CHAPTER 5.6

Applying Soil Ecological Knowledge to Restore Ecosystem Services

Sara G. Baer, Liam Heneghan, and Valerie T. Eviner

5.6.1 Introduction

Environmental degradation resulting from resource extraction, land-use change, and invasion by exotic species alters numerous functions and services provided by intact and unexploited ecosystems. Ecological restoration is the human-facilitated improvement of a degraded ecosystem and represents an important means to repair or reinstate many natural services in degraded ecosystems (Table 5.6.1). Restoration can be initiated from any point along a continuum of degradation and restoration goals can vary from focused improvements (e.g., amelioration of unsuitable pH, soil stabilization, and re-establishing rare species) to holistic recovery of biological diversity, efficient nutrient cycling, and complex energy flow pathways (Hobbs & Harris 2001). Restorations that aim to re-establish ecosystem structure and function “prior to degradation” may find that historical and extant targets can be difficult to define considering the variability of natural systems in space and time (White & Walker 1997) or unrealistic to attain if multiple abiotic and/or biotic factors have been highly modified through human activity (Hilderbrand et al. 2005). Furthermore, restorations are now conducted under novel conditions including invasive species pressure, greater inputs of nutrients through atmospheric deposition, and higher atmospheric CO₂ levels that may restrict the ability to restore systems to some state in the past (Hobbs & Harris 2001; Hobbs et al. 2009).

Degradation of terrestrial ecosystems is often strongly reflected as damage to the soil system. It can take tens to thousands of years for some soil properties to develop through the interaction of parent material, climate, topography, and organisms (Jenny 1941). Soil degradation can result in the loss of or alteration to many soil properties and functions. We define soil legacy as the physical, chemical, and biological attributes and interactions that remain following a significant change to an ecosystem. This definition of legacy is aligned with ecological legacy (White & Jentsch 2004), but differs from disturbance legacy, which has been used to indicate the residual effects of an abiotic or biotic disturbance on ecosystem properties (e.g., Reinhart & Callaway 2006). Disturbance legacy, Soil legacy is the degree to which soil properties (e.g., horizonation, porosity, texture, nutrient storage, organic matter content, aggregation, etc.) and functions (e.g., nutrient supply, infiltration, etc.) at the onset of restoration reflect characteristics before the degrading influence.

The range of variation in ecosystem degradation produces varying soil legacy at the onset of restoration. Heneghan et al. (2008) proposed that more soil ecological knowledge (defined as the integrated understanding of soil physical, chemical, and biological factors and processes in the context of plant-soil feedback) may be required to restore complex interactions following disturbance (Fig. 5.6.1). This chapter presents the utility of soil ecological knowledge to the practice of ecological restoration along a continuum of ecosystem degradation that results in varying legacy of the plant and/or soil system. Mineral resource extraction can result in severe ecosystem degradation that leaves little to no soil legacy, initially. Restoration of these highly degraded lands...
has revealed the importance of physical, chemical, and biological properties of soil to revegetation, as well as the role of soil heterogeneity in providing refugia for the recolonization of soil biota. Addition of topsoil to mined land can rapidly increase the amount of soil legacy at the onset of restoration with consequence for improved ecosystem functions. Restoration of agricultural systems often represents moderate soil legacy at the onset of restoration. Soil degradation resulting from agriculture varies with the type of production system. Most development and application of soil ecological knowledge to the restoration of agricultural systems has been gleaned from those that have been cultivated. Although recovery of many aspects of soil structure and function can proceed passively following revegetation of cultivated soils, there are increasing efforts to restore biological and physical complexity to better represent historic or extant systems. Restoring biodiversity and structural complexity may

### Table 5.6.1 Ecosystem goods and services provided through ecological restoration.

<table>
<thead>
<tr>
<th>Ecosystem service*</th>
<th>How ecological restoration can provide ecosystem goods (functions) and services</th>
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<tbody>
<tr>
<td>Gas and climate regulation</td>
<td>Revegetation of degraded lands through reforestation, grassland establishment, and wetland restoration can aid in mitigating atmospheric CO₂; conversion of agricultural land to perennial vegetation can reduce N₂O emissions if nitrification rates are reduced.</td>
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<tr>
<td>Disturbance regulation</td>
<td>Restoration of degraded lands to perennial vegetation increases transpiration of water to the atmosphere and improved soil structure promotes infiltration to reduce runoff and provide flood control.</td>
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<td>Water supply</td>
<td>Improved soil structure promotes infiltration to groundwater; hydrologic manipulations in wetland and floodplain restorations can promote groundwater recharge.</td>
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<td>Erosion control and sediment retention</td>
<td>Conversion of highly erodible arable lands and riparian buffer zones to perennial vegetation reduces erosion and traps sediment.</td>
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<tr>
<td>Soil formation</td>
<td>Restoration of degraded lands to perennial vegetation promotes organic matter accrual; organic acids from root exudates and decomposition can facilitate weathering and soil formation.</td>
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<td>Nutrient cycling</td>
<td>Establishing plants associated with N-fixing microorganisms on degraded lands can promote N and organic matter accrual; developing root systems, microbial biomass, and organic matter during restoration of degraded soil can promote nutrient conservation; conversion of agricultural lands to perennial vegetation reduces nutrient inputs and pollution.</td>
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<td>Biological control</td>
<td>Perennial vegetation restored within agricultural landscapes can provide refugia for predators of crop pests.</td>
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<td>Pollination</td>
<td>Floristically diverse restorations can provision pollinators for plant populations.</td>
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<td>Refugia</td>
<td>Restoration can reduce landscape fragmentation and provide resources and/or reproduction habitat requirements for local and transient wildlife populations.</td>
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<td>Food production</td>
<td>Restoration of degraded land and wetlands with perennial vegetation can increase game populations.</td>
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<tr>
<td>Raw materials</td>
<td>Reforestations can be managed for production of lumber; perennial grasslands can be used for biofuel and forage production.</td>
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<tr>
<td>Genetic resources</td>
<td>Restoration conducted with high fidelity to local gene pools represents a means to preserve genetic variation for medicinal purposes or crop improvement (e.g. resistance to plant pathogens).</td>
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<tr>
<td>Recreation</td>
<td>Forest, wetland, and grassland restoration increase habitat for wildlife and opportunity for hunting; restoration can improve water quality (increase clarity through less sedimentation, reduced eutrophication through nutrient abatement) and conditions for fish populations; restorations provide areas for hiking and nature appreciation.</td>
</tr>
<tr>
<td>Cultural</td>
<td>Restorations and re-creations, especially when conducted to achieve a historic community, can preserve cultural heritage.</td>
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* List modified from Costanza et al. (1997).
require more soil ecological knowledge and an explicit focus on plant–soil feedbacks (where a plant species or community alters soils in a way that impacts its own success as well as that of other species). These plant–soil feedbacks can be key mechanisms by which species become invasive. Thus, ecosystems under dynamic change through invasion may contain high soil legacy that has become altered in subtle ways. Restoration of these systems may require considerable soil ecological knowledge to establish rare, historically dominant, or a diversity of species that depend on specific or historic soil properties, processes, and/or biotic composition (Heneghan et al. 2008; Eviner et al. 2010), particularly if that system has attained a self-organizing alternative stable state (Suding et al. 2004). In no-analog environments, large shifts in the abiotic and biotic components of an ecosystem have occurred, resulting in new and self-sustaining assemblages of plant species that have never before coexisted and perhaps a novel soil legacy. In these novel systems, it is critical to recognize that the new communities can provide ecosystem services (i.e. beneficial functions, as defined by the Millennium Ecosystem Assessment 2005), and attempts to restore these systems to a former state could result in failure and compromise ecosystem services provided.

Disturbance to the soil system has potential to alter ecosystem services (Daily et al. 1997) such as efficient and conservative nutrient cycling, soil formation, and/or water holding capacity (to name only a few) that are provided by structurally heterogeneous soils with a thriving biota. In the absence of restoration, soil structure and functioning, as well as ecosystem services, would remain in a degraded state, continue to decline, or recover slowly (Insam

**Figure 5.6.1** Relationship between the degree of soil legacy in degraded lands (including interaction among physical (P), chemical (C), and biological (B) properties and processes) and ecosystem functioning in the context of restoration. Restoration is human-facilitated improvement of a degraded ecosystem’s functioning (indicated by stair-step line). Abiotic and biotic constraints may need to be alleviated to achieve proportionally greater improvement in ecosystem functioning (indicated by the dashed line within gray windows). Three general circumstances of varying soil legacy are depicted, although a continuum exists within the realm of each example (regions I-III). Region I represents restoration of highly disturbed lands (e.g. some mine land reclamations), where P, C, and/or B properties and processes may be disconnected, and reconnection of these components is required to restore vegetation. Region II depicts restoration from disturbance such as agriculture, where P, C, and B properties and processes may be present and interactive, but altered in status and/or composition. Revegetation drives the recovery of P, C, and B properties and processes towards a target state in region II, but recovery may be constrained by limited species, development of complex plant-soil feedback, or altered representation of higher trophic levels (e.g. aboveground herbivores). Region III represents restoration scenarios where soil legacy may be significant, but plant communities are undergoing dynamic change (invasion) or have been replaced by self-perpetuating assemblages of species that have never before coexisted (novel ecosystems). In Region III, aspects of soil biota, nutrient status, and/or biogeochemical processes may be highly altered, but P, C, and B properties and interactions are considered more complex and tightly coupled to aboveground community dynamics. (Modified from Heneghan et al. 2008, with permission from John Wiley & Sons.)
<table>
<thead>
<tr>
<th>Soil property</th>
<th>Knowledge or manipulation during ecological restoration.</th>
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<tbody>
<tr>
<td>Structure</td>
<td>In soil degraded through cultivation, development of soil macroaggregates corresponds to soil microbial community recovery, particularly arbuscular mycorrhizal fungi in restored grassland (Jastrow et al. 1997).</td>
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<tr>
<td>Texture</td>
<td>Higher levels of organic carbon supply in soils with higher clay content lead to faster recovery of soil properties (Baer et al. 2010).</td>
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<tr>
<td>Organic matter</td>
<td>High-nutrient availability is often linked to high species richness and diversity. Addition of organic chelators can enhance phytoextraction of metals in contaminated soils (Huang &amp; Cunningham 1996).</td>
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<tr>
<td>Nutrient status</td>
<td>pH affects plant growth through its regulation of nutrient solubility and metal toxicity. In general, soil with pH around 6.5 contains the highest nutrient availability and lowest metal toxicity (Wong 2003).</td>
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<tr>
<td>Heterogeneity</td>
<td>Inoculating soil dominated by invasive species with soil derived from native plant communities can reduce invasive species cover and promote native perennial species (Rowe et al. 2009).</td>
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Example: Severe soil compaction limits root growth and water infiltration. Soil ripping has been applied in extreme circumstances to promote establishment of vegetation (Ashby 1997).
& Haselwandter 1989). Restoration can facilitate recovery or reinstate numerous ecosystem services in degraded lands and landscapes (Table 5.6.1) largely through revegetation efforts, and establishing key species that promote a specific ecosystem service (Eviner & Chapin 2001). This chapter synthesizes how knowledge of soil processes, belowground heterogeneity, roles of soil biota, controls by state factors, and potential feedbacks with the aboveground community can be applied to promote restoration success (Table 5.6.2).

5.6.2 Low to high legacy: lessons from restoration of mined land

Soil ecological knowledge is an asset to restoring severely disturbed ecosystems, particularly with respect to understanding the role of soil properties and plant–soil relationships that promote revegetation. Mineral resources exist underground and their extraction requires the removal of vegetation and soils, which can result in complete environmental destruction; however, a continuum of ecosystem degradation from mining activity does exist.

Mine workings (materials produced by mining) generally contain factors that limit ecosystem development over the short term in the absence of reclamation practices (Bradshaw 1997). In the extreme case, deposition of waste rocks (i.e. host rock with insufficient mineral amounts for extraction) and mine tailings (i.e. remnant slurry post mineral extraction) at the surface become sources of pollution, eliminate biodiversity, and drastically reduce the production capacity of the environment. Restoration of mine workings to an improved ecosystem state has elucidated that physically and chemically altered soils are critical constraints to plant growth. Transport of materials by heavy machinery inevitably results in severe soil compaction, and mechanical soil treatment (e.g. soil ripping) is commonly applied prior to revegetation to loosen compacted soil and promote root penetration (Ashby 1997). Mine waste materials can include weathered subsoils and overburdens with deficiencies in mineral amounts or unweathered to the extent that nutrients cannot be released quickly enough to sustain plant growth. Thus, nutrient deficiencies must be determined. Fertilizers or amendments (topsoil, residues, sewage sludge, etc.) are commonly added to alleviate nutrients that are too limiting to sustain plant growth (Bradshaw 1997; Wong 2003).

Knowledge of physico-chemical properties of soil is required for restoration of extremely disturbed mined environments. Mining for coal and metal ores results in the oxidation of sulphide minerals, and consequently, severe acidification of soil (pH 2–2.5; Bradshaw & Chadwick 1980; Bradshaw 1997). Soil pH may be one of the most important properties to consider in mined land restoration because it influences the solubility of nutrients and metal ions, activity of soil microorganisms and fauna, and pH-sensitive processes such as nitrification and nitrogen fixation (van Breeman 2004). Remediating pH levels requires knowledge of soil acidity, the potential acidity that can arise from further oxidation of metal sulphides, and the acid neutralizing capacity of the soil to determine effective amounts of calcium carbonate (lime) to increase and maintain pH for successful restoration (Costigan et al. 1981). Waste materials produced from the mining for heavy metals can contain significant amounts of residual metals, even after processing, with little to no potential for natural reduction (Li 2006). The concentration and chemical forms of metals (as affected by pH) determine soil toxicity. Many heavy metal ions exhibit reduced solubility at low pH; however, the solubility (i.e. availability) of essential metals (e.g. molybdenum) decreases at high pH and results in metal deficiencies (van Breeman 2004). Organic acids derived from soil organic matter and root exudates represent important sources of chelators present at low levels in mined soils. Phytoextraction of metals using hyperaccumulating plant species, coupled with the addition of metal-chelating compounds can enhance metal uptake and removal to 1) render the soil more suitable for growth of microorganisms that are inhibited by heavy metals (e.g. rhizobia), 2) promote development of symbioses important for plant growth (e.g. legume-rhizobia), and 3) facilitate desired plant communities (Wong 2003).

Heavy metals and persistent organic pollutants can render soil toxic to belowground organisms and plants. Physicochemical properties of soil are important for decontamination of organic pollutants, which bind to soil constituents (e.g. clay, organic
matter, organomineral complexes) over time. Once contamination levels begin to decline, microbial populations can recover. For example, Yin et al. (2000) found that the arrival of bacterial species along a restoration gradient that included a mine spoil, restored mined land, and undisturbed forest was dependent on time since disturbance. Refugia for soil organisms, provided by uncontaminated soil microsites in physically heterogeneous soil, can serve as important sources of soil flora and fauna for recolonization (Eijsackers 2004) that might be necessary for some plants to establish. Delayed arrival of microbial species could represent a constraint to restoring plant diversity (Harris 2003). Recognition that soil health (vital whole soil) is imperative for successful revegetation has resulted in formulation of policy in many countries to conserve and replace surface soils in mined sites. Mined land amended with topsoil can, in some cases, represent a rapid transition from a low to moderate or even high soil legacy starting point for restoration. Topsoil amendments provide biological or biologically-produced soil components such as organic matter, stored nutrients, available nutrients, soil biota, and plant propagules (Brenner et al. 1984). Topsoil replacement, however, has resulted in varied restoration success and care must be taken in how it is managed. For example, if topsoil is added to a dissimilar or compacted underlying material, then hydraulic discontinuity and instability can result (Bradshaw 1997). Depth of topsoil addition can also influence the trajectory of plant community recovery. Paschke et al. (2003) reported that deep additions of topsoil encouraged grasses and forbs to outcompete mountain shrubs that are adapted to the historically shallow soils. “Live handled” topsoil is preferred over stockpiled topsoil to provision restorations with symbiotic soil organisms. Preservation of topsoil through long-term stockpiling has been shown to reduce soil organic content (according to many of the same mechanisms as cultivation) and be detrimental to symbiotic arbuscular mycorrhizae fungi. These physical and biological changes to soil during long-term stockpiling, coupled with uniform re-application of the stored soil, has revealed important soil-related constraints to restoration. Mummey et al. (2002) documented that disturbance to soil structure (through removal and stockpiling) and absence of an associated plant community to sustain symbiotic microorganisms during stockpiling imposed long-lasting effects on vegetation and spatial organization of surface mined land. Failure of native shrubs to establish in stockpiled and re-applied topsoil impacted root distribution, water relations, fire cycles, and spatial resource heterogeneity in the restored mined lands. This study underscores the importance of soil physicochemical properties and the soil microbial community to ecosystem restoration. In some cases (e.g. shallow soil on steep terrain), topsoil conservation and replacement is difficult and mine spoils are substituted for topsoil, despite that their properties and growth of native species therein can be different than native soils (Showalter et al. 2010).

5.6.3 Moderate legacy: restoration of agricultural systems

Agriculture represents the most globally widespread anthropogenic influence on ecosystems (Ellis & Ramankutty 2008). The degree of soil perturbation from agriculture depends upon the type of production system (e.g. annual crops, pasture, vs. timber) and historic management (e.g. tillage and rotation regimes, fertilizer application, grazing intensity, and selective harvest vs. forest clearcutting). Restoration goals for agricultural systems vary considerably, partly due to differences in historical communities (i.e. grassland, forest, or wetland) that were converted to production systems. Soil ecological knowledge is increasingly considered to restore multiple ecosystem services in these systems, particularly those provided by biodiversity.

5.6.3.1 Restoration to grassland

Long-term conventionally cultivated systems generally contain no legacy of the historic plant community and limited potential for colonization of historic species from the regional species pool due to few native propagules in landscapes dominated by agriculture. It is well recognized that long-term cultivation degrades soil structure, promotes more extreme wet-dry cycles, alters soil microbial com-
position, increases decomposition, and lowers soil carbon (C) and other nutrients to new equilibrium levels (Dick 1992). Furthermore, long-term fertilized soils may exhibit high residual nutrient levels, high nitrification rates, and lower pH. In general, simple goals such as revegetation to reduce erosion can be easily achieved and concomitant improvements in soil structure and functions can proceed passively. The development of perennial grass root systems in long-term conventionally cultivated soil can promote soil macroaggregate formation, microbial and fungal biomass, and soil C accrual on a decadal time scale (Matamala et al. 2008), but recovery can vary drastically between highly contrasting soil textures (Bach et al. 2010; Baer et al. 2010). Paustian et al. (1998) reviewed the potential for agricultural systems to mitigate increasing atmospheric CO₂ and suggested that planting perennial vegetation such as grass represents one of the most favorable scenarios for increasing soil C stocks following land degradation. Erosion reduces land productivity and ability to maintain or improve C stocks in biomass and soil; therefore, measures to reduce soil erosion are very important. Despite improvement in numerous ecosystem services provided by simple erosion control measures (functional restorations), these practices generally do not restore biodiversity and associated ecosystem services (e.g. genetic resources, pollination, cultural heritage).

Restoration of some plant communities may require specific soil conditions. In Europe, liming has been used to raise pH of naturally acidic soils to promote crop production; however, high soil pH limits restoration of grassland and heathland communities that prefer acidic soil conditions. Applications of elemental S and pyritic peat have been used to effectively lower pH, promote establishment of species that require acidic soil conditions, and reduce ruderal species (Owen et al. 1999). High residual soil fertility from nutrient management in agricultural soils can constrain the restoration of diverse plant communities, particularly if soil fertility results in asymmetric competition for nutrients and dominance by a few species (Baer et al. 2003). High species coexistence is generally associated with low levels of soil fertility (Janssens et al. 1998), further supported by the consistent phenomenon of declines in plant diversity under nutrient enrichment. Manipulating soil fertility has been explored as a restoration tool to increase plant species diversity, reduce invasive or non-target species, and increase soil heterogeneity prior to, or during restoration. Walker et al. (2004) reviewed efforts to reduce soil fertility in arable lands to recreate species-rich grasslands in Europe. Measures used to reduce phosphorus (P) availability include haying or cropping to promote off-take of P, addition of aluminum (Al) or iron (Fe) (ferric) sulfate to increase P adsorption capacity, and deep cultivation or addition of inert or organic materials to dilute nutrient pools. In the UK, nutrient reduction through deep cultivation combined with seed addition has been shown to increase plant community similarity to grassland targets with conservation value on a decadal time scale (Walker et al. 2004). Carbon addition can be an effective tool to reduce inorganic nitrogen (N) availability by promoting the growth of the soil microbial biomass and immobilization of N, with significant consequence for reducing non-target plant cover during grassland restoration (Baer et al. 2003; Blumenthal et al. 2003). Reducing N availability at the onset of restoration may be a valuable tool to prevent invasive species establishment. However, the effectiveness of C addition is variable, and efficacy of such manipulations should be considered in the context of long-term temporal dynamics of N availability modulated by development of soil C stocks and increasing plant–soil feedback over time (Baer & Blair 2008).

5.6.3.2 Restoration to forest

Forest restoration on agricultural land has generally employed fewer soil manipulations relative to restoring grasslands, but there are studies that demonstrate soil properties affect forest regrowth and CO₂ mitigation. Soil fertility and land-use history (as it has affected soil) are critical factors influencing forest regrowth (Tucker et al. 1998). The tropics, in particular, are subject to a continuous cycle of forest clearing for agricultural purposes and socioeconomic constraints to maintaining the productive capacity of soil, which results in rapid soil degradation and further clearing for agriculture (Lavelle
1987). Soil C loss due to cultivation of tropical soils occurs at a much faster rate than in subhumid regions due to faster decomposition, which is further exacerbated in mountainous regions by erosion. Due to the amount of C lost from forest conversion to agriculture, Paustian et al. (1998) contended that the most significant opportunity for mitigating CO₂ emissions is to reduce the rate of tropical land conversion to agriculture. Change in soil C stocks in response to reforestation is not well documented for the tropics. Paul et al. (2010) found no change in soil C pools in response to reforestation of rainforest species, but improvement in many other soil properties (i.e., extractable inorganic N, plant available inorganic N, nitrification rate, pH, and bulk density) occurred on a decadal time scale.

Our understanding of soil-related factors that influence forest regrowth and/or composition on former agricultural lands comes mostly from studies of reforestation following land abandonment. For example, differential rates of forest regrowth following agricultural land-use in the tropics have been attributed to a suite of soil properties associated with different soil orders. Clay-rich Alfisols hold more nutrients and support faster forest regrowth relative to Ultisols and Oxisols with higher sand content and lower fertility (Lu et al. 2002). Over half of the forest cover throughout Europe and eastern North America occurs on former agricultural land (Vellend 2003). Residual impacts of cultivation on soil have been documented in secondary forest following 90–120 years of abandonment from agriculture. Compton and Boone (2000) demonstrated that formerly cultivated secondary forest sites contained less forest floor C, more mineral soil N and P, lower C:N and C:P ratios, and higher nitrification rates relative to sites that were selectively logged, with no cultivation disturbance to mineral soil. Furthermore, forest composition of abandoned agricultural lands can remain distinct from forests that have never been cleared for agriculture for centuries, particularly with respect to herbaceous richness (Flinn & Marks 2007). Although the cause of compositional variation among secondary forests on formerly cultivated soil and uncultivated soil has not been deduced, Flinn and Marks (2007) speculated that soil properties and processes play an important role, particularly in the reduction of microtopography, which influences small scale species distributions and the variable history of agricultural intensity and management among sites.

5.6.3.3 Restoration to wetland

Globally, over half of wetland area has been lost, most of which has been converted to agriculture. Costanza et al. (1997) estimated that shallow waters, which cover <2% of the Earth’s surface, provide up to 40% of global renewable ecosystem services; thus, restoration of these systems has important consequences for ecosystem services. Restoration of wetland systems generally involves restoring or manipulating hydrology to promote recovery of ecosystem services such as disturbance regulation, water supply, sediment retention, and nutrient cycling (Table 5.6.1). However, the vast array of restoration approaches coupled with variation in landscape factors, disturbance regime, invasive species pressure, historic seed banks, and nutrient supply constrain predictability of wetland restorations to achieve specific targets (Zedler 2000).

Soil moisture, as affected by texture properties and hydrology, is probably the most frequently considered soil-related factor in wetland restoration because it regulates biogeochemical processes and aboveground community structure. Wetting and drying, of soils affect nutrient dynamics. Nitrate supplied by mineralization is stimulated by soil drying, and removal of nitrate through denitrification requires temporary inundation to induce dissimilatory reduction of N conducted by facultative anaerobic microorganisms (Venterink et al. 2002). Drained and cultivated agricultural soils are generally considered to contain limited denitrification potential due to aerobic conditions and depleted soil organic matter. Restoring wetlands has been promoted as a mechanism to reduce surface water nutrient loads through vegetation uptake and denitrification (Mitsch et al. 2001). However, Orr et al. (2007) documented no change in actual and potential denitrification rates in former agricultural soils following cessation of agriculture and hydrologic reconnection in a leveed floodplain. Thus, processes assumed to self-repair under certain conditions
may not always develop from recreating the physical template (Hilderbrand et al. 2005).

Water depth is a key controller of wetland structure and function, and long-term drainage and tillage of former wetland soils has led to organic matter loss and subsidence of soil (Verhoeven & Setter 2010). In addition to hydrology, soil wetness and variation in soil properties (e.g. texture, organic matter storage, and nutrient availability) are influenced by microtopography. Meyer et al. (2008) demonstrated differential recovery rates of belowground structure and function in re-created sloughs containing slight topographic variation between the temporally inundated central channels of sloughs and slightly elevated slough margins. Microtopographic variation also imparts variation in vegetation composition (VivianSmith 1997). Thus, soil texture and moisture characteristics will need to be considered (potentially re-created) to successfully restore all species and assemblages associated with topographic transition.

Attaining biodiversity targets and associated services through wetland restoration is generally impeded under nutrient enrichment, as species richness is commonly low where nutrient supply is high (Green & Galatowitsch 2002). Managing nutrients will require active consideration of inputs from the landscape, as well as soil properties and processes that modulate nutrient availability through adsorption and microbial transformations, respectively. There can be a great disparity between recovery rates of vegetation and soil properties during wetland restoration (Craft et al. 1999), which may impose temporal constraints on realizing ecosystem services that in-tact wetlands perform.

5.6.4 High legacy under dynamic change: preventing invasion and restoring invaded systems

Invasion of natural and managed lands by new, undesirable species can displace species and impair ecosystem services provided by diverse communities (e.g. efficient nutrient cycling, pollination, refugia, genetic resources, recreation, and cultural heritage). Efforts to understand biological invasion into habitats of biodiversity conservation concern have largely focused on 1) traits of invading species, 2) habitat and soil-related factors linked to facilitating or resisting invasion, 3) post-colonization effects of invasive species on a variety of soil-mediated ecosystem processes, and 4) complex interactions of all of these factors. There has been a large effort to quantify how invasive plants modify soil properties over the past two decades. Recent studies have provided detailed information on the effects of invasive species (not only plants) on ecosystem productivity, decomposition, soil nutrient dynamics, and soil food webs. Consequently, the prospect of developing a new array of restoration tools to manage native communities or control invasive species is growing.

Efforts to identify physiological or life history traits that differentiate invasive from non-invasive species, as well as highly invisible from less invasible habitats have been largely inconclusive. For instance, an analysis of 79 independent native versus invasive plant comparisons revealed that invaders did not consistently have higher growth rates, competitive abilities, or fecundity (Daehler 2003). In fact, the success of non-native plants generally depended on growing conditions, illustrating the importance of habitat and often soil-based factors influencing the invasion process. One particularly influential hypothesis on habitat factors facilitating invasion has been the “fluctuating resource hypothesis” (Davis et al. 2000). This hypothesis suggests that plant invasion depends on soil resource supply rates augmented by the availability of propagules of the invasive organism. Although there is some support for this hypothesis (Foster & Dickson 2004) other studies have been either less emphatically supportive (Kercher et al. 2007) or concluded the contrary (Walker et al. 2005). The search for patterns of habitat susceptibility to invasion has also examined whether species-rich or low resource environments are more resistant to invasion, but this potential mechanism has not been supported consistently (Lonsdale 1999; Funk & Vitousek 2007). Thus, a variety of life history strategies can be associated with invasive species and many habitat types are susceptible to invasion, which limits the development of generalities about the mechanisms driving biological invasion.

Intimate knowledge of local systems and their potential invaders remain essential to preventing
invasion or restoring invaded environments. Such knowledge forms the basis for developing and implementing management. For instance, the invasion and establishment of *Alliaria petiolata* (garlic mustard), an herbaceous biennial prevalent in Eastern and Midwestern woodlands, is sensitive to both woodland density and site fertility, but light availability appears to be the most important factor affecting the proliferation of this species (Meekins & McCarthy 2000). Other biennial weeds in these systems, including *Dipsacus sylvestris* (common teasel) and *Barbara vulgaris* (garden yellowrocket), flourish in response to soil disturbance (Roberts 1986). Managers can use these specific understandings to protect systems from a suite of potential invaders (e.g. managing for high woodland density with low light levels, coupled with minimal soil disturbance). Management based on well-understood ecological traits of invasive species, potential novel invaders in the regional species pool, and environmental conditions are needed to predict and prevent invasion.

Conservation programs should prioritize the protection of sites with high legacy of native biota, particularly if restoring highly invaded areas is not cost effective and probability of success is low (Hobbs & Harris 2001; Hobbs et al. 2009). For example, Chicago Wilderness is a consortium of over 250 conservation-oriented organizations that prioritizes habitat conservation and management in exactly this manner. Traditional management of areas retaining some residual biodiversity has been to cut and remove invasive plants, but other trophic levels that may interact with invasion processes are typically not managed, such as non-native earthworms that impact soil processes in ways that can have consequence for plant composition (Heneghan et al. 2006). The success of invasive species removals is largely determined by the degree of invasion, as the “early detection, rapid response” method to controlling invasive species is generally most effective. Ecosystem changes resulting from invasion increase with time since invasion; therefore, restoration in the early stages of invasion is likely to be more successful because there is less modification to the historic system (or higher legacy) relative to long after an invader has established (Strayer et al. 2006). Although removal of invaders followed by the re-establishment of historical disturbance regimes (e.g. fire) may conserve and enhance native biodiversity (Hobbs & Huenneke 1992), there has been growing concern that methods exclusively targeted at physical removal of an invader can leave a habitat vulnerable to rapid reinvasion (Iannone & Galatowitsch 2008). Furthermore, invasive species that share similar physiological traits and response to management as native species can pose a real dilemma for managers (Reed et al. 2005).

### 5.6.4.1 Using soil ecological knowledge to control invasion

On a large scale, there has been less active management of soil properties and/or processes to prevent or reduce biological invasion relative to active management of vegetation (Callaham et al. 2008). Several studies have quantified the effects of invaders on soil properties and processes, and a few studies have manipulated soil to reduce invasive species. Because soil and plants interact, a modification to the plant community, such as invasion and dominance by a new species, is expected to change soil conditions (Wardle et al. 2004; van der Putten et al. 2009). Common impacts of invaders on soil include alteration to microbial communities and decomposition rates with consequence for nutrient supply (Corbin & D’Antonio 2004b; Belnap et al. 2005), and these changes may persist even after removal of invasive species (Ehrenfeld & Scott 2001). There is limited knowledge about the passive recovery of soil physical, chemical, and biological components following removal of invasive species. If feedback processes develop, there is potential for the system to persist in a self-organizing alternative stable state (Suding et al. 2004).

Development of restoration strategies that ameliorate soil conditions modified by invasive species may be needed to successfully increase desired species. Invasive plants may benefit themselves by altering soil biota, soil structure, amount and quality of organic matter, form of available nutrients (e.g. nitrate vs. ammonium), and/or by adding allelochemicals to the soil. Restoration techniques that mediate these changes to soil include: using plant species that reverse invader-cultured soil
conditions, adding microbial-containing inoculum to soil, and adding charcoal to bind allelochemicals (Eviner et al. 2010). Kulmatiski and Beard (2006) added 1% activated C to soil dominated by two exotic species and found reduced extractable organic C and N coupled with consistent shifts in community composition (reduction in cover of two target exotic species and an increase in overall cover of native species). Despite these promising results, not all native species responded positively and other (non-target) exotic species increased in cover. This example does illustrate the potential utility of soil-based tools to reduce invasive species.

A common observation is that invasive plant species enhance the availability of limiting nutrients, N and P in particular (Ehrenfeld 2003). Numerous methods, similar to ones used in restoring arable land, have been used to reduce nutrient availability in invaded environments. Carbon amendments (e.g. mulch, sawdust, and sugar additions) can be effective at reducing invasive species and promoting plant diversity. However, some studies found that benefits are short lived and that strategies targeted at manipulating propagule availability were more effective (Morgan & Seastedt 1999; Corbin & D’Antonio 2004a). Rowe et al. (2009) compared the efficacy of nutrient reduction through sucrose application to inoculation of invaded communities with soil from uninvaded communities and found that both tools reduced the focal invasive species’ cover and increased perennial native species cover; however, nutrient reduction also increased non-native annual/biennial cover.

Although the tool box of soil-related approaches to reducing invasion is growing, there is not an immediate prospect of applicability, particularly on a large spatial scale. Because invasive species can alter many aspects of soil, the most promising management option will vary with invader. Conflicting outcomes of soil-based restoration tools to control invasive species limit the ability to make general recommendations. To successfully manage ecosystems undergoing dynamic change through the invasion of undesirable species it will be prudent to: 1) study invasion on a local scale, 2) acquire comprehensive information on life history strategies and resource requirements (including interactions with belowground flora and fauna) of local invaders, 3) know the environmental conditions prior to invasion, 4) quantify the impacts of invasion on biological communities and soil, and 5) develop restoration tools that target reducing invasive species and promoting desired communities, coupled with evaluating the efficacy of those tools. Finally, reporting failures of soil-related manipulations used to manage invasive species can be just as valuable as the knowledge gained from restoration success.

5.6.5 Novel legacy: no-analog ecosystems and environmental conditions

There is increasing recognition that restoring ecosystems of the past may not be feasible under rapid and widespread anthropogenic-driven changes to the Earth’s atmosphere, climate, land, disturbance regimes, and available nutrients, in combination with invasion of non-native organisms and corresponding loss of diversity (Vitousek et al. 1997). These environmental changes have led to the development of novel ecosystems, defined as self-perpetuating communities that contain no historic analog in terms of species composition and potential functions (Fig. 5.6.1, Scenario III) (Hobbs et al. 2009). Novel ecosystems represent a self-sustaining stable state under new biotic and abiotic conditions. They are often characterized by exotic (either actively or formerly invasive) assemblages of species that have never before coexisted. Because invasive plants commonly alter soils in ways that benefit themselves (Kulmatiski & Kardol 2008), they can facilitate the creation of a new stable state and partly explain the emergence of some novel ecosystems.

The development of novel ecosystems can be due to 1) shifts in abiotic conditions, which then drive biotic changes, 2) shifts in the biotic community, which then alter abiotic conditions, or 3) interactions of biotic and abiotic changes (Hobbs et al. 2009). Increased N deposition in coastal sage scrub habitats of southern California has driven major shifts in the biological community, with consequences for ecosystem structure and functioning. Increased N input through deposition has increased productivity, fuel loads, and fire frequency, which has resulted in the conversion of native shrubland to grasslands dominated by exotic species (reviewed
in Fenn et al. 2003; Fenn et al. 2010). Even with efforts to control exotic grasses and planting native species, these grasslands persist over the long-term, and represent a new stable state (Cox & Allen 2008). Wolkovich et al. (2010) reported that this grass-dominated system was nine times more productive than the native system, had lower erosion rates, and a 1.4-fold greater C storage in soil and litter, which shifted the system from a variable C source to a C sink.

Shifts in biotic composition can strongly affect abiotic components of the ecosystem. In fact, the direct impacts of environmental changes on ecosystem processes are often small compared to the indirect ecosystem effects mediated by changes in the plant community (Chapin 2003). For example, in Western Australia, clearing of native vegetation for agriculture leads to a shift from vegetation with deep roots and high evapotranspiration rate, to agricultural species that have shallower roots and use less water. Low evapotranspiration rate in the system dominated by agricultural species leads to a rise in the water table and salinization of the soil surface (with negative consequences for crop production). These abiotic shifts, caused by conversion to agriculture also limit which plant species can thrive in the surrounding natural landscape (George et al. 1997). Furthermore, the saline soils can contain 2.5-fold lower soil organic C stocks, lower soil N, decreased soil aggregation, and increased bulk density (Wong et al. 2008). Ecosystem transformations such as these can also be mediated by species extinctions, invasion of exotic species, and even shifts in dominant native species (Hobbs et al. 2009).

State changes can also be driven by an interaction between shifts in biotic and abiotic changes. For example, 80–87% of Inner Mongolia’s grasslands are undergoing desertification due to overgrazing, which causes shifts in vegetation composition and exacerbates drought (Li et al. 2000). Plant composition shifts resulting from overgrazing in Inner Mongolia’s grasslands leads to decreased plant diversity and cover, increased erosion, decreased soil C and nutrients, and increased aridity at a larger scale (Li et al. 2000). Nitrogen additions to these degraded grasslands can enhance the prevalence of perennial drought-tolerant species. Although N addition, in this circumstance, does not necessarily restore historic community composition, it does enhance ecosystem function and resilience of the system to drought. Conversely, N addition to non-degraded perennial grasslands in this region can lead to dominance by annual, early successional species that may not establish in a drought, and leave the system susceptible to massive erosional losses and potentially desertification after a large windstorm (Bai et al. 2010).

In novel systems, manipulations to soil structure, chemistry, and/or biota could be key to retaining some presence of historic species, but restoration to historic communities in most cases would require extreme modification. Effective restoration of novel ecosystems will require knowledge of factors that caused state changes (Beisner et al. 2003). Threshold changes in system states are more likely to occur in ecosystems with strong interactions (Suding & Hobbs 2009). Thus, understanding abiotic and biotic interactions is critical to predict and manage state changes. Restoration of a novel system to some past condition may not be feasible (or reasonable) if the environmental change needed to reverse a state change exceeds the environmental change that initiated the state change, a phenomenon known as “hysteresis.” For example, successful restoration of coastal wetlands may require large decreases in salinity, because salinity tolerance of establishing seedlings is much less than that of mature wetland plants (Zedler 2005).

Key factors that contribute to the resilience/recoverability of an ecosystem include regulation of abiotic conditions (including nutrient supply), propagule availability in the the regional species pool, and landscape connectivity. All of these factors must be considered to conserve and restore communities and ecosystem services. The role of regulating abiotic conditions has proven critical for restoration of southern California salt marshes. In these systems, small patches cleared for restoration have been successful, but larger-scale restoration efforts have been unsuccessful because large expanses of bare ground heat up and lead to high evaporation, high levels of salinity, and minimal plant establishment (Zedler 2005). Securing ecosystem functions will require a diversity of genotypes and species tolerant of harsh abiotic conditions in the regional or restoration pool of
propagules (Eviner & Chapin 2001). Finally, proximity and/or connectivity to remnant patches across the landscape can be critical to maintaining abiotic conditions, providing resources and species through migration and propagule dispersal, and mediating disturbance regimes critical to the maintenance of a system (Bengtsson et al. 2003).

Rapidly changing environmental conditions may necessitate shifting some restoration goals to maintaining or reinstating ecosystem services. Restoration and management to some historic plant communities could, in fact, promote species and communities that can no longer persist without intense management (and eliminate plants that can), potentially leading to a collapse in the provision of multiple ecosystem services (Hobbs et al. 2009). Although novel ecosystems have received negative attention because they are often dominated by non-native species, in some scenarios, these communities have and will represent the most effective way to provide ecosystem services in greatly altered environmental conditions (Ewel & Putz 2004).

5.6.6 Conclusions

The importance of soil ecology in the science and practice of ecological restoration has been repeatedly recognized (Bradshaw 1999; Young et al. 2005; Heneghan et al. 2008). To synthesize the role of soil ecological knowledge in guiding restoration science and practice is challenging because failures are commonly unreported and most published studies on ecological restoration reflect only a brief excerpt (temporally and spatially discrete) from a continuous process that inherently involves change over time. Furthermore, it is difficult to identify generalities across varying types and degrees of disturbance among an array of ecosystems that are restored and managed in unique ways for different purposes. This summary of restoration from the soil legacy continuum perspective elucidates the following:

1. Slower recovery of soil properties and processes relative to plant components (cover and productivity) is consistent across many types of restored ecosystems. Many studies report improved soil structure, C stocks, microbial populations, and nutrient cycling in the trajectory of a target state within decades, but full recovery is anticipated to take much longer.

2. Inconsistent patterns in plant community recovery are commonly attributed to soil properties and/or processes altered through disturbance, which can persist in some cases for over a century.

3. There is more knowledge about singular soil-related constraints to restoration than complex soil or plant-soil interactions. For example, soils with high nutrient availability typically support species-poor plant assemblages. Direct physical and chemical (reduction in P availability through dilution or adsorption) and indirect biological (C addition to increase microbial demand for N) methods used to reduce nutrient availability can be effective. Similarly, pH can be manipulated to alter metal toxicity to promote revegetation or promote restoration of communities adapted to specific pH conditions.

4. The proverbial “black box” of species and their interactions with physical and chemical properties of soil truly demonstrates that a whole soil connected to the aboveground community is greater than the sum of all the parts. This is evidenced by attempts to preserve vital topsoil for restoration, but discovery that displacement, disconnection (from plants), and replacement alters properties of soil enough to constrain restoration of key species.

5. Where substantial elements of the native biota persist in ecosystems undergoing dynamic change through biological invasion, it may be prudent to integrate knowledge of the soil factors that may promote invasion (i.e. disturbance or nutrient supply) and invasive species impacts on soil into management.

6. In highly invaded sites, where the native biota is vestigial, managers may want to consider amelioration of soil properties and processes affected by the invasive species. Novel tools have been tested in attempt to
ameliorate allelopathic effects of invasive species on soil and supply microbial propagules through inoculum additions, but they are limited thus far in knowledge of their effectiveness across ecosystems and at a large spatial scale.

7. Under changing environmental conditions, traditional restoration targets may need to be reconsidered, particularly if restoration requires continued intensive management to sustain species that are no longer suitable for the environment or restoration will require modification to the extent that will cause ecosystem degradation and compromise services. Novel ecosystems may maintain ecosystem services such as productivity, nutrient provision and retention, erosion control, soil C storage and protection, as well as water infiltration, storage, and supply.

Despite many uncertainties, the increasing number of studies that have monitored or manipulated soil properties and processes (successfully or not) tangibly achieve the ultimate goal of restoration ecology, which is to use ecological knowledge to steer restoration practice and test our basic understanding of ecology.

References


