Landscape Legacies

Jennifer M Fraterrigo, University of Illinois, Urbana, IL, USA

Glossary

Carbon (or nutrient)-accumulation rate   The rate at which carbon or nutrients, such as nitrogen and phosphorus, accrue in biomass and soils.

Deforestation   The most intense form of timber extraction, wherein forests are converted for another land use either permanently or for a long term.

Landscape legacy   The long-term impact of historical events on ecosystem structure, composition, or function.

Natural disturbances   Any relatively discrete event in time that is not directly caused by humans; disrupts ecosystem, community, or population structure; and changes resources, substrate availability, or the physical environment (White and Pickett, 1985).

Nitrification   The step in the nitrogen cycle wherein ammonia is oxidized and converted to nitrite and then oxidized again to form nitrate.

Plow horizon   The homogenous soil layer, typically at 0–20 cm depth, that results from plowing. Designated as the "Ap" horizon in soil morphology.

Selective logging   A less intense form of timber extraction involving removal of select trees, often based on species, size, or age class. The forest canopy is typically maintained under this process.

Site history   The collection of past events involving natural disturbance or land use conversion at a given site.

Soil organic matter (SOM) depletion   The loss of organic matter from the soil. The main constituent of SOM is soil organic carbon. Consequently, this measurement relates directly to soil organic carbon loss and storage.

Introduction

At the start of the twenty-first century, appreciation for the importance of site history was emerging, yet most ecological studies tended to focus on the here and now, and many ecologists were unconcerned with the events that occurred in the distant past. There was a general perception that site history was unimportant for understanding the patterns and processes of modern ecosystems (Foster *et al.*, 2003). However, over the past two decades, ecologists have come to recognize that historical events can have lasting impacts on ecosystem structure, composition, and function. Indeed, many studies now show that site history can explain a substantial amount of the variation in contemporary ecological patterns and processes in both terrestrial and aquatic ecosystems. The strong, lingering effects of historical events on ecosystems are known as landscape legacies.

The duration of such impacts can be surprisingly long, particularly for ecosystem properties that are physically affected by past events. Soil and vegetation communities, as well as the processes they influence (e.g., nutrient cycling and primary production), often retain the imprints of past events for decades to centuries. In several cases, recovery from past events has not yet been observed, thereby leading the scientists to ask whether some ecological changes might persist indefinitely (Peterken and Game, 1984). In areas of northeastern France deforested during the Roman occupation and farmed during AD 50–250, species richness and plant communities of modern forests, as well as the chemical and structural properties of soil, still varied for more than 1500 years later with the intensity of former agriculture (Dupouey *et al.*, 2002). Similarly, modern forest composition, microtopography, soil texture, and the lake and wetland sediment deposits are strongly associated with the Mayan practice of deforestation in

AD 700–900 (Turner *et al.*, 2003). Changes brought about by past events can also act indirectly to produce lasting alterations in animal assemblages. In southeastern USA, fish and stream invertebrate communities are less diverse today because historical agriculture has persistently increased the amount of sediments in nearby streams (Harding *et al.*, 1998). Examples such as these have called into question the long-standing assumptions about trajectories of ecosystem recovery and compelled ecologists and managers to rethink of traditional concepts about natural or reference ecosystem states, as well as the controls on species distribution and abundance (Foster *et al.*, 2003; Flinn and Vellend, 2005). The knowledge gained from the studies of landscape legacies could, therefore, be important for directing management policies and more accurately predicting how biodiversity will change in the future.

Drivers of Landscape Legacies

Land Use

Human land use is a primary driver of landscape legacies. Humans have long used the land in ways that would modify the native ecosystems, and a growing body of evidence demonstrates that these changes can persist even long after human activities cease. Agriculture is the quintessential example, having been practiced in the form of cultivation and livestock husbandry since plants and animals were domesticated 10,000 years ago (Diamond, 2002). Although agricultural land use is expanding in some regions, other regions have experienced widespread agricultural abandonment (Ramankutty and Foley, 1999). For example, many modern forests in Western Europe and eastern North America existed as farms or pastures during the nineteenth and twentieth centuries (Rackham,

1980; Peterken and Game, 1984; Foster, 1992; Verheyen et al., 1999).

Despite long periods without additional disturbance, most lands with an agricultural history have characteristics distinct from those of lands without a similar disturbance history. Such agricultural legacies have been observed in a broad range of native ecosystems, including temperate mixed and deciduous forests in Europe and eastern North America (Motzkin et al., 1996; Foster et al., 1998; Compton and Boone, 2000; Richter et al., 2000; Hermy and Verheyen, 2007), grasslands and arid lands in the central and western USA (Burke et al., 1995; Coffin et al., 1996; Lewis et al., 2006), and in tropical forests (McGrath et al., 2001; Thompson et al., 2002; Turner et al., 2003). Although agricultural legacies are pervasive, their longevity and magnitude vary because the intensity and duration of agriculture, and specific management practices attending to agriculture, can differ widely (Coffin et al., 1996; Compton et al., 1998; McLauchlan, 2006). Empirical studies and meta-analyses demonstrate that the effects of cultivation and pasturing on soil carbon and nitrogen pools, for example, can vary markedly depending on farm-residue management, crop rotation, and tillage practices (Fearnside and Barbosa, 1998; Murty et al., 2002). Despite this variation, cultivated lands consistently show more persistent and profound legacies than pastured lands due to the high, sustained intensity of cropping (Compton and Boone, 2000; McGrath et al., 2001; Gerhardt and Foster, 2002; Brown and Boutin, 2009).

Timber extraction can also generate landscape legacies. These legacies tend to be smaller in magnitude and of shorter duration than those attending agriculture, but understanding the legacies of timber extraction is vital due to global importance and long history (spanning for more than two millennia) of this practice (Williams, 2000; FAO, 2006; Hansen et al., 2010). Timber extraction, like agriculture, is practiced with varying intensity. Deforestation (or clearcutting) is the most detrimental of such practices, characterized by wholesale forest clearance and substantial soil disturbance. Selective logging represents the opposite extreme and is characterized by the removal of a few individuals (often economically desirable species) and minimal soil disturbance. The extent of land conversion can be substantial under practice (Asner et al., 2005), but selective logging is generally thought to have less appreciable and short-term effects compared with deforestation (Williams, 1990). Indeed, in studies examining the impacts of historical land use, former selectively logged stands are frequently used to characterize reference ecological conditions when undisturbed stands are unavailable.

Forest loss associated with deforestation has occurred heterogeneously over the past 2000 years. Europe and Asia experienced significant deforestation during both pre-1650 and from 1750 to 1849 but are now undergoing afforestation in many parts (Williams, 1990; FAO, 2006). Extensive forest clearance in eastern North America began in the early nineteenth century and has been followed by rapid afforestation. Today, the regions suffering the largest losses due to deforestation are in South America and Africa, where forests are being cleared for cropping or livestock grazing (FAO, 2006). Tropical forest recovery is of particular concern because of its potential to impact global carbon and nutrient budgets and plant and animal biodiversity.

Detecting land-use legacies is often challenging because of preexisting differences in site conditions. From a statistical standpoint, variation in the initial conditions of sites with similar histories may be large enough to swamp variation associated with previous land use. Legacies may still be present within a given site but may be statistically undetectable because the signal is weak relative to that produced by the physical gradients. Relying solely on mean values to evaluate the effects of land-use history may therefore be misleading, and patterns of spatial heterogeneity or structure may yield a more comprehensive depiction of enduring changes (Fraterrigo et al., 2005, 2006b). Initial site conditions can also confound detection of historical land-use effects by biasing land use. For example, sites with good drainage were favored for cultivation relative to sites with poor drainage, which were avoided. As a result, ecological patterns on historically cultivated and uncultivated lands may not be comparable. Approaches for dealing with this problem include pairing or blocking sites with different histories to control for environmental variation.

Natural Disturbance

Natural disturbances can also leave legacies that persist for decades to centuries. For example, research conducted across a chronosequence of burned lodgepole pine stands in Yellowstone National Park indicates that large, stand-replacing fires contribute to variation in stand density and growth rate for nearly two centuries (Kashian et al., 2005a, 2005b). Previous disturbance history can also influence the severity of future disturbances. In the subalpine forests of western USA, spruce beetle outbreaks appear to reduce the susceptibility of forest stands to low-severity fires by elevating forest floor moisture (Kulakowski et al., 2003), whereas previous blow downs result in more severe burns decades later (Kulakowski and Veblen, 2007).

Despite the potential for natural disturbances to generate considerable variation in ecological patterns and processes, evidence suggests that ensuing dynamics will be constrained by patterns initiated by past land use. In tropical forests of Puerto Rico, successional vegetation trajectories following hurricanes, landslides, and local treefalls correspond more to land use in the nineteenth and early twentieth centuries than to the severity of recent natural disturbances (Thompson et al., 2002). Similarly, patterns of plant and soil variation on New England sand plains closely relate to historic variation in nineteenth-century agriculture, and repeated episodes of fire have had little effect (Motzkin et al., 1996; Eberhardt et al., 2003). These studies reinforce the need to consider historical context when interpreting disturbance effects.

Legacies in Plant Communities

What are the dominant legacies of human land use and natural disturbance on plant communities, and what factors influence them? Research conducted in temperate forest ecosystems demonstrates that previous land use strongly controls the species composition of contemporary forests

(Foster, 1992; Motzkin *et al.*, 1996; Hermy and Verheyen, 2007). Overstory composition of forests in eastern and mid-western USA has shifted has shifted from long-lived and shade-tolerant species to more rapidly growing and short-lived species as a result of historical agriculture and logging (Foster *et al.*, 1998; Rhemtulla *et al.*, 2009). In southern New England, for example, primary forests are dominated by *Acer saccharum*, *Acer rubrum*, *Fagus grandifolia*, and *Tsuga canadensis*, whereas secondary forests abandoned from agriculture a century ago are dominated by *A. rubrum* and *Pinus strobus* (Flinn and Marks, 2007). The species attaining dominance in secondary forests are generally those that sprout effectively or aggressively invade cleared or cultivated lands (Eberhardt *et al.*, 2003; Foster *et al.*, 2003). Studies from tropical and temperate forests demonstrate that non-native invaders, in particular, can quickly become dominant in anthropogenically disturbed stands and persistently preclude re-establishment of native species (Brown and Gurevitch, 2004; DeGasperis and Motzkin, 2007). Selection for species with disturbance-adapted traits has also contributed to the homogenization of overstory species composition at a regional scale (Schulte *et al.*, 2007; Rhemtulla *et al.*, 2009). Such is the case in New England, a region characterized by a history of agriculture, logging, and reforestation (Foster *et al.*, 1998). Paleoecological data indicate that pre-European patterns of forest vegetation that corresponded with differences in climate, substrate, and fire regime have been obscured by European settlement, which has produced a more homogenous regional flora (Fuller *et al.*, 1998). Similarly, the density, age, and size structures of contemporary forests with a history of anthropogenic or intensive natural disturbance often have a more uniform distribution relative to old-growth forests (Goodale and Aber, 2001; Kashian *et al.*, 2005b; Rhemtulla *et al.*, 2009).

Long-term changes in overstory composition and structure can result in lasting changes on the forest floor. Cultivation is generally associated with decreases in foliar litter mass and carbon content due to increased decomposition rates that can accompany the shift to tree species with more degradable litter (i.e., lower foliar C:N) (Compton and Boone, 2000). Working across a chronosequence of formerly farmed sites, Hooker and Compton (2003) estimated that forest-floor carbon content may take over a century to recover after land abandonment. Effects of logging are more equivocal (Yanai *et al.*, 2003), with both increases and decreases in foliar litter carbon content reported (Covington, 1981; Goodale and Aber, 2001; Latty *et al.*, 2004). There is evidence that variation in the magnitude and longevity of logging effects can be explained by differences in logging intensity, which is determined not only by the amount of biomass removed but also by the degree of mechanical disturbance (Yanai *et al.*, 2003). Likewise, logging combined with fire, which often ignited slash piles left on-site after harvests, produce more lasting changes due to increased disturbance intensity (Goodale and Aber, 2001; Latty *et al.*, 2004).

Changes in the amount and size distribution of coarse woody debris are another legacy of land use and natural disturbance. Work conducted at Harvard Forest shows that 73-year-old pine stands planted on abandoned agricultural lands have slightly higher masses and a uniform distribution of smaller size class coarse woody debris compared with

deciduous stands without an agricultural history (Currie and Nadelhoffer, 2002). Naturally reforested lands accumulate woody debris more slowly – at a rate of 0.05 mg ha^{-1} year^{-1} – and thus may require more than a century to return to pre-agricultural levels (Hooker and Compton, 2003). Similarly, intensive logging by itself or combined with fire has led to long-term decreases in coarse woody debris, especially in larger size classes, both as a direct result of tree removal and persistent changes in site quality or successional status (McCarthy and Bailey, 1994; Sturtevant *et al.*, 1997; Gough *et al.*, 2007). Fire alone removes considerably less coarse woody debris than logging and, consequently, its effects are smaller in magnitude and shorter in duration (Tinker and Knight, 2000).

Herbaceous plant communities are among the most severely impacted by past land use activity. In European and North American temperate forests, previous agriculture has led to striking changes in understory assemblages, a prominent and consistent feature of which is the reduced abundance or absence of native understory species for a century or more (Peterken and Game, 1984; Flinn and Vellend, 2005; Hermy and Verheyen, 2007). In contrast, most studies indicate that recovery from logging occurs within decades of disturbance (Halpern and Spies, 1995; Roberts and Gilliam, 2003), although long-term effects have been found (Duffy and Meier, 1992). There is also the potential for wide variation in recovery. This is illustrated by semiarid grassland plant communities cultivated half a century ago, where some old fields are compositionally similar to uncultivated grasslands and some are distinct (Coffin *et al.*, 1996). Regardless, these studies have led to important insights about the factors controlling ecosystem response to disturbance. It is clear that life-history traits play a key role in the colonization dynamics of disturbed lands (Verheyen *et al.*, 2003b). Overwhelming evidence supports the hypothesis that species mobility (i.e., dispersal capacity) determines the colonization of disturbed lands (Dzwonko and Loster, 1992; Matlack, 1994; Brunet and von Oheimb, 1998; Bossuyt *et al.*, 1999; Bellemare *et al.*, 2002; Verheyen *et al.*, 2003a). Not surprisingly, the spatial arrangement of disturbed relative to undisturbed lands is important for predicting the nature and rate of species colonization and interacts with dispersal capacity to affect community recovery via its influence on seed availability (Dzwonko and Loster, 1992; Brunet and von Oheimb, 1998; Bossuyt *et al.*, 1999; Butaye *et al.*, 2002). Working in young, secondary stands that varied in isolation from older, species-rich stands, Matlack (1994) demonstrated that diversity increases with proximity to source populations, mainly due to increased representation of poorly dispersing species. The spatial configuration of disturbed habitat relative to the source populations is also important for recovery after large, intense natural disturbances such as fire and flooding (Turner *et al.*, 1998).

Dispersal is the primary factor explaining the colonization of historically altered lands, but site conditions can also affect the distribution of herbaceous plant species by influencing plant recruitment. Indeed, variation in the establishment of species with similar dispersal abilities (Singleton *et al.*, 2001) suggests that site conditions should not be overlooked. Assembly of herbaceous plant communities on disturbed lands likely occurs as a two-stage process in which restricted seed

availability followed by a low recruitment limits colonization (Verheyen *et al.*, 2003a; Baeten *et al.*, 2009a, 2009b). Yet it remains unclear which site conditions affect recruitment. For some species, a lack of microtopographic variation or micro-site disturbance hampers establishment (Verheyen and Hermy, 2004; Flinn, 2007; Baeten *et al.*, 2009b), whereas other species appear to be influenced by edaphic characteristics (Verheyen *et al.*, 2003a). Undoubtedly, a species' life-history traits influence its requirements for establishment, which makes it challenging to identify factors that influence all species equivalently. Another complicating factor is that effects of past land use may vary with plant life stage. Several studies demonstrate that previous agriculture has neutral to positive effects on seed germination and adult plant performance (Donohue *et al.*, 2000; Singleton *et al.*, 2001; Endels *et al.*, 2004; Verheyen and Hermy, 2004; Fraterrigo *et al.*, 2006c; Flinn, 2007, but see Vellend, 2005), but negative effects on seedling and juvenile survival and growth, as well as juvenile and adult survival (Endels *et al.*, 2004; Jacquemyn and Brys, 2008). The mechanisms underlying these patterns are poorly understood. One hypothesis is that due to competition from early colonizing, disturbance-adapted species reduces the ability of native species (many of which are slow-migrating perennials) to acquire resources, thereby creating bottlenecks during some stages (De Keersmaeker *et al.*, 2004). Further work is needed to evaluate the role of these and other factors.

Legacies in Soils

Land use, especially agriculture, can impose long-term changes on the physical, chemical, and biological properties of soils. A plow horizon, that is, the depth at which plowing homogenizes the soil, is one of the most apparent legacies of previous cultivation and may persist for centuries after land abandonment (Motzkin *et al.*, 1996). In addition to being visibly distinct, plow horizons are often depleted of carbon (C) and nitrogen (N) due to accelerated decomposition, reduced organic matter inputs, degradation of soil physical structure, and erosion. Labile or reactive soil C and N fractions in the plow layer can see even greater losses than total C and N pools because they are highly degradable and slower to recover (Compton and Boone, 2000). Such conditions can in turn affect soil microbial communities (Buckley and Schmidt, 2001) and contribute to changes in carbon and nutrient cycling (see legacies in ecosystem processes; Compton and Boone, 2000; Fraterrigo *et al.*, 2006a).

However, not all sites subjected to past cultivation show soil C or nutrient depletion. The specific impacts of cultivation vary with soil amendments, such as liming or fertilization, and crop management (Compton *et al.*, 1998; Knops and Tilman, 2000; Richter *et al.*, 2000). Effects on soil organic carbon, for example, depend on the amount and type of organic amendment, method of incorporation, and size and length of time of application (McLauchlan, 2006). As a result, soil C and nutrient content can increase, decrease, or show no change following agricultural land use. The stability of a chemical pool can also influence the longevity of impacts. Phosphorus, for instance, is relatively biogeochemically stable compared with C and N and often remains substantially

altered well after other chemical pools have returned to pre-cultivation levels (Honnay *et al.*, 1999; Compton and Boone, 2000; Dupouey *et al.*, 2002; Grossmann and Mladenoff, 2008).

Relative to agriculture, logging and natural disturbance have a more limited impact on soils. Mineral soil C and N content of sites logged approximately 100 years ago is comparable with that of old-growth forests, although logging and fire together can slightly reduce soil C and N (Goodale and Aber, 2001; Latty *et al.*, 2004; Gough *et al.*, 2007). Regional studies of disturbance impacts on soil C and nutrient content suggest that the long-term effects are greatest following agriculture, followed by logging and fire (Grossmann and Mladenoff, 2008).

Despite slow rates of accumulation, depleted soil C and N pools recover eventually in most ecosystems (Knops and Tilman, 2000; Hooker and Compton, 2003; Matlack, 2009). The factors that influence C and N recovery operate via their effects on soil development and C and nutrient inputs and include vegetation recovery, climate, and soil texture and mineralogy (Burke *et al.*, 1995; Ihori *et al.*, 1995; Knops and Tilman, 2000; Post and Kwon, 2000; Springob *et al.*, 2001; McLauchlan, 2006). Because these factors differ across sites, rates of recovery vary widely within and among the ecosystems (McLauchlan, 2006). Empirical and modeling work indicate that active soil organic matter in once-cultivated grasslands returns to precultivation levels within 30–50 years, whereas total soil C may take 100–150 years to recover (Burke *et al.*, 1995; Baer *et al.*, 2002; McLauchlan *et al.*, 2006). Similarly, accrual rates of soil C in formerly cultivated temperate forests range from 1.5 to 5.8 g C m^{-2} year^{-1}, which suggests at least a 100-year recovery period (Hooker and Compton, 2003; Paul *et al.*, 2003). Climate and soil texture may ultimately constrain ecosystem C accrual by regulating biomass production, but more work is needed to evaluate how this relates to soil C accumulation (Johnson *et al.*, 2000; Johnson and Curtis, 2001).

Ecosystem Process Legacies

Persistent changes in soil properties can result in altered ecosystem processes. Globally, primary production is controlled by climate and soil texture (Johnson *et al.*, 2000), but within regions, previous land use can influence site quality, thereby reducing the rates of growth and biomass accumulation. These effects are most severe under repeated disturbance or when the duration of previous land use is long. For example, forest stands in the Great Lakes region that were disturbed twice by harvest and fire stored on an average 45% less C annually than those receiving the same disturbance only once due to reduced site quality (Gough *et al.*, 2007). Similarly, pine stands in southeastern USA that were previously farmed for cotton and other crops show acute N deficiency and reduced growth, despite fertilization during cropping and 50–125 years of forest development (Richter *et al.*, 2000).

Previous land use can also result in changes in N cycling and retention. Northern hardwood forests logged and burned 80–110 years ago have lower nitrification rates and export less nitrate to adjacent streams compared with old-growth forests

due to an increase in the strength of the biomass N sink (Goodale *et al.*, 2000; Goodale and Aber, 2001). By contrast, cultivation is associated with increased nitrification rates. The reasons for this are unclear, but one hypothesis is that increased nitrification is related to soil organic matter depletion. As soil microbes become substrate-limited, they may increase the rate at which they degrade soil organic matter and nitrify more N in the process (Compton and Boone, 2002).

Implications

Given the strong influence of historical events on ecosystem structure and function, it is clear that understanding the land use and disturbance legacies is fundamentally important for managing and restoring ecosystems. In many cases, ecosystem responses to current landscape-change drivers cannot be interpreted without knowing the historical context. For example, experimental and observational studies indicate that the N saturation status of forests cannot be accurately predicted without knowing the forest history (Aber *et al.*, 1998; McLauchlan *et al.*, 2007). Rates of C accrued and sequestered in biomass also depend on land-use history, making it an important factor in explaining global C dynamics (Caspersen *et al.*, 2000). Past events can influence the success of ecosystem restoration activities by altering the pool of species available for reintroduction. One result might be that the restoration activities such as prescribed burning have little effect on the patterns imposed by past land use (Motzkin *et al.*, 1996). The composition of disturbed and undisturbed communities may also be so different as to respond to management activities in unique ways (Brudvig and Damschen, 2011). More work is needed to develop strategies for managing landscapes with diverse histories.

Conclusions

Land use and disturbance legacies can be detected in plant communities, soils, and ecosystem processes, resulting in altered ecosystem structure, composition, and function. Recognizing historical legacies aides in interpreting contemporary ecosystem patterns and responses to modern landscape-change drivers. For these reasons, landscape legacies should be viewed as an integral component of ecological science and landscape management.

> *See also*: Deforestation and Land Clearing. Forest Ecology. Human Impact on Biodiversity, Overview. Land-Use Patterns, Historic

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