt et al. 2003), and including extensive comparison with European woodlands, indicate that these compositional imprints are most apparent between continuously wooded sites (i.e., ancient woodlands and primary woodlands) and adjoining forests that were once cleared (secondary woodlands; figure 3). Although these floristic differences may be driven by site differences that predate the land use or arise from it, studies on environmentally homogeneous sites across which history varies indicate that the patterns are often controlled by land use alone (Motzkin et al. 1996, Donohue et al. 1999). At least two mechanisms are operative: (1) Intensive land use may act as an editor, removing native species that vary in their ability to disperse and reestablish when the intensity of use declines; (2) the site may be colonized by opportunistic species that may persist for considerable time once established (Motzkin et al. 1996, Eberhardt et al. 2003). Similarly, in Puerto Rico, localized impacts such as charcoal production have created distinctive forest patches that add to landscape-scale heterogeneity (Thompson et al. 2002).

Land-use imprints on soils

The imprints of past land use on soil properties are equally enduring and may have important ramifications for the function and dynamics of ecosystems ranging from forests to grasslands (Trimble 1999). Many persistent physical, chemical, and biological changes are imposed on soils by agriculture, burning, and grazing (Haas et al. 1957, Burke et al. 1989, Davidson and Ackerman 1993, Compton et al. 1998, Pouyat and Effland 1999). Plowing homogenizes the upper soil horizons to a depth of 10 to 30 centimeters (cm), leaving a uniform Ap (i.e., plow) horizon (cf. figure 2) that may be depleted of C and N, although specific impacts will vary with soil amendments, such as liming and fertilization, and cropping type and duration (Compton et al. 1998, Knops and Tilman 2000, Richter et al. 2000). Under changed vegetation and environmental conditions, microbial populations are altered, and the invasion of exotic organisms, including earthworms, is often facilitated (Callaham and Blair 1999).

When farmed sites are abandoned and native vegetation reestablishes, physical and biological soil development proceeds slowly. Ap horizons may persist for hundreds of years

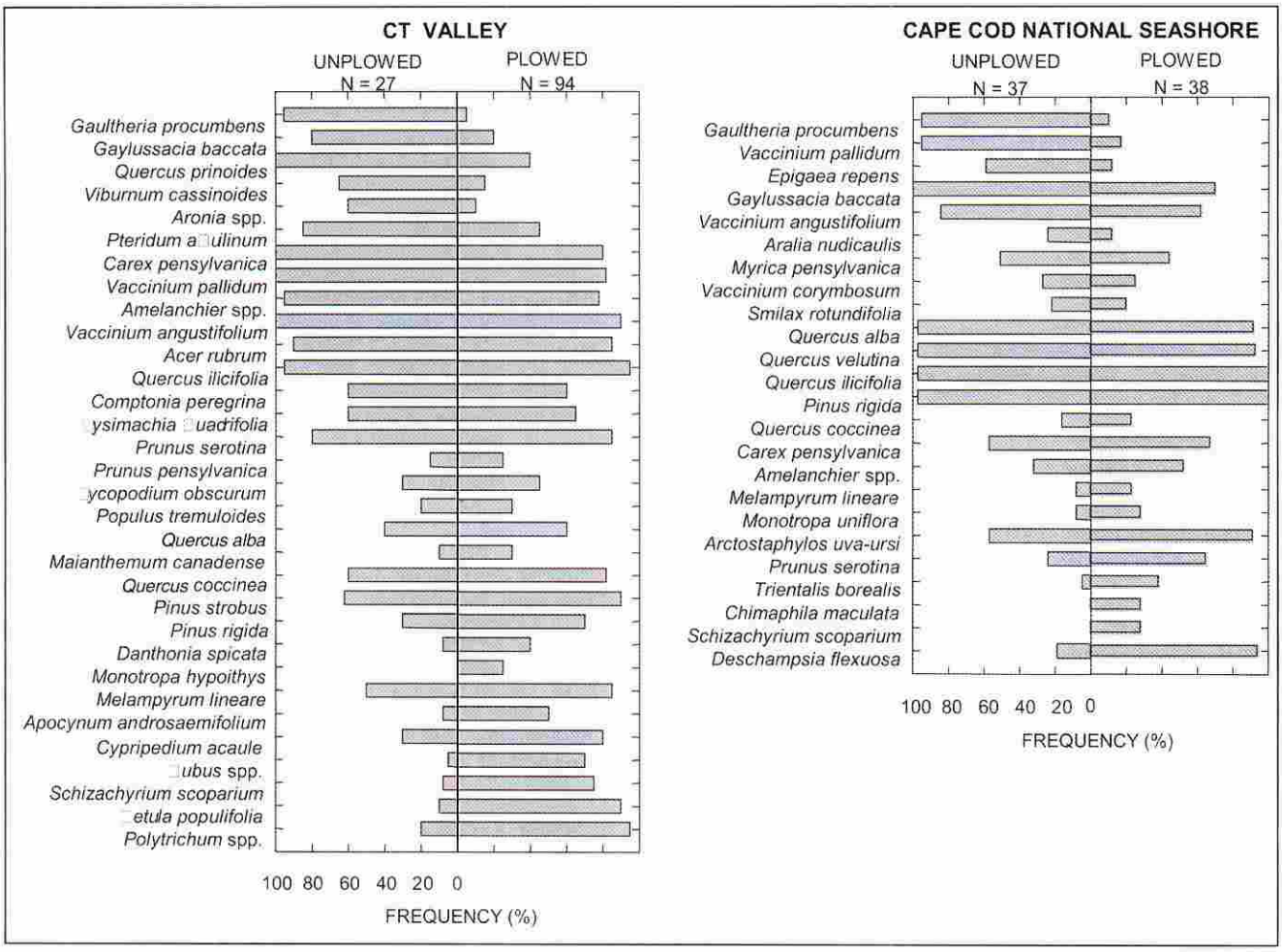

Figure 3. Persistent variation in the understory flora of woodlands generated by century-old land use. In both the Connecticut Valley in central Massachusetts (left) and the Cape Cod National Seashore (right), two major land-use histories occurred across environmentally similar sites: Areas were deforested, plowed, and subsequently allowed to reforest naturally (plowed) or remained continuously in woodland (unplowed, woodlot). Both areas have been forested and unmanaged since the late 19th century. Three distinct patterns may be seen: (1) Species (especially ericaceous shrubs) preferentially occurring in former woodlots, and presumably widespread across the area initially, that were eliminated by agriculture and have failed to reestablish over the past 100 years; (2) ubiquitous species that have great mobility and environmental flexibility; and (3) weedy species that established and have persisted on former agricultural sites but are incapable of establishing widely in intact forest areas. Modified and used with permission from Motzkin and colleagues (1996) and Eberhardt and colleagues (2003). (N is the number of plots sampled.)

as new A, E, and B layers gradually differentiate. Studies at forested sites (Hubbard Brook, Harvard Forest, Coweeta, Cedar Creek, and the Calhoun Forest in South Carolina) and grassland sites (Shortgrass Steppe and Konza Prairie) indicate that differences in pH, C, and N imposed by agriculture can endure for decades to centuries after use is discontinued and native species and processes reestablish (Burke et al. 1995, Coffin et al. 1996, Compton et al. 1998, Baer et al. 2002).

At Cedar Creek, Knops and Tilman (2000) used a combination of chronosequences, long-term measurements, and modeling to investigate the trajectories of soil recovery on sand plains reforesting after field abandonment. Up to 75% of the N and 89% of the C were depleted from the upper 10 cm of mineral soil at the time of agricultural abandonment, relative to intact sites. Over subsequent decades the recovery trajectories for different soil attributes vary: For example, organic C, total N content, and total plant biomass increase at different rates than the recovery of the ratio of C to N, microbial C, and microbial N. From these results it is estimated that legacies of past land use in soil C and N on this dry oak–woodland landscape will persist for 150 years. A comparable period was proposed by Burke and colleagues (1997) for the time required for soil C levels in shortgrass prairie to recover following two decades of cultivation (figure 4). In similar fashion, researchers from the Konza tallgrass prairie document that total C across a range of restored grasslands remained 36% lower (4390 grams [g] C per square meter [m^2]) than in

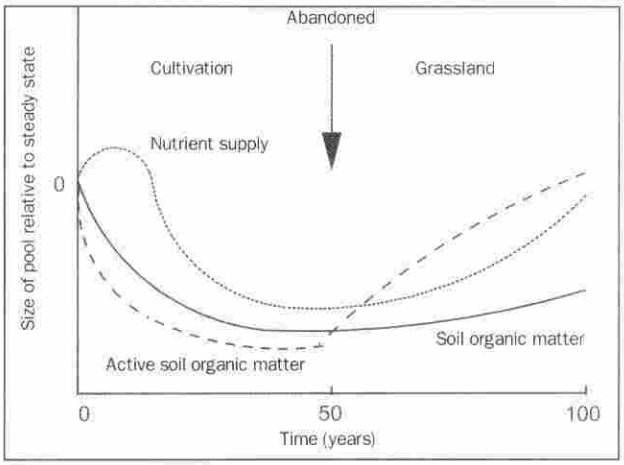

Figure 4. Conceptual representation of the responses of total soil organic matter, soil organic matter that is biologically active and subject to active modifications, and nutrient supply to 50 years of cultivation followed by 50 years of recovery in perennial grasslands such as the shortgrass steppe, the tallgrass prairie, and adjoining prairie–forest margin.

comparable native prairie (6830 g C per m^2; Baer et al. 2002). Rates of C accrual (in the upper 5 cm of soil) in the first 12 years averaged 58 g per m^2 per year, which suggests at least a 30-year recovery period.

These land-use legacies may greatly affect the productivity of the subsequent vegetation (Richter et al. 2000). Across much of the southeastern United States, broad expanses of second-growth pine forest occupy sites that were previously harvested for cotton and other crops before abandonment and natural succession (Trimble 1974). Nitrogen and soil organic matter were removed by repeated cropping and erosion, whereas fertilization, although not fully counteracting these effects, enhanced N concentrations in the residual soil organic matter. After 50 to 125 years of forest development, the upper 30 cm of soil in these old-field pine forests contain only 64% of the N and 59% of the C of continuously wooded hardwood forests. The nature and character of the forest rotations and harvesting regimes across the Southeast are extremely varied. However, in all cases the current land use is largely a product of the history of land use, and a substantial fraction of the N cycling in these pine forests comes from fertilizer applied many decades ago (Richter et al. 2000). The variety of current forest management practices will most certainly produce very complex legacies in the future, overlaid on today's legacies.

Land use and aquatic ecosystem structure and function

The legacies of past agriculture extend to the aquatic ecosystems embedded in secondary forest landscapes. In assessing faunal diversity of southern Appalachian streams around Coweeta, Harding and colleagues (1998) determined that the modern composition and diversity of invertebrates and fish were best predicted, not by current forest cover or environment, but by watershed land use over five decades earlier. These legacies result from a combination of biological and habitat factors. For example, macroinvertebrates are slow to disperse upstream, and therefore, once removed, populations reestablish only gradually. In addition, large physical structures, such as debris dams that control stream environment and habitat diversity, are slow to develop following intensive activities like clear-cutting or agriculture.

Coarse wood, which originates in terrestrial ecosystems, is a critical element in aquatic ecosystems. Boles, root mass, branches, and smaller organic material form debris dams that dissipate stream energy and diversify habitat structure in riverine and lake environments. In old-growth forests, inputs of wood to streams occur episodically, related to tree death or damage (Bilby 1981). Massive logs make effective dams that deflect water and trap fine organics like leaf litter, enabling it to decompose and release nutrients (Bilby and Likens 1980). Large logs resist dislodging by storm events and decay slowly, thereby maintaining persistent structures. For decades following logging, the input of large, dead logs is interrupted, and existing material decays. The result is an ongoing release of stored organic matter, an increase in stream flow velocities, a decrease in channel complexity, and simplification of stream habitat. Experimental watershed manipulations at Hubbard Brook and Coweeta allow these impacts to be quantified and linked mechanistically. In the New Hampshire streams, large exports of organic matter occurred after logging, with 84% of the downstream movement of organics tied to increased erodibility of the material and 16% to increased stream flow (Bilby 1981).

Regional surveys by Hubbard Brook researchers show that, as a consequence of logging in the late 19th and early 20th centuries, organic debris dams remain rare on moderate-sized streams (i.e., streams greater than 7 m wide) and will require many additional decades to recover (Bilby and Likens 1980, Bilby 1981). Because of changes in stream hydrology and the quality of allochthonous inputs, the quality and quantity of stream organic matter also requires considerable time to recover in secondary forests. In general, the organic matter in undisturbed watersheds is refractory and has a long residence time. In contrast, in logged and old-field forests, C compounds are easily decomposed and more labile and transient. Analogous processes operate in lake ecosystems. In many watersheds land use has effectively eliminated a pulse of woody debris to riparian and near-shore environments, with a long-term, detrimental impact on the recruitment of large fish and impacts on the entire food web (Christensen et al. 1996).

Past conditions and land-use impacts exert other persistent influences on modern lakes. Development and associated nutrient inputs drive many lakes to progressively more eutrophic conditions through time. Reversal of this condition is a major objective of lake management; however, studies by researchers at the North Temperate Lakes LTER site suggest that legacies of land use in surrounding watersheds may thwart these efforts (Bennett et al. 1999, 2001). Agricultural

and suburban fertilizer applications result in substantial storage of phosphorus (P) throughout the landscape. Consequently, even with substantial reduction in inputs, watersheds may continue releasing P and maintaining eutrophic conditions for decades.

The pattern of slow recovery of lakes from land use is seen in many settings. Widespread reforestation leaves many eastern US watersheds in less disturbed conditions than centuries earlier and enables an evaluation of the recovery rate of lake ecosystems (Francis and Foster 2001). Surprisingly, studies by Harvard Forest researchers indicate that 100 to 150 years after reforestation major physical and biological aspects of the aquatic environments—including sediment accumulation rates and organic content, assemblages of fossil chironomids, and productivity—remain altered and exhibit little reversion to earlier conditions.

Land-use history and terrestrial ecosystem process

Legacies of historical activity condition the susceptibility and response of some ecosystems to stress and disturbance and assume a critical role in the assessment of ecosystem vulnerability to these factors. Over much of the earth's surface, N is a limiting nutrient that controls productivity and aspects of the biosphere–atmosphere system. Human activity has altered the global N cycle, with the result that large regions receive greatly increased levels of N through dry and wet deposition. In excess, N can disrupt plant metabolism and key ecosystem processes, affect forest composition and health, and leach into groundwater and aquatic systems, where it can become a pollutant and health hazard (Aber et al. 1989). Consequently, an understanding of the mechanisms controlling forest susceptibility and response to this anthropogenic stress are major scientific and policy concerns.

Harvard Forest and Hubbard Brook collaborators have produced and tested a set of hypotheses concerning N saturation in forested ecosystems (Aber et al. 1989, 1998). Long-term experiments, coupled with regional field studies, indicate that landscape history is a major factor conditioning ecosystem status and response to N deposition (Goodale et al. 2000, Goodale and Aber 2001). Oftentimes prior history is more important than either forest composition or deposition amounts in predicting ecosystem response to N or stream and soil characteristics such as N concentration and the loss rates of nitrate (NO_3^-) and dissolved organic and inorganic N (Goodale et al. 2000, Ollinger et al. 2002). In watersheds where disturbance by fires or logging during the 19th and early-20th centuries had triggered N losses through volatilization, NO_3^- leaching, and organic matter export, forest ecosystems are currently accumulating N more rapidly than in neighboring old-growth watersheds. This control over watershed-scale nutrient dynamics can persist for well over a century (Goodale and Aber 2001).

Parallel experiments in which N has been added chronically to forests for more than a decade confirm that land-use history conditions the rate at which N saturation occurs and excess N begins to leach into the groundwater system (Aber et al. 1998). In continuously wooded hardwood sites that have been cut and burned intensively, N leaching was not observed for up to 10 years, even under very high applications of NO_3^- and ammonium (NH_4^-): that is, 150 kilograms (kg) per hectare (ha). In contrast, adjoining pine forests on sites that were farmed in the 19th century and amended with manure applications experienced NO_3^- leaching in 3 years on high N sites and in 9 years under low application rates. The pines on the high N sites were also less productive. This result is all the more striking because pine stands, with longer foliar retention, lower quality litter, and a tighter N cycle, would be expected to be more N limited and capable of storing more N than neighboring hardwood forest. Overall, these results suggest that site history strongly determines the trajectory to saturation (Aber et al. 1998).

In the semiarid grassland, which is not typically recognized as N limited, N amendments may become a legacy. Today, sites that were enriched with N 30 years ago still have higher N availability and greater exotic plant cover than control plots (Milchunas and Lauenroth 1995). The annual exotic species have tissues with low C to N ratios, which maintain high N mineralization rates, suggesting that feedbacks between N additions and exotic species generate a persistent influence on ecosystem functioning.

Because land-use history plays an equally important role in local C dynamics, history becomes a critical issue in the global C cycle and figures strongly in related policy discussions. The rate of increase in atmospheric carbon dioxide (CO_2) is determined by balances between the release and storage of C in terrestrial and marine pools. Many lines of evidence suggest that a substantial C sink is located in the midlatitudes of North America, a region undergoing long-term changes as a consequence of past logging, fire suppression, and reforestation (Casperson et al. 2000, Tilman et al. 2000). This regional sink is a major legacy of shifting patterns of land use; consequently, its magnitude and duration will be largely determined by the lags in ecosystem response and recovery from these impacts. Despite major uncertainties regarding such processes as CO_2 enhancement, N fertilization, and climate feedbacks on C dynamics, inclusion of historical factors and their ecological legacies greatly improve the performance of models at all scales (Casperson et al. 2000).

On former farmland and logged sites where land-use intensity has declined over past centuries, the restoration of depleted soil C and forest regrowth are sequestering considerable amounts of C in above- and belowground pools (Compton et al. 1998, Goodale and Aber 2001). With current timber growth exceeding levels of extraction in most of the eastern United States, the net effect of these processes may be substantial (Casperson et al. 2000). As forests mature, and as activities including forest conversion increase, these balances will shift. Consequently, to understand and project these processes forward is a critical challenge.

In extensive areas subjected to 20th-century fire suppression, C storage is occurring through forest growth and maturation, woodland invasion onto previous grass- or shrub-

dominated lands, infilling of open forests, and accumulation of deeper organic soil horizons and coarse dead woody material (figure 5; Vose 2000). These processes are occurring rapidly. For example, at an LTER site in the Flint Hills of Kansas, researchers document that gallery forests and cedar woodlands are expanding broadly onto former prairies and are only locally controlled by fire, mowing, or cutting (Knight et al. 1994, Briggs et al. 1998). The 60- to 80-year-old red cedar stands that have replaced native grassland have accumulated up to 10,600 g C per m^2 in aboveground biomass and an average of nearly 700 g C per m^2 in forest floor mass, resulting in a substantial increase in net ecosystem C storage and a change in allocation of C aboveground compared with the native grasslands. In the oak woodlands of southeastern Minnesota, areas that are subject to fire suppression also exhibit marked differences in C sequestration in comparison with experimentally burned sites at Cedar Creek (figure 5; Tilman et al. 2000).

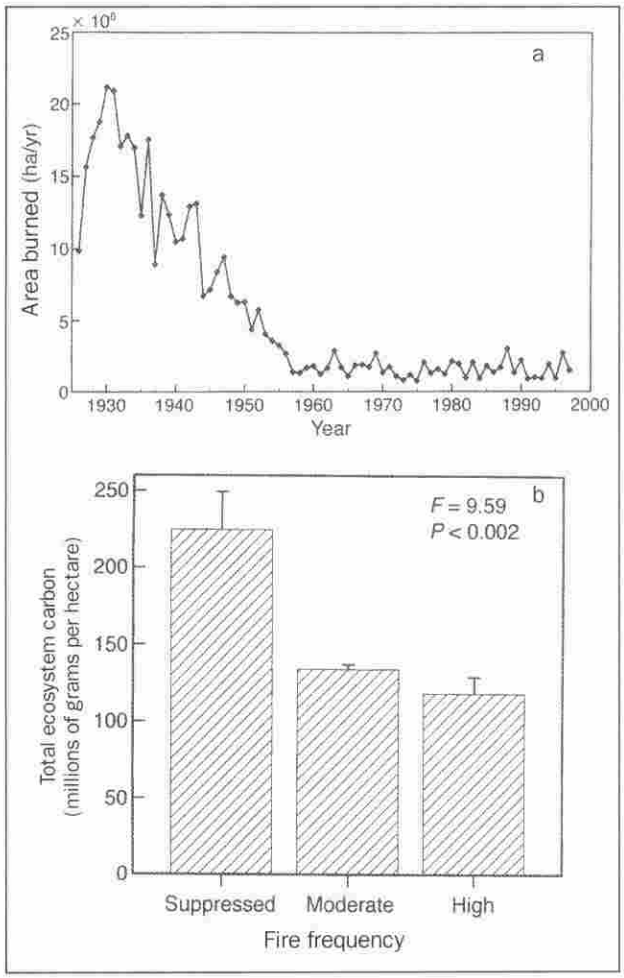

Figure 5. (a) Changes in ecosystem burning in the United States in the past century (1926–1997) have generated major changes in ecosystem structure, composition, and function, including changes in terrestrial carbon storage. (Data from the US Census and USDA Forest Service, as modified and used with permission from Tilman and colleagues [2000].) (b) Effect of three experimental fire treatments on ecosystem carbon in an oak savanna ecosystem at the Cedar Creek LTER site. Modified and used with permission from Tilman and colleagues (2000).

In the Alaskan boreal region, fire suppression results in C storage in deep soil organic layers, which provide insulation resulting in cooler, moister soils and a tendency for permafrost development or a reduction in the active layer of seasonal soil thawing. Studies at the Bonanza Creek LTER site indicate that long-term consequences of this process include a reduction in site productivity as root metabolism, decomposition, and nutrient availability decline.

Persistence of land-use legacies through natural disturbance

The legacies of past land use interact with natural disturbance processes and may confound the interpretation of disturbance regimes in many landscapes. Vegetation structure and composition strongly control landscape susceptibility and ecosystem response to fire, wind, and mass movement, and consequently vegetation modification by past land use can alter these responses, with important implications for policy and management. Of equal significance is the persistence of land-use legacies through several episodes of disturbance. This finding is critical, because scientists who are investigating disturbance-prone landscapes often incorrectly describe post-disturbance responses and conditions as "natural" in the sense that natural processes were the proximate cause of the pattern of disturbance and ecosystem response (Eberhardt et al. 2003). The longevity of land-use legacies also belies a common assumption that natural processes and conditions may be restored on human-modified landscapes simply by applying historically relevant disturbances like prescribed fire (Stephenson 1999).

Following severe damage by Hurricane Hugo to Puerto Rico, researchers at Luquillo noted that striking patterns of floristic variation and successional trajectory corresponded more to land use in the 19th and early 20th centuries than to the actual severity of a blowdown. These results arose unexpectedly when scientists who were documenting species distributions and diversity in long-term monitoring plots uncovered patterns of prior land use that were previously unrecognized (Zimmerman et al. 1995, Thompson et al. 2002). Similarly, well-differentiated patterns of plant and soil variation on New England sand plains relate to historic variation in 19th-century agriculture and show little change despite repeated episodes of fire (Motzkin et al. 1996, Eberhardt et al. 2003). Even intense fire exerts little effect on belowground conditions in this vegetation and, as in Puerto Rico, the plants recover vegetatively through sprouting. Consequently, although fire, like hurricane winds, greatly affects vegetation structure by creating a new age and size distribution, it does not alter the floristic pattern established by land use a century earlier. Thus, an investigation that proceeds without historical context might easily ascribe the resulting vegetation solely to site conditions and natural disturbance.

Perspectives and implications for management

Recognition that the history of disturbance shapes the long-term structure, composition, and function of most ecosystems and landscapes can increase the effectiveness of management (Swetnam et al. 1999). In contrast, ignoring historical legacies may lead to the development of ill-conceived conservation and management schemes (Foster 2000). Historical perspectives aid the interpretation of landscapes that we wish to manage and contribute to the identification of realistic goals and appropriate tools and approaches to achieve those ends (Landres et al. 1999). Historical studies may also inject sober reality into the planning process by highlighting constraints to our efforts. After all, the changes in ecosystems that are derived from historical legacies and natural ecosystem processes create landscape conditions that significantly constrain policy and management choices. In all cases historical studies underscore the multiplicity of past states and potential directions for management and consequently reinforce the conviction that, although science and history may inform management, the ultimate driver of policy is human values and perceptions.

Land-use legacies have different relevance in the context of varying landscape and management objectives. These contexts are diverse and span a broad range: wildlands, such as national parks or wilderness areas, where naturalness is the management objective or the intended context of research projects; natural resource landscapes that are managed for production while sustaining native species and processes; plantations and other intensively managed commodity lands that may include exotic chemicals and nonnative crop species; and cultural landscapes where traditional land-use practices are used to sustain nonnatural attributes in the context of specific objectives such as maintenance of species assemblages or a historic condition. In the section below, we give examples on this continuum, noting cases where science and policy meet in planning management and conservation.

Wildlands and managed natural resource landscapes

Across North America 500 years ago, grazing by large herbivores like bison, elk, and moose undoubtedly imposed varying patterns of species diversity, vegetation structure and composition, and ecosystem function (Axelrod 1985, Milchunas et al. 1998, Knapp et al. 1999). In some areas large grazers persist, but for much of the continent, removal of these species or replacement with domestic livestock initiated a series of changes that are easily overlooked—legacies of human activity. Long-term studies highlight the role of native grazers, provide motivation for their reestablishment, and sometimes identify cultural substitutes for their activity in areas where commodity production is an important objective (Knapp et al. 1999).

At the Konza Prairie, long-term experimental manipulations examine the range of impacts and interactions among bison (or cattle) grazing, fire, mowing, or no management. It is interesting that, although fire reduces grass thatch, mineralizes nutrients, and enhances productivity in desirable ways that are not replicated by mowing, adding bison is essential for maintaining high levels of native plant diversity (Collins et al. 1998). Bison graze predominantly on graminoids, avoiding most of the diverse forbs and preferentially feeding on burned areas where grasses, with tall stature and dense cover, tend to outcompete other species. Under a grazing regime the smaller stature forbs thus increase in number and abundance.

Bison also create distinct grazing patterns at three spatial scales that enhance habitat diversity. Grazing patches of 20 to 50 m^2 are intensely cropped, whereas grazing lawns form larger areas (> 400 m^2) of less intensive defoliation. Gradual shifting of these areas, selective reduction of the dominant grasses, and other impacts, including nutrient redistribution, wallowing, and bison carcasses, create a dynamic mosaic of microhabitats. On a broader scale, bison historically migrated seasonally, which shifted this patchwork geographically over decades. Clearly, the reintroduction of bison, such as has been accomplished at Konza and a few other sites, is a critical element in the restoration of the tallgrass prairie, which once covered 68 million hectares (and which now totals 150,000 ha) with some 30 million to 60 million bison. More important, Konza research indicates that, although cattle do not mimic all aspects of bison ecology (e.g., they do not wallow and seldom are left to die on the reserves), they are similar enough to argue for putting cattle, managed for their ecological role, on sites where bison will not meet landowner objectives. Similarly, 50 years of experiments on the shortgrass steppe highlight the importance of cattle grazing for maintaining ecosystem structure (Milchunas et al. 1998).

Long-term and historical research has provided fundamental insights for management of prairie, woodland, and forest regions where fire has been suppressed over much of the past century. In many cases forest management, prescribed fire, and "prescribed natural fire" have been implemented, based on an understanding of the natural wildfire disturbance regime and in an effort to reverse conditions that are legacies of former policy (Knops and Tilman 2000, Vose 2000). These approaches include using an understanding of historic fire regimes to design forest management that will sustain native species and processes in landscapes where commodity production and conservation objectives are balanced (Cissel et al. 1998). A premise of this approach is that creating and sustaining habitats that are within the range of conditions that native species occupied in the past will favor these species' survival.

This concept is being explored at the H. J. Andrews Experimental Forest LTER site in Oregon (Cissel et al. 1998). Various techniques have been used to interpret the past disturbance regime of this complex landscape, where fire recurrence intervals ranged from less than one to several centuries, depending on topography, vegetation, and other factors. This information was then used to develop a landscape management plan for a 23,900 ha watershed adjacent to the Andrews Forest. The frequency, severity, and spatial patterns

of forest cutting in that plan are based in part on the natural disturbance regime. Approximately 25% of the area had previously been clear-cut in dispersed patches, creating substantial fragmentation of the forest pattern; thus one objective is to restore landscape structure to within the range of historic conditions. A longer-range objective is to develop a management system that accommodates wood extraction, while creating land-use legacies that protect native species and processes. Implementation of the plan is now underway using an adaptive management approach that involves monitoring and further research to collect new information to be used in plan adjustments. In a sense this is a conscious effort to minimize the land-use legacy in what is inherently a dynamic landscape.

Cultural landscapes restored to their cultural past

In eastern North America and northwestern Europe, among the most rapidly declining and highly threatened species are those of the grasslands, shrublands, and early successional woodlands that have progressively reverted to mature forest, been developed, or been placed under intensive agricultural management (Birks et al. 1988, Vickery and Dunwiddie 1997, Askins 2000). Regional studies by researchers at the Harvard Forest LTER site underscore the anthropogenic legacies in these patterns. On the island of Nantucket, Massachusetts, which supports one of the greatest concentrations of uncommon and rare species in the eastern United States, an extensive survey of the grassland, shrubland, and heathland conservation areas confirmed that essentially all sites had been intensively altered for agriculture in the past 300 years. Although originally wooded, the island was cleared and supported 10,000 to 15,000 sheep in the mid-19th century. Although much of Nantucket and neighboring Martha's Vineyard appear natural today, the landscape and biotic assemblages are very much the product of the history of anthropogenic activities (Motzkin and Foster 2002, Foster et al. 2002). Encroachment of woody vegetation and human development threaten to eliminate nonforest species from many areas. Although fire is used increasingly to counteract this trend, studies suggest that practices responsible for creating this landscape, notably sheep grazing, are likely to be the most effective at perpetuating it. Conservation organizations have recently begun experimenting with exactly these approaches.

General considerations and sobering reality for restoration

Conservation is often driven by a desire to restore natural areas to a previous condition characterized as fitting within the "natural range of variability" or "indigenous nature of the system" (Landres et al. 1999). In most cases in which this perspective is adopted, the consequences of land-use history (outside of Native American activity) are viewed as negative, and an effort is made to remove the legacies of prior human activity (Moore et al. 1999). In these situations, the historical and ecological work in LTER and similar research programs enable identification of the consequences of land use, the desired future condition or activity to be restored, and some of the means of achieving ecosystem restoration.

However, the persistence of land-use legacies should inject some cautionary reality to restoration activities. Streams and lakes in which decades of reforestation have resulted in little recovery of the fauna or physical and chemical conditions indicate some of the constraints to restoration (Harding et al. 1998, Bennett et al. 1999, Francis and Foster 2001). The relationships between physical, chemical, and biological recovery processes mean that in many cases lengthy legacies of prior conditions and disturbances will persist in many settings where superficial physical appearances suggest otherwise.

In like fashion, the persistent signatures of past human activity in soils and the patterns of vegetation in the face of subsequent disturbance underscore the limitations of restoration through reintroduction of natural disturbance regimes (Zimmerman et al. 1995, Stephenson 1999). Prescribed fire is often used to restore altered communities or ecosystems that are considered degraded as a consequence of prior land use, including fire suppression. However, studies from a range of ecosystems suggest that plant composition and soil characteristics may be relatively unchanged by this renewed wave of burning (Motzkin et al. 1996). In essence, the reintroduction of historically natural processes does not necessarily restore historic ecosystem conditions (cf. Stephenson 1999).

Many valued landscapes and biotic assemblages have developed as a consequence of past human activity (Birks et al. 1988). Maintenance of these cultural landscapes and their biota often requires the continuation or reintroduction of traditional management activities. However, recognition of a land-use imprint often poses a conundrum for American conservationists committed to natural processes and native communities. In many of the early Euro-settler landscapes, centuries of grazing, mowing, plowing, and burning have produced a disturbance mosaic that supports unusual floral and faunal assemblages. As traditional land-use practices change or are discontinued, these landscapes are changing and their culturally maintained biota are declining, as in the Nantucket example.

Introduced species are another legacy of human activity that must be accommodated in many ecosystems. In Puerto Rico, for example, bats are the only extant native mammals, but mongooses (introduced in 1877) and rats (perhaps arriving with Columbus in 1493) are now important carnivores, seed predators, and insectivores in some ecosystems (Willig and Gannon 1996). These aliens cannot be exterminated, and thus conservation and restoration efforts must deal with their presence and impacts as well.

Trajectories of legacies into the future

This critical look at land-use legacies places the present conditions of an ecosystem in the context of its trajectory of change that embodies past land use, climate, and natural disturbance, as well as endogenous successional processes. It underscores the insights into current landscape patterns and processes that may come from a consideration of these his-

torical developments and highlights the need to incorporate this lengthy temporal perspective and awareness of legacies in the framing of conservation and management objectives. Past dynamics shape current conditions and constrain future responses. Meanwhile, our ongoing suite of land-use activities continues to add further complexity and future legacies across current patterns. From this perspective we can view our present research on contemporary land uses as laying the foundation for understanding their legacies far into the future. This suggests the importance of designing and implementing very long-term experiments and monitoring programs that will facilitate interpretation of legacies and interactions of land use, natural disturbance processes, and climate variation, an appropriate task for long-term ecological research.

Acknowledgments

This manuscript benefited greatly from suggestions from John Hobbie, Steve Carpenter, Tim Seastedt, Glenn Motzkin, Tim Parshall, Dave Orwig, Nancy Grimm, Monica Turner, Matthew Greenstone, and two anonymous reviewers. Dorothy Recos Smith, Audrey Barker Plotkin, and Debbie Scanlon contributed extensively to the development of the manuscript. The work described in this article was broadly supported by the National Science Foundation's Long Term Ecological Research program and other state and federal agencies.

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