

Ecosystem Impacts of Exotic Plants Can Feed Back to Increase Invasion in Western US Rangelands

By Valerie T. Eviner, Sarah A. Hoskinson, and Christine V. Hawkes

Invasive, nonnative plant species have become one of the most pressing rangeland management issues. In the western United States (the 17 US states from North Dakota, south to Texas, and west to the Pacific coast), 51 million hectares of rangeland are now dominated by invasive plants considered to be noxious weeds.¹ In over two-thirds of western rangelands, nonnative annual grasses account for 50–85% of vascular plant cover.² Invasive plants have large negative impacts on the prevalence and diversity of native species, and many decrease livestock production through decreases in forage quantity and/or quality (Table 1). Invasive species on US rangelands have an estimated annual cost of US\$2 billion³ due to lost production and costs of control efforts. There are also hidden costs associated with invasive species in the form of degraded ecosystem services—key functions provided by ecosystems that benefit humans (e.g., water provisioning, flood control, erosion control, carbon storage, nutrient supply, climate regulation). In some cases, invasive species change ecosystem processes in ways that are self-reinforcing, making the system more suitable for the invader than for the previous inhabitants, in what is known as a positive feedback loop. The combination of degraded ecosystem properties and positive feedbacks can make invasive plant control and rangeland restoration much more challenging because in these cases, it is not sufficient to simply remove the invaders. The ecosystem impacts of invasive species can persist long after the plants have been removed, and when this occurs, the system can remain vulnerable to reinvasion until the ecosystem effects are mitigated or reversed. We review the ecosystem impacts of the current major rangeland invaders in the western United States, discuss the potential for these ecosystem changes to further promote invasion through positive feedbacks, and suggest strategies to address persistent ecosystem effects in order to enhance invasive

plant control and restoration of native (or otherwise desirable) plant communities.

Ecosystem Impacts of Plant Invasions

Most of the major rangeland invaders in the western United States have large impacts on at least some aspects of ecosystem function, ranging from forage productivity to soil and water quality¹ (Table 1). Invasive plants in western rangelands typically reduce livestock production by 30–75% (however, not all invasive plants are detrimental to livestock production, and the effects of a given invader can be beneficial to some livestock species but detrimental to others; Table 1). Although forage quality and production are the most immediate concerns for ranchers, invasive species can also change many other ecosystem characteristics that can negatively impact both the ranch itself and the surrounding areas that rely on ecosystem services provided by rangelands. These ecosystem services include regulation of water flow and quality, soil fertility, soil carbon storage, and wildlife habitat. Water use by yellow starthistle, for example, can remove 15–25% of annual precipitation, decreasing soil water availability for other plants and ultimately reducing downstream water flow. In California's Sacramento River watershed alone, the costs of lost water associated with yellow starthistle amount to US\$16–75 million annually.⁴ Medusahead has been shown to decrease soil carbon stores, which can have major implications for those seeking credits for carbon sequestration on rangelands. Goatgrass, cheatgrass, medusahead, and spotted knapweed can reduce nitrogen recycling rates, thus potentially limiting rangeland productivity because nitrogen is the most commonly limiting nutrient to plant growth in these systems. Even when invaders do not alter the total amount of soil resources, they can change the timing of resource availability, restricting which plant species have access to soil resources.⁵

Table 1: Effects of major invasive plants in western US rangelands. Empty cells indicate that data were unreported for these properties (either because they are unmeasured, or because differences that are not statistically different tend not to get reported). Citations provide specific references (see web appendix), and much of this information is reviewed in DiTomaso (2000), Ehrenfeld (2003), and Duncan and Clark (2005)

Invaser and its coverage in hectares across 17 western US states	Plant productivity	Costs or economic losses	Diversity/composition	Water availability and quality	Carbon storage	Nitrogen availability and litter turnover	Soil microbes	Disturbance regime	Other	References
Barbed goatgrass (<i>Aegilops triuncialis</i>), data on area covered not available	Decreases productivity on nonserpentine soils; on serpentine, increases productivity compared to serpentine natives	40–75% decrease in livestock productivity	Can often form monotypic stands; decreases diversity particularly in serpentine soils, which had been a refuge for native species			Decreases decomposition compared to serpentine natives.	Alters soil microbial community composition		Increases soil aggregation	Batten et al. 2005
										Batten et al. 2006
						Decreases nitrogen stored in microbial biomass				Batten et al. 2008
										Canals et al. 2005
Canadian thistle (<i>Cirsium arvense</i>), 2.86 million ha		Decreases livestock carrying capacity by 42%, can injure livestock	Decreases plant diversity						Allelochemicals	Drenovsky and Batten 2007
										Eviner and Chapin 2005
										Jacobsen 1929
										Malmstrom et al. 2009
										Pritekel et al. 2006

Table 1. Continued

Invader and its coverage in hectares across 17 western US states	Plant productivity	Costs or economic losses	Diversity/composition	Water availability and quality	Carbon storage	Nitrogen availability and litter turnover	Soil microbes	Disturbance regime	Other	References
Cheatgrass (<i>Bromus tectorum</i>), 22.68 million ha	Changes from patchy vegetation to continuous cover	\$20 million per year in firefighting costs	Can facilitate other invasives (medusa-head)	Increase or no change in soil moisture	Alters distribution of soil carbon (disrupts islands of fertility)	Decreases nitrogen fixation by soil crusts	Decreases arbuscular mycorrhizal fungal abundance and diversity	Changes fire return interval from 60–100 years to 5 years	Palatable and used extensively by livestock	Belnap and Phillips 2001
			Decreases native perennial grasses and shrubs (through fire)	Decreases water infiltration	Increases surface soil carbon pools	Impacts on plant-available nitrogen vary with site and duration of invasion; range of 50% decrease to increase in net nitrogen mineralization.	Shifts arbuscular mycorrhizal community in soil	Mixed impact on wildlife: some use as forage, others do not	Mixed impact on wildlife that rely on shrub habitat	Bolton et al. 1993
	Increased or decreased due to 10-fold variation in productivity year to year (vs. natives, which have more reliable production)		Decreases biological soil crusts			Increases surface soil's total nitrogen in most sites	Shifts soil fungal composition and decreases pathogens			Boxell and Drohan 2009
							Direction of effects on particular microbes depends on native community			Hall et al. 2009
										Hawkes et al. 2006
										Hooker et al. 2008
										McHenry and Murphy 1985
										Ponzetti et al. 2007
										Rimer and Evans 2006
										Rowe and Brown 2008
										Sperry et al. 2006
										Whisenant 1989
										Wolfe and Klironomos 2005
										Zouhar 2003

Table 1. Continued

Invader and its coverage in hectares across 17 western US states	Plant productivity	Costs or economic losses	Diversity/composition	Water availability and quality	Carbon storage	Nitrogen availability and litter turnover	Soil microbes	Disturbance regime	Other	References
Diffuse knapweed (<i>Centaurea diffusa</i>), 0.75 million ha		Low palatability, injures livestock \$42 million per year in Montana (for <i>C. diffusa</i> and <i>C. maculosa</i>)	Tends to form monotypic stands	Reduces infiltration, increases runoff					Allergen Good wildlife forage (e.g., bighorn sheep) Allelochemicals	Callaway and Aschehoug 2000
Leafy spurge (<i>Euphorbia esula</i>), 1.49 million ha	Decreases production by as much as 75%	\$130 million per year in Montana, North Dakota, South Dakota, and Wyoming 50% decrease in grazing capacity. Cattle avoid areas with as little as 10% cover	75% decrease in plant species richness						Decreases use by deer, bison, elk Decreases some birds	Belcher and Wilson 1989 Duncan et al. 2004 Olson 1999 Trammell and Butler 1995
Medusahead (<i>Taeniatherum caput-medusae</i>), 2.4 million ha	Decreases productivity	50–80% decrease in livestock productivity; can cause injury to livestock	Decreases plant diversity, decreases natives, increases exotic forbs		Decreases soil carbon	Lowers total soil nitrogen, nitrogen mineralization, and nitrification High silica content leads to slow decomposition	Changes bacterial community composition and function	Increases fire frequency in Great Basin		Davies and Svejcar 2008 DiTomaso 2000 Eviner et al., unpublished data Malmstrom et al. 2009 Trent et al. 1994

Table 1. Continued

Invader and its coverage in hectares across 17 western US states	Plant productivity	Costs or economic losses	Diversity/composition	Water availability and quality	Carbon storage	Nitrogen availability and litter turnover	Soil microbes	Disturbance regime	Other	References
Musk thistle (<i>Carduus nutans</i>), 1.89 million ha	Even at low densities, can decrease forage production by 23%	Decreases livestock carrying capacity by 38%							Allelopathy suspected	Rees et al. 1996
Spotted knapweed (<i>Centaurea maculosa</i> , <i>C. stoebe</i>), 2.12 million ha	Decreases grass productivity 60–90%	\$42 million per year in Montana (for <i>C. maculosa</i> , <i>C. stoebe</i> , and <i>C. diffusa</i>) Interferes with livestock access to more desirable forage, leads to 63% reduction in livestock capacity	Decreases native diversity Decreases cryptogamic crusts, which are important for soil stability, nitrogen fixation, and moisture retention	Decreases water infiltration, increases runoff, leads to increased sedimentation	Impact depends on site: often no effect, increases at some sites, decreased at one site	Varied effects, tends to decrease nitrogen availability	Changes fungal and arbuscular mycorrhizal fungal communities, decreases arbuscular mycorrhizal fungal diversity and hyphal length, mixed effects on quantity of arbuscular mycorrhizae	Reduces fire frequency	Decreases elk use Allergen Allelochemicals, mixed evidence Alters spider community, increases density by 46- to 74-fold, with 89-fold increase in invertebrate predation by spiders	Blair et al. 2005 Broz et al. 2007 Carey et al. 2004 Hook et al. 2004 Lacey et al. 1989 Marler et al. 1999a, b Mummey and Rillig 2006 Pearson 2009 Sheley et al. 1998

Invader and its coverage in hectares across 17 western US states	Plant productivity	Costs or economic losses	Diversity/composition	Water availability and quality	Carbon storage	Nitrogen availability and litter turnover	Soil microbes	Disturbance regime	Other	References
Yellow starthistle (<i>Centaurea solstitialis</i>), 5.98 million ha	Lowers productivity	US\$12.5 million per year in management costs	Decreases plant diversity	Decreases soil moisture by drawing down the equivalent of 15–25% of annual precipitation.			Changes microbial community composition			Batten et al. 2006
		US\$16–75 million per year due to water loss in Sacramento River watershed, California								Enloe 2002
		Toxic to horses								Gerlach 2004
		Lowers forage crude protein, but good forage for goats and sheep in early stages								Jetter et al. 2003
				In Siskiyou County, California, water loss is more than 100,000 m ³ per year						Malmstrom et al. 2009

References available online at www.srmjournals.org.

Some ecosystem impacts of invasive species may be rapidly reversible upon removal of the invader. For example, decreased soil water availability caused by high plant transpiration rates should reverse quickly once the invasive plant is removed. In contrast, many invader-induced ecosystem effects can persist even after invasive removal, a concept known as legacy effects. For species that alter soil properties such as soil structure, water infiltration, water holding capacity, carbon storage, nitrogen availability, and so forth, it may take from months to decades to reverse these changes even with active management.⁶ Extensive erosion of topsoil in invaded systems, for example, can take decades to centuries to reverse via soil formation processes and the gradual buildup of organic matter by the restored plant community.

Understanding the ecosystem impacts of key invasive plants in western US rangelands can be difficult because even for a given species, ecosystem effects are often not constant but vary with site conditions, invader prevalence, and duration of the invasion.^{5,7,8} Continued research into the context-dependence of invasive species effects will help us better predict which sites will be most impacted by a particular invader, which ecosystem processes will need to be restored at a given site, and how these ecosystem effects change over time—giving us critical tools for prioritizing our eradication and restoration efforts.

Feedback Effects of Plant Invasions

Although the ecosystem effects of invasive plants are a concern in their own right, invaders can also change the soil conditions to such an extent that the new conditions alter which plant species can grow successfully at that site. Feedback effects, where a change in plant composition alters conditions that can further alter the plant community, can be either positive or negative. In a positive feedback, the effects of invasive plants on ecosystem properties will further promote the persistence and growth of the invader. In a negative feedback, changes to the ecosystem caused by invasive plants promote other species and thereby limit abundance of the invader. Feedbacks are typically mediated through changes in soil biota, microenvironment, disturbance regime, and/or the soil physical or chemical environment.^{9,10}

In general, feedbacks play an important role in community dynamics. In native communities, negative feedbacks are most common, and can decrease plant biomass by an average of 37%.¹¹ Invasive plants are less likely to have negative feedbacks and are more likely to alter soils in ways that increase their own prevalence and biomass (by an average of 43%).^{6,11,12} In some cases, a given invasive plant alters the soil to benefit other invaders, as well as itself. For example, cheatgrass invasion can make a system more vulnerable to medusahead, and medusahead can increase the prevalence of exotic forbs (Table 1).

Positive feedbacks are common for a number of invasive species in western US rangelands, making their control a greater challenge (Table 2). Many of these invasive plants alter soil biota in ways that favor themselves, or inhibit

natives more strongly than themselves. For example, Italian thistle decreases densities of symbiotic arbuscular mycorrhizal fungi, which limits the growth of native forb species. Black mustard displays a different type of feedback strategy; it inhibits native grasses by increasing consumption of the native species by small mammals. The effects of this feedback extend up to 30 m away from mustard patches. Rangeland invaders also generate feedbacks through changes in the fire regime (cheatgrass), changes in soil nitrogen availability (cheatgrass), and addition of allelochemicals (knapweed) that inhibit growth of other plant species (Table 2). Native communities may also resist invasion by altering soils in ways that suppress the growth of invasive species.¹³

The study of feedbacks created by invasive species is still a relatively new field, and although it is clear that feedbacks can play an important role in invasions, not all invader-induced ecosystem changes will feed back to benefit invaders. Just as the ecosystem impacts of invaders can be context-dependent, the strength and direction (positive or negative) of feedbacks can also vary with environmental conditions, the amount of time that the invader has been present, and with which plant species are interacting.

Management Considerations

Removing an invasive species through burning, grazing, or herbicide is a common and necessary starting point, but in some cases, successful management requires disruption of invader-induced soil changes, which can persist for weeks to decades after the invasive plant has been removed.⁶ Without management to reverse the effects of invasive species on soils, the system can often remain susceptible to reinvasion. Because plant–soil feedbacks operate through many mechanisms, there is no easy, one-size-fits-all management plan. Some of the common management practices that have the potential to alter plant–soil feedbacks in favor of native and other desirable species include selecting plants for restoration that can reverse the ecosystem impacts of invasive species, manipulating soil microbes, and adding carbon and charcoal to soil (described below and in Table 3). For these practices to be successful, we must identify the mechanisms driving the feedbacks and select the approaches that have the greatest likelihood of interfering with those specific mechanisms. These tools have been effective in controlling some invaders under specific conditions, but also have failed to work or even increased the prevalence of invaders (Table 3). Mitigating feedbacks is a relatively new approach, and a close collaboration is required between managers and researchers in order to rapidly fine-tune these tools for effective management of invaders.

Selection of Intermediate Plant Species for Restoration

Although restoration often aims to reestablish the preinvaded plant community, this may not be an immediately feasible goal if invader-induced feedbacks are strong enough to prevent the original native species from persisting long

Table 2. Feedbacks impacting invasive plants in western US rangelands

Invader, study location	What does the invader change?	How do these changes affect native vs. invasive species?	What does this mean for managing the invader?	References
Barbed goatgrass (<i>Aegilops triuncialis</i>), California	Changes soil microbial community composition on serpentine soils	Decreases growth and flowering time of <i>Lasthenia californica</i> (native forb)	Need to alter soil community for successful restoration of this native species	Batten et al. 2008
Crested wheatgrass (<i>Agropyron cristatum</i>), Great Plains region	Changes soil biota	Increases its own growth and decreases growth of some native forbs (also increases growth of the invasive <i>Bromus inermis</i>)	Consider planting native species that are relatively insensitive to soils altered by the invader	Jordan et al. 2008
Black mustard (<i>Brassica nigra</i>), California	Increases consumption of the native <i>Nassella pulchra</i> by native small mammals	Curtails establishment of <i>N. pulchra</i> within 30 m of <i>B. nigra</i> patches	May not be able to reestablish <i>N. pulchra</i> close to <i>B. nigra</i>	Orrock et al. 2008
Smooth brome (<i>Bromus inermis</i>), Great Plains region	Changes soil biota	Increases its own growth and decreases some native forbs (also increases growth of the invasive <i>Euphorbia</i>)	Consider planting native species that are relatively insensitive to soils altered by the invader	Jordan et al. 2008
Cheatgrass (<i>Bromus tectorum</i>), Great Basin	Increases fire frequency	Decreases survival of native perennials	Must decrease fire frequency for restoration of perennials	Knick and Rotenberry 1997
Cheatgrass (<i>Bromus tectorum</i>), Utah	Increases soil nitrate deep in the soil profile through leaching from litter, inhibition of nitrogen supply from soil crusts	Natives cannot access this deep-soil nitrogen source	Need to restore surface soil nitrogen availability for reestablishment of natives	Sperry et al. 2006
Italian thistle (<i>Carduus pycnocephalus</i>), California	Decreases AMF densities	Decreases growth of a native forb (<i>Gnaphalium californicum</i>); <i>C. pycnocephalus</i> grows best in soils without AMF and in nonnative soils	If species that do not maintain AMF communities invade an area, it may be difficult to restore the area to a native community that is reliant on AMF, potential for use of native AMF inoculum	Vogelsang and Bever 2009
Knapweed (<i>Centaurea maculosa</i> and <i>C. diffusa</i>), Intermountain West	Releases allelochemicals	Decreases growth of some native species, but species may be able to evolve resistance to allelochemicals over the long term	<i>Centaurea maculosa</i> and <i>C. diffusa</i> may exclude native species when they invade a new area, but plants that have been exposed to these invaders for a long time may be less affected	Blair et al. 2005
				Callaway and Aschehoug 2000
				Callaway and Vivanco 2007
				Thorpe et al. 2009

Table 2. Continued

Invader, study location	What does the invader change?	How do these changes affect native vs. invasive species?	What does this mean for managing the invader?	References
Spotted knapweed (<i>Centaurea maculosa</i>), Montana	Alters AMF function	Enhances ability for <i>C. maculosa</i> to competitively suppress <i>Festuca idahoensis</i> (native bunchgrass); <i>C. maculosa</i> parasitizes <i>F. idahoensis</i> through AMF, increasing invader growth 87–168% in presence of AMF	Further study is needed, may need to suppress or alter AMF community	Carey et al. 2004 Marler et al. 1999a, b
Leafy spurge (<i>Euphorbia esula</i>), Great Plains region	Changes soil biota	Decreases growth of native forbs, as well as other invaders	Consider planting native species that are relatively insensitive to soils altered by the invader	Jordan et al. 2008

AMF indicates arbuscular mycorrhizal fungi.
References available online at www.srmjournals.org.

enough to alter soil conditions. Instead, a multistage successional approach can be employed by initially planting species that are more tolerant of the invaded soil conditions. Once these initial plantings ameliorate the invaded soil conditions, the native community that is ultimately desired can be seeded in (Tables 2 and 3). This approach is similar to agricultural use of cover crops to disrupt pathogen cycles, increase soil fertility, and build up organic matter. In Australian grasslands, a specific grass species is used to reduce high levels of soil nitrate created by invasive species, which prevents reinvasion (Table 3). To prevent spotted knapweed reinvasion after weed control measures, plant species are being tested for resistance to knapweed's allelochemicals (Table 3). The establishment of these resistant species can prevent knapweed from reinvading and eventually facilitate the establishment of native species that are susceptible to allelochemicals.

Soil Microbial Communities as a Tool for Restoration

Soil biota can strongly affect plant success, but their manipulation is not straightforward and our understanding of these interactions is still rudimentary. Two groups that are often targeted in restoration efforts are mycorrhizal fungi and biological soil crusts (Table 3). Mycorrhizal fungi are available as a commercial inoculum, but this is primarily a tool for severely degraded sites that have little to no soil biota remaining. In systems where native plants have a stronger benefit from local mycorrhizas than do invasive plants, a local native mycorrhizal inoculum may be useful if it can be obtained. Biological soil crusts have been used as a tool to enhance native seed germination at the expense of

invasive plants and can additionally increase nitrogen availability and soil stability in degraded ecosystems. Attempts to reestablish crusts at large scales using cultured, pelleted algae have had limited success (Table 3).

Carbon Additions to Decrease Soil Nitrogen

To manage invasive species that increase nutrient availability, carbon additions (e.g., sawdust, sugar) have sometimes been used with the goal of tying up excess soil nitrogen in microbial biomass by stimulating microbial growth. Although this approach can be successful in reducing some invasive species (e.g., diffuse knapweed), its effectiveness in reducing soil nitrogen availability and controlling invasives is variable (Table 3; also see article by Alpert in this issue).

Activated Carbon to Mitigate Allelochemicals

Activated carbon, also known as activated charcoal, is often used for chemical purification and pollutant removal from water and air because of its ability to efficiently sequester organic compounds on its highly porous surface area. In soils, the effects of activated carbon are not completely understood, but it is believed to play a large role in binding allelochemicals, removing them from the soil solution, and reducing their effects on native plants. The native grass *Festuca idahoensis*, when grown with spotted knapweed, grew 85% larger with activated carbon than without (Table 3). A single application of activated carbon combined with native seed additions in ex-arable fields also reversed dominance from invasives such as cheatgrass and diffuse knapweed to natives (largely bluebunch wheatgrass). Allelochemicals generally are short-lived in the soil (hours to days),¹⁴ suggesting that activated carbon may be most

Table 3. Some potential management practices for disrupting positive plant–soil feedbacks created by invasive species

Management option	Successful management	Management limitations/ failures	References
Successional approach: rather than directly planting in desired plant community, initially plant species that can make system more amenable to native reestablishment	Use of species that can decrease soil-available nitrate, making restoration sites more resistant to reinvasion and more conducive to the persistence of desirable species	The ability of species to decrease soil nitrate may fluctuate seasonally, creating windows of opportunities for invaders	Herron et al. 2001
			Prober et al. 2005
			Prober and Lunt 2009
	Use of species that are resistant to allelochemicals (currently being tested)	Few species are resistant to allelochemicals at all life stages, so diversity of restored community may be limited initially	Alford et al. 2008
			Perry et al. 2005
	Use of species minimally impacted by invader effects on soil microbial community	Untested, based on studies that suggest that invader effects on soil microbes limit reestablishment of some natives	Jordan et al. 2008
			Vogelsang and Bever 2009
Application of commercial mycorrhizal inocula	Can increase productivity and survival of target species, reduce invasive plant fitness, and increase soil aggregation	Can also decrease target species, increase invasive species, reduce soil carbon	Reviewed in Schwartz et al. 2006
Reestablishment of biological soil crusts	Can increase soil stabilization, native seed germination, adult plant establishment, and soil nutrient availability. Various inoculation methods exist; most successful approach requires destruction of intact crusts for inoculum used to restore crusts at local scales	Mass culturing and pelletization of cyanobacteria produce crusts in lab but not in field tests; introduction of cyanobacteria cultured on cloth resulted in short-term growth at only one of five sites	Reviewed in Bowker 2007
			Buttars et al. 1998
			Kubecková et al. 2003
			Lesica and Shelly 1992
			St. Clair et al. 1984
Addition of carbon (e.g., sawdust, sugar) to decrease soil available nitrogen through microbial immobilization	Can be very effective in controlling some invaders (e.g., diffuse knapweed)	Can have no impact or increase other invaders. Carbon additions do not always decrease nitrogen (and can sometimes increase nitrogen). There may be site-specific threshold levels of carbon that must be added to decrease nitrogen	Alpert, this issue
			Blumenthal et al. 2003
			Blumenthal 2009
Activated carbon to sequester allelochemicals	Has been effective with spotted knapweed, diffuse knapweed, and cheatgrass	Can also increase invaders and/ or decrease natives. Because binding is indiscriminate, additions can decrease allelochemicals, change nitrogen availability, and alter microbial communities, making the mechanism of impact uncertain	Kulmatiski, in press
			Kulmatiski and Beard 2006
			Lau et al. 2008
			Ridenour and Callaway 2001

References available online at www.srmjournals.org.

useful to minimize the effects of invaders currently at a site. To ameliorate potential longer-term legacies of allelochemicals deposited through plant litter,¹⁴ best practices should include removing all invasive plant material from a site. Activated carbon not only binds organic substrates, but can also change soil nitrogen availability, the ratio of carbon to nitrogen in soil, and soil microbial communities, so its effects on soils and plants may be for different reasons in different trials (Table 3).

Summary

Invasive plants in western US rangelands not only greatly decrease native diversity and cover, but also compromise many ecosystem services, resulting in millions of dollars lost each year due to diminished productivity, water quantity, water quality, erosion control, and other key services. These invader-induced changes to the ecosystem can also benefit the invasive species at the expense of natives, making invasive plant control even more intractable. In cases in which invasive species cause positive feedbacks, simply eradicating invaders will only lead to reinvasion. Thus, management needs to go beyond basic invader control by reversing the changes invaders make to ecosystem properties, with a particular emphasis on soils. There is considerable variation in effects of invasive species across sites and time and our understanding of feedbacks and their management is still developing. Yet there are some underexploited tools that show promise in disrupting plant–soil feedbacks and collaborations between managers and researchers can accelerate our understanding and control of these feedbacks.

Acknowledgments

Eviner was supported by the National Research Initiative of the USDA Cooperative State Research, Education, and Extension Service Managed Ecosystems Program grant 2007-55101-18215, and Weedy and Invasive Species Program grant 2006-55320-17247. Hawkes was supported by the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service Managed Ecosystems Program, grant 2006-35101-16575. Hoskinson was supported by the California Department of Food and Agriculture Weed Management Area Program, grant 08-0610.

References

1. DUNCAN, C., AND J. K. CLARK [EDS.]. 2005. Invasive plants of range and wildlands and their environmental, economic,

- and societal impacts. Lawrence, KS, USA: Weed Science Society of America. 222 p.
2. BELNAP, J., AND S. L. PHILLIPS. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* 11:1261–1275.
3. DiTOMASO, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Science* 48:255–265.
4. GERLACH, J. D. 2004. The impacts of serial land-use changes and biological invasions on soil water resources in California, USA. *Journal of Arid Environments* 57:365–379.
5. EHRENFELD, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503–523.
6. VAN DER PUTTEN, W. H., R. D. BARDGETT, P. C. DE RUITER, W. H. G. HOL, K. M. MEYER, T. M. BEZEMER, M. A. BRADFORD, S. CHRISTENSEN, M. B. EPPINGA, T. FUKAMI, L. HEMERIK, J. MOLOFSKY, M. SCHADLER, C. SCHERBER, S. Y. STRAUSS, M. VOS, AND D. A. WARDLE. 2009. Empirical and theoretical challenges in aboveground–belowground ecology. *Oecologia* 161:1–14.
7. STRAYER, D. L., V. T. EVINER, J. M. JESCHKE, AND M. L. PACE. 2006. Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution* 21:645–651.
8. EVINER, V. T., AND C. V. HAWKES. 2008. Embracing variability in the application of plant–soil interactions to the restoration of communities and ecosystems. *Restoration Ecology* 16: 713–729.
9. EHRENFELD, J. G., B. RAVIT, AND K. ELGERSMA. 2005. Feedback in the plant–soil system. *Annual Review of Environment and Resources* 30:75–115.
10. REINHART, K. O., AND R. M. CALLAWAY. 2006. Soil biota and invasive plants. *New Phytologist* 170:445–457.
11. KULMATISKI, A., AND P. KARDOL. 2008. Getting plant–soil feedbacks out of the greenhouse: experimental and conceptual approaches. *Progress in Botany* 69:449–472.
12. KULMATISKI, A., K. H. BEARD, J. STEVENS, AND S. M. COBBOLD. 2008. Plant–soil feedbacks: a meta-analytical review. *Ecology Letters* 11:980–992.
13. KULMATISKI, A., K. H. BEARD, AND J. M. STARK. 2004. Finding endemic soil-based controls for weed growth. *Weed Technology* 18:1353–1358.
14. REIGOSA, M. J., N. PEDROL, AND L. GONZALEZ. 2006. Allelopathy: a physiological process with ecological implications. Dordrecht, Netherlands: Springer. 637 p.

Authors are Assistant Professor, Dept of Plant Sciences, University of California, Davis, CA 95616, USA, veviner@ucdavis.edu (Eviner); Graduate Student, Graduate Group in Ecology, University of California, Davis, CA 95616, USA (Hoskinson); and Assistant Professor, Section of Integrative Biology, University of Texas, Austin, TX 78712, USA (Hawkes). Additional references available online at www.srmjournals.org.