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Gone but Not Forgotten? Invasive Plants' Legacies on Community and Ecosystem Properties

Jeffrey D. Corbin and Carla M. D'Antonio*

The widespread recognition that nonnative plants can have significant biological and economic effects on the habitats they invade has led to a variety of strategies to remove them. Removal alone, however, is often not sufficient to allow the restoration of altered communities or ecosystems. The invasive plant's effects may persist after its removal thus exerting a ''legacy'' that influences community composition or the ecosystem properties or both over some ensuing period. Here, we review evidence of such legacy effects on plant and soil communities, soil chemistry, and soil physical structure. We discuss this evidence in the context of efforts to restore community composition and ecosystem function in invaded habitats. Legacies are especially likely to develop in cases where invasive species cause local extirpations of resident species, alter resource pools, and interact with other aspects of global change including land-use changes, atmospheric N deposition, acid rain, and climate change. In cases where legacies of invasive plants develop, the removal of the nonnative species must also be accompanied by strategies to overcome the legacies if restoration goals are to be achieved.

Key words: Biodiversity, exotic plants, plant–soil interactions, nonnative plants, nutrient cycling, restoration.

Invasive alien species are widely recognized as a major component of anthropogenic global change with wide-ranging ecological and economic effects (Mack et al. 2000; Pejchar and Mooney 2009; Pimentel et al. 2005; Vitousek et al. 1997). Several individual studies, as well as summary and meta-analysis articles have demonstrated effects of invasive species on processes that operate at population (e.g., Anttila et al. 1998; Olden et al. 2004; Sakai et al. 2001), community (e.g., Levine et al. 2003; Vander Zanden et al. 1999; Wilcove et al. 1998), and ecosystem (e.g., D'Antonio and Vitousek 1992; Ehrenfeld 2010; Liao et al. 2008) scales. Estimates of the annual, economic effects of invasive plant and animal species typically exceed \$100 billion in the United States alone (e.g., Pimentel et al. 2005).

The biological effects and associated costs of invasive plant species in natural and managed landscapes have led to the development and use of tools to remove unwanted species as part of the management of those habitats. Such tools include the development and release of biocontrol agents, chemical control, manual excavation, controlled ungulate grazing, and prescribed fire. The success of each technique depends on the particular species and habitat. Successful eradication has been achieved only at relatively small spatial scales (Simberloff 2001)—we are not aware of an example of the successful eradication of a widespread invasive plant species throughout its introduced range.

Even where local eradication is achieved, removal by itself is unlikely to allow restoration of broader community or ecosystem characteristics. For example, the number, relative abundances, or composition of native species in postremoval environments may be significantly different from nearby uninvaded habitats (Heleno et al. 2010; Rey Benayas et al. 2009). Similarly, invader-mediated changes in ecosystem conditions may persist even after the nonnative species is removed or dies (Haubensak et al. 2004; Maron and Connors 1996; Maron and Jefferies 1999; Vitousek et al. 1989). In such cases, management beyond invasive plant control must be considered if the community or the ecosystem effects or both of the invasive plants are to be reversed.

In this article, we review examples of how legacies of invasive plants (sensu Corbin and D'Antonio 2004; Cronk and Fuller 1995; D'Antonio and Meyerson 2002) may inhibit or interfere with the restoration of invaded habitats. We differentiate *legacies* of species invasions from the *effects* of invasive species on community or ecosystem conditions.

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Legacies are a specific type of effect in which measurable changes in biological, soil chemical, or physical conditions are evident even after the invader has been removed from an ecosystem. To date, there have not been enough studies on the subject to permit a quantitative analysis of the conditions in which we might expect to see legacies (e.g., a meta-analysis) and how long they are likely to last. Instead, we review the available studies to understand the implications of legacies for habitat restoration and for prioritization of invasive plants for control.

Legacies of Plant Invasions

Removal of nonnative plants is often the first (and in some cases, the only) action taken to restore an invaded habitat. In some cases, removal alone can result in a return to predisturbance, or at least markedly better, conditions than those that existed before removal (Ray Benayas et al. 2009). For example, removal of the invasive estuarine macrophyte smooth cordgrass (*Spartina alterniflora* Loisel.) in Willapa Bay, WA—without any further restoration efforts—was sufficient for the recovery of at least some species. Holsman et al. (2010) found that the catch of the commercially important Dungeness crab (*Metacarcinus magister* Dana) was 4 to 19 times higher in areas where *S. alterniflora* was removed compared with areas where the abundant cordgrass was left in place. Similarly, Patten and O'Casey (2007) found that both herbicide and mechanical tilling to control *S. alterniflora* in Willapa Bay, WA, increased the abundance of a variety of shorebirds: the abundance of "peeps" (sandpipers [*Calidris* spp.]) and waterfowl, respectively, were 62 and 16 ha^{-1} in herbicide-sprayed *S. alterniflora* meadows and 700 and 27 ha^{-1} in tilled meadows. These abundances compare to 7 and 0.8 birds ha^{-1} in untreated *S. alterniflora* meadows.

In other cases, however, eradication of an invasive species either does not lead to the recovery of valued ecosystem properties or the successional trajectory toward a more desired condition is extremely slow. In these situations, altered community and ecosystem properties may be a legacy of the past plant invader. Indeed, as we discuss later, although Dungeness crab and shorebird populations recovered following control of *S. alterniflora* in Willapa Bay, WA, removal of the invasive species in a nearby estuary did not lead to the recovery of other ecosystem conditions, including soil physical structure.

The concept that species composition may have effects on ecosystem processes after they are gone from the system is not new nor is it restricted to the study of invasive species. For example, the Connell and Slatyer (1977) facilitation model of succession and the ideas of Clements (1916) that early colonizing species influence soil in ways that lead to species change and turnover are based on the concept that species have legacies. The influences of species on the development of soil structure and on the alteration of nutrient availability (e.g., inputs of N) are broadly recognized as pathways influencing the course of primary succession (e.g., Del Moral and Bliss 1993; Vitousek et al. 1989). What is different about legacies in the context of invasive species is that lasting effects of nonnative plants are considered detrimental to succession (from the perspective of human benefits), inhibiting our ability to return the ecosystem to a more desirable state. In cases in which invasion legacies develop, removal of the species is not likely to be enough for recovery of the desired services (D'Antonio and Meyerson 2002; Suding et al. 2004). Instead, other strategies are likely required to achieve restoration goals, including seeding or planting of target vegetation (e.g., Cione et al. 2002), decreasing or amending soil resources (Perry et al. 2010), or the active reintroduction of natural disturbance regimes (D'Antonio and Vitousek 1992; Sheley and Krueger-Mangold 2003).

Biotic Legacies. The introduction of a new genetic lineage in a community is, by definition, an increase in biodiversity and indeed it has been noted that nonnative species have increased biodiversity at intermediate to large scales (Davis 2003; Sax and Gaines 2008). However, at smaller scales, nonnative species are frequently associated with net decreases in biodiversity (Levine et al. 2003). They can decrease biodiversity via predation, herbivory, competition, and hybridization, among other pathways. Global extinction is, by definition, not reversible, although local extirpation (the loss of a species from a particular habitat when it persists elsewhere) may be reversible. Although plant invaders have been associated with local extirpations within a given community and dramatic shifts in community dominance, there are relatively few, if any, cases of global extinctions from plant invaders (Gurevitch and Padilla 2004; Sax and Gaines 2008). Local extinction may last for decades or longer because of propagule limitations (e.g., Seabloom et al. 2003). Then, assisted dispersal in the form of seeding or planting of established individuals may be required during restoration (Corbin et al. 2004; Martin and Wilsey 2006). The reversibility of shifts in composition from past invasion is likely dependent on the extent to which the habitat was altered simultaneous with (but not due to) invasion, as well as the legacies left by the invaders after control. Where native seedbanks persist intact or large stands of native species occur nearby for recolonization, recovery may not require further human intervention. However, there are few long-term studies of invasive plant effects, so we know very little about the conditions governing "natural" recovery after death or removal of an invader.

Gene flow and hybridization between native and nonnative species is a pathway through which invasive plants can have long-term influences on the biodiversity of a habitat, including influences long after removal of the invasive plant (Vilà et al. 2000). For example, Bleeker et al. (2007) found that 17 threatened plant species in Germany experienced outbreeding depression because of hybridization with nonnative species and that the gene pools of 8 species were affected by introgression of exotic genes. Likewise, Ayres et al. (2004) demonstrated that the native California cordgrass (*Spartina foliosa* Trin.) is disappearing from the San Francisco Bay, CA, region because of hybridization with an introduced congener, *S. alterniflora*. Removal of *S. alterniflora* will not result in *S. foliosa* recolonization if no (genetically) true *S. foliosa* remains in the region. Such changes in the gene pools of native species can cause significant changes in the responses of vegetation to environmental conditions. For example, common cordgrass (*Spartina anglica* C.E. Hubbard) is an invasive species and the product of a spontaneous doubling of the chromosomes of the hybrid of small cordgrass [*Spartina maritima* (M.A. Curtis) Fernald] and *S. alterniflora*. It is capable of occupying a wider ecological range than either of its genetic antecedents (Daehler and Strong 1996), and as a result, the area of open mudflat has declined in estuaries invaded by *S. anglica*. In another example, Meyerson et al. (2010) found that co-occurring native and invasive subspecies of common reed [*Phragmites australis* (Cav.) Trin. ex Steud.] are capable of producing fertile hybrids, although hybrids had not been detected in wild populations.

Invasive plants have been shown to alter soil microbial and fungal communities in ways that can influence plant–plant interactions, plant community composition, and plant–soil interactions (Kourtev et al. 2002; Pringle et al. 2009; Reinhart and Callaway 2006; Stinson et al. 2006). As summarized by Pringle et al. (2009), plant–mycorrhizal symbioses are sensitive to invasive plants, with a variety of implications for the community and the ecosystem. First, the ability of invasive plants to alter the soil mycorrhizal community (Mummey and Rillig 2006) and the symbioses of adjacent species (Hawkes et al. 2006; Mummey et al. 2005) could lead to feedbacks among the composition of plant and fungal species in ways that influence competitive interactions in plants (van der Heijden et al. 1998). Second, changes in fungal communities have the potential to influence nutrient availability, soil C structure and storage, and abundance and composition of other soil microorganisms that directly interact with vegetation. In a dramatic example, garlic mustard [*Alliaria petiolata* (Bieb.) Cavara & Grande], a nonmycorrhizal herb invading forests in temperate North America, has been shown to disrupt mycorrhizal associations in co-occurring native tree seedlings (Stinson et al. 2006). Pringle et al. (2009) also hypothesized that the invasion of nonmycorrhizal plant species into an ecosystem dominated by species that associate with mycorrhizae could "tip a system into a more nonmycorrhizal state" (p. 710). In this way, an invasive plant species could indirectly benefit nonmycorrhizal species, including subsequent invaders, even after it is removed.

Plant-mediated shifts in soil biota can persist after community composition has changed. Experimental work has demonstrated that accumulation of positive and negative feedbacks between plants and soil biota can influence productivity, community composition, and the likelihood of invasion, although most of these studies have been conducted in the laboratory (e.g., Klironomos 2002; Van der Putten et al. 1993; Wolfe and Klironomos 2005). For example, Grman and Suding (2010) created soil legacies in containers by growing nonnative species for 5 wk, removing them, and then, planting native species in the same containers. They found that native colonization of containers with nonnative "legacies" was significantly less and the colonists were smaller than in containers without any previous nonnative species growth. There was no legacy of native species on nonnative colonization or growth. Changes in the relative abundances of soil biota rather than the elimination of certain taxa may allow for quick recovery of the soil microbial and fungal communities following the removal of the invasive plant. Alternatively, the complete elimination of taxa may require inoculation with fungal or microbial taxa to achieve restoration goals. This restoration approach has been performed in cases of revegetation following intense agriculture or other severe disturbances (e.g., Richter and Stutz 2002; Zubek et al. 2009).

Soil Chemical Legacies. Invasive plants have been shown to alter ecosystem N dynamics, including soil N pools and rates of N cycling (Ehrenfeld 2010; Liao et al. 2008). The clearest examples come from the invasion of nitrogen-fixing shrubs and trees into habitats without a history of N-fixers. For example, the invasion of fayatree [*Morella faya* (Ait.) Wilbur] in volcanic soils in Hawaii (Vitousek and Walker 1989; Vitousek et al. 1987), acacia (*Acacia* Mill. spp.) in South African fynbos (Stock et al. 1995), and black locust (*Robinia pseudoacacia* L.) in inland New York sand barrens (Rice et al. 2004) have all increased soil N pools and rates of N cycling. Generalizing across the published studies of invasive plants' effects on N dynamics—including N-fixing and non–N-fixing species—Liao et al. (2008) used a meta-analysis to conclude that soil N pools were nearly 20% larger ($n = 88$) and rates of net N mineralization were 51% faster ($n = 58$) in soils associated with invasive plants as compared with uninvaded soils. Rates of litter decomposition were more than double in invaded, compared with uninvaded, sites ($n = 58$).

Thus far, the extent to which such changes in N pools and rates of N cycling have the capacity to last after the removal of the invasive species—that is, to act as a legacy of invasion—is not well-known and deserves further study. Maron and Jefferies (2001) found soil N levels were higher in soils that had formerly been invaded by the N-fixer bush lupine (*Lupinus arboreus* Sims) as much as 35 yr earlier, as compared with uninvaded soils, and levels remained high for at least 5 yr after bush lupine removal. This was despite active management that included mowing and removal of aboveground biomass to reduce N pools. The elevated N also fed back to plant community composition by facilitating the invasion of nonnative grasses, thereby shifting plant community composition (Maron and Jefferies 1999). Yet, compositional effects were reversible, despite the soil N not being fully restored after lupine removal. In other cases, soil N dynamics may not exhibit legacies after restoration. For example, invasion of the N-fixer black locust into sandy soils in New York increased total soil N concentration by 1.3 to 3.2 times, compared with soils dominated by the native pine–oak (*Pinus*–*Quercus*) vegetation (Rice et al. 2004). Rates of net nitrification were 25 to 125 times greater in the invaded stands. However, 4 yr after mechanical removal of black locust stems and roots from these sites, followed by mechanical mixing of the soil and planting of native forb and grass seeds, soil N concentrations, rates of net nitrification, and rates of net N mineralization declined to the point that they were largely indistinguishable from paired, uninvaded plots (Malcolm et al. 2008). In this case, there was little legacy of the black locust invasion observed after its removal, perhaps because soil mixing associated with site preparation diluted the effects of black locust on the upper horizons (S. K. Rice, personal communication).

Invasive plants can also exert legacies by altering other aspects of soil chemistry and structure, including pH, salinity, and organic content. In what is probably the earliest published study on invader effects on soils, Vivrette and Muller (1977) demonstrated that the annual crystalline iceplant (*Mesembryanthemum crystallinum* L.) redistributed salts from the soil profile into plant tissue and then to the soil surface with annual plant death. The leaching of salts from decomposing plant tissues created a buildup of salts at the soil surface that limited colonization by other species even after iceplant removal. D'Antonio (1990) and Molinari et al. (2007) demonstrated that a related species of iceplant—the Hottentot fig [*Carpobrotus edulis* (L.) N.E. Br.]—which is also invading coastal California, reduced soil pH, calcium and magnesium, and increased sodium. D'Antonio (1990) found these effects persisted for at least 18 mo after removal. Conser and Conner (2009) demonstrated that in soil where *C. edulis* had been removed, germination, survival, growth, and reproduction of manyleaf gilia (*Gilia millefoliata* Fisch. & C.A. Mey.), a rare dune annual, was significantly lower, indicating strong legacy effects of the invasive plant. Accumulation of salt in the leaves of saltcedar (*Tamarix ramosissima* Ledeb.) has been shown to contribute to soil salinization and reduce subsequent growth of native species (e.g., Ladenburger et al. 2006), but such legacies may be context-dependent (Lesica and DeLuca 2004) or short lived in riparian habitats where ample winter flooding can rapidly reset surface soils.

Soil Physical Legacies. Invasive plants can alter the physical structure of soil in ways that can persist long after the removal of the nonnative species because both rates of soil erosion and rates of soil accumulation can increase in the presence of invasive plants. Such species have been termed *ecosystem engineers* (sensu Crooks 2002; Jones et al. 1994) for their ability to change rates of soil erosion or accumulation, water table depth, and stream channel structure. For example, invasion of black wattle (*Acacia mearnsii* de Wildeman), Sydney golden wattle [*Acacia longifolia* (Andr.) Willd.], orange wattle [*Acacia saligna* (Labill.) Wendl. f.], and the maritime pine (*Pinus pinaster* Ait.) in riparian habitats of the South African fynbos has increased rates of riverbed erosion and widened stream channels (Enright 2000). Likewise, Lacey et al. (1989) used simulated rainfall events in semiarid rangelands in Montana dominated by native grasses versus areas dominated by spotted knapweed (*Centaurea stoebe* L.) to demonstrate that surface runoff and sediment erosion were both significantly greater under spotted knapweed than under native vegetation. They hypothesized that this was due to greater bare ground associated with the invasive plant than with the native vegetation. In contrast to these examples, invasion of pasture grasses into lowland tropical riparian habitats in Queensland, Australia, has been shown to significantly increase soil capture along stream edges (Bunn et al. 1998). The result is reduced stream width and flow capacity. Likewise, invasion of coastal dunes in the Pacific Northwest of North America by European beachgrass [*Ammophila arenaria* (L.) Link] has increased rates of sand accumulation and, as a result, has dramatically changed dune topography (Wiedemann and Pickart 1996).

Such ecosystem engineers change abiotic conditions and, therefore, community and ecosystem dynamics even after their removal. Common cordgrass, an invader of mudflats and salt marshes in Oregon and Washington, has dense root systems that accumulate sediment and significantly alter sediment biogeochemistry, including tidal elevation, sediment water content, water evaporation, and salt accumulation (Hacker and Dethier 2009; Thompson 1991). Reeder and Hacker (2004) documented that, although removal of common cordgrass in Puget Sound, WA, resulted in colonization by native plants, the recruiting species were typically uncommon in uninvaded habitats. Hacker and Dethier (2009) hypothesized that the shift in community composition was due to common cordgrass–induced changes in sediment, soil hydrology, and salinity and that the long-term trajectory of these communities is likely dependent on the extent to which the sediment persists in the habitats. For example, greater wave action in cobble beaches is expected to scour sediment and foster a more ‘‘natural’’ restored community; by contrast, sedimentation may persist in habitats, such as mudflats and salt marshes, which experience lower forces of water movement. In the latter case, a return to the preinvasion community composition may not be possible, and the legacies of common cordgrass will persist.

Potential for Restoration of Invasive Species' Legacies

Not all, or even most, invasive species are likely to exhibit legacies after their death or extirpation from an ecosystem. However, those that do can present unique challenges to the habitats that they invade and to managers designing strategies to restore invaded communities. Understanding the conditions under which legacies are likely to develop is an important step toward developing appropriate control and restoration strategies.

First, invasive species that influence species number, via either local or global extinction, are more likely to leave behind legacies than those that influence relative abundances of species without extinction or local extirpation. Even when species eliminated by the invader are present elsewhere in the landscape, recovery may be limited by the arrival and establishment of propagules. In such cases, active seeding or seedling planting (Corbin et al. 2004; Martin and Wilsey 2006) or microbial inoculation or both (Richter and Stutz 2002; Zubek et al. 2009) may be necessary. For example, a variety of native perennial grass and forb species in California grasslands have been shown to be limited by seed availability (e.g., DiVittorio et al. 2007; Hamilton et al. 1999). In these habitats, strategies to control exotic species, including prescribed fire, grazing, herbicide, mechanical control, and carbon addition, are relatively unsuccessful without supplemental seeding or planting of native species (Corbin et al. 2004).

Second, invasive species that alter resource pools in the ecosystem, such as soil N, sediment, or salt, may be especially likely to leave behind legacies after removal, especially if there is no ready mechanism for the alteration of those pools during or after removal. For example, elevated N in the form of organic matter that has become integrated in the soil organic horizon may have long-term persistence in the ecosystem and may require further treatments beyond removal of the nonnative species. Pickart et al. (1998) found that removal of bush lupine, along with litter and duff on the soil surface, was more effective in limiting subsequent invasion by nonnative grasses and in promoting the establishment of native dune vegetation than was removal of bush lupine alone. Mechanical manipulation of topsoil, including mixing with deeper, less-fertile horizons (Malcolm et al. 2008) or even topsoil removal (Buisson et al. 2008; Choi and Pavlovic 1998), have been applied in attempts to reduce soil N or nonnative seedbanks or both. Soil amendments, including the application of labile C to soil to reduce plant-available N have received a good deal of attention as a strategy to overcome the legacy of elevated soil N (Perry et al. 2010). The persistence of resource pools is likely a function of other dynamics in the ecosystem as well. For example, depending on the nature of water availability at the site, salts that accumulated in the upper layers of the soil surface following invasion by saltcedar may be rapidly leached, leaving behind little legacy of invasion. As described above, Hacker and Dethier (2009) hypothesized that the success of restoration of habitat invaded by *Spartina* sp. was a function of the wave energy—sediment in Puget Sound, WA, is more likely to return to preinvasion levels in the cobble beaches that experience heavier scouring than in the mudflats and salt marshes.

Third, the interactions among multiple factors—including those already discussed related to species invasion but also other elements of global change, including land-use changes, atmospheric N deposition, acid rain, and climate change—are likely to reinforce each other and influence the return to preinvasion conditions. Hobbs and coauthors have argued that such interactions are leading to more and more ‘‘novel ecosystems,’’ which contain new combinations of species (Hobbs et al. 2006, 2009; Seastedt et al. 2008). In such cases, the alteration of biotic and abiotic conditions may be so extreme that a return to ‘‘unaltered’’ community composition or ecosystem state may be impossible. Hobbs and his coauthors have argued for the acceptance of the reality of these ecosystems as stable and semipermanent fixtures in our landscapes, and in some cases, ones that can provide significant ecosystem services. Where novel ecosystems have developed, resources may be applied more efficiently and effectively in preventing subsequent invasions than in restoring historical community composition.

Conclusions

The effects of invasive plants on community composition or ecosystem properties may persist after removal, thus exerting a ‘‘legacy’’ that persists over some ensuing time period. Association with legacies is not usually an explicit consideration when invasive species are characterized for ecological threat. Although the detailed mechanisms by which the effect of an invasive species persists after its extirpation—by reducing biodiversity, altering soil chemistry, or acting as an ecosystem engineer—are often considered, the most useful application of the concept of legacies of invasion is in the design of restoration strategies.

In such cases, the removal of the nonnative species must also be accompanied by strategies to overcome the legacies if restoration goals are to be achieved.

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