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Plant invasions in western North America : implications for temperate grasslands worldwide

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Key points : To varying degrees, temperate grasslands world-wide have become invaded by non-native plants and animals, products of both accidental and deliberate introductions. The susceptibility of these grasslands has been strikingly different and not strictly a function of the intensity of human occupation. Grasslands dominated by rhizomatous-spreading grasses have generally been more resilient to disturbance and plant invaders, while those in which caespitose grasses dominate have displayed decidedly lower resilience to agriculture, particularly the combined forces of farming and livestock. As outlined here, the fate of the steppe in the Intermountain West of North America in the last 100 years is emblematic of the severity of damage that results from a radical change in the disturbance regime in a temperate caespitose-dominated grassland, coupled with an onslaught of alien species pre-adapted to these new factors (Mack , 1986, 1989).

Temperate grasslands in the Intermountain West of the United States occur in a region with diverse geomorphology bounded east and west by the Rocky Mountains and the Sierra Nevada , respectively , and north and south by the forested northern Rocky Mountains and the Sonoran Desert , respectively . Several smaller mountain ranges and other highlands occur within this region , such as the Blue Mountains and the Owyhee Plateau , which support both forests and grassland . Grasslands within what is commonly referred to as the Great Basin and its extensions are steppe , i.e., grasslands dominated by perennial grasses on zonal soils too dry to support trees (Mack , 1986) .

Vulnerability of this steppe to plant invasion is largely attributable to the dominant grasses consistent life form as caespitose (bunchgrass) grasses. These grasses (e.g. *Pseudoroegneria spicata [A gropyron spicatum]*, *Festuca idahoensis*, *Poa secunda*) are characterized by spreading exclusively by seeds; none are rhizomatous, and all are readily damaged by recurring grazing, trampling and other physical damage by large, congregating mammals. Their persistence in the Great Basin steppe owed much to the general lack of herds of large, congregating mammals (e.g. elk, antelope and particularly bison) throughout most of the Holocene (Mack and Thompson, 1982). As a result of bison s paucity in the Great Basin-in sharp contrast to the massive herds that migrated across the temperate grasslands east of the Rockies-these communities were characterized by a canopy of caespitose grasses along with shrubs (e.g. *A rtemisia* spp., *Chrysothamnus nauseosus* and *Purshia tridentata*), overlying a low stature assembly of herbs (e.g. *A stragulus* spp., *Balsamorhiza sagittata*, *Lomatium* spp., *Lupinus* spp.). Conspicuous in the undisturbed communities was a carpet of cryptogams (mosses, lichens, liverworts and cyanobacteria) (Daubenmire, 1970).

These steppe communities , whether shrub/grass dominated or grass dominated and regardless of floristic composition , were swiftly and catastrophically altered beginning in the mid to late 19^{th} century by the almost simultaneous entry of alien species : livestock (principally cattle , but also sheep and horses) along with a growing assembly of non-native grasses , herbs and some shrubs (Mack , 1981 , 1986 ; Mack and Thompson , 1982) . Livestock largely destroyed these communities through grazing , manuring , wallowing , congregating and especially trampling .So fragile is the cryptogamic crust that usually a single episode of intense community occupation by livestock is sufficient to destroy these exceptionally slow growing organisms . The caespitose grasses and shrubs are only marginally more tolerant of routine damage by livestock than the cryptogams .Recurring removal of flowering culms by grazers restricts the grasses sole mode of persistence on a site through sexual reproduction . Trampling dismembers the adult grasses into fragments from which regeneration is unlikely . Native shrubs , such as *Artemisia* spp ., while varying in their palatability to livestock , are probably more damaged through severe trampling ; for example sagebrushes do not re-sprout after breakage . None of these community dominants displays consistently high seedling recruitment each year , which exacerbates the loss of seeds to livestock (Mack and Thompson , 1982 ; and references therein) .

None of this widespread damage by livestock would probably have caused the wholesale alteration of these ecosystems physical features had the other group of alien species-grasses , herbs and some shrubs-not arrived . Most of these alien plant species (e . g . *Elymus caput-medusae* , *Halogeton glomeratus* , *Salsola iberica* , *Sisymbrium altissimum*) are native to Eurasia , a huge source region for species long associated with humans and their livestock and cereal agriculture (Mack , 1986 , 1989) . Most of these species were likely introduced accidentally as contaminants in cargo , livestock bedding and perhaps livestock fur and fleeces (although the role of this last dispersal mode may be largely apocryphal) (Mack , 1981 , 1986) . The most damaging of these invaders , the annual grass *Bromus tectorum* (cheatgrass) , most likely arrived repeatedly (Novak and Mack , 1991) as a seed contaminant in wheat seeds because the northern portion of the Great Basin was converted to cereal agriculture (wheat , barley , oats) in the last quarter of the 19th century , site of the first regional detection of cheatgrass (Mack , 1981) .

Cheatgrass and other plant invaders capitalized on the ongoing disturbance caused by livestock in steppe that had previously had a much lower level of animal disturbance (mainly trampling by small herds of deer, elk and antelope, local burrowing by ground

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squirrels, mice, and other small mammals) (Mack and Thompson, 1982). Unlike the native species, these alien plants thrive with recurring disturbance. They rapidly supplanted the destroyed or damaged native species locally and have transformed these steppe communities into almost entirely alien plant communities (Daubenmire, 1970; Mack, 1986). The rate at which these invasions and the consequent transformations occurred ranks as one of the swiftness known through biological invasion : within less than 40 years, for example, the Columbia Basin of Washington became dominated by the annual Eurasian grass B. *tectorum* (Mack, 1981). It has been joined by other alien species, that while not necessarily invasive, have directly benefited from the demise of the native steppe : e.g. *Avena fatua*, *Cirsium vulgare*, *Erodium cicutarium*, *Poa pratensis* (Mack, 1986), 1989). Although species, such as the annual cheatgrass, provide little competition for the large, long-lived native grasses and shrubs, they are superior competitors to the seedlings of these native species. Cheatgrass, for instance, resumes growth from its over-wintering stage weeks before many of the native species even germinate. Its head start in root growth allows it to usurp the limited soil water, thereby placing a consistent constraint in seedling survival (Harris, 1967). Consequently, as adult native plants die, they are no longer replaced in the community by their offspring.

Almost insidiously, species such as cheatgrass not only thrive in the disturbance created by livestock and the annual plowing with cereal agriculture, they have also provided the *coup de grace* to the natives by so completely altering the region s fire regime. Fire was a component of pre-European settlement ecosystems in the Intermountain West. But the frequency (increased from once every 40-50 yrs to fires every decade or less) has consistently destroyed the native species. These fires have been particularly devastating to the seed banks of natives, assuming that any adult plants survive spring/summer fires to flower (Knick and Rotenberry, 1997; and references therein). In contrast, invasive species, such as cheatgrass are not damaged as extensively and some of their seeds always survive these conflagrations. In effect, the emergence of cheatgrass within the region s steppe communities has served as a positive feedback mechanism in which more than a century of recurring fires has completed the demise of the native steppe that began with arrival of livestock and was furthered by introduction of cereal agriculture.

The regional destruction of temperate grassland is not yet complete-some small fragments of the original steppe that were never plowed or used by livestock remain . But in sum , these are pathetically small remnants of an array of communities that stretched across hundreds of thousands of square kilometers in North America . And new hazards , in the form of more recently introduced alien plants continue . In the last 40 years members of the genus *Centaurea* (Asteraceae) have become increasingly important in the northern half of the Great Basin . Unlike cheatgrass and some other alien grasses , these dicots are completely unpalatable by livestock because of their stiff , dense spines ; they consequently render a paddock totally unusable (Roche and Roche , 1988) . It is not clear yet whether one or more *Centaurea* spp . or some other invader will replace the current regional dominant , cheatgrass . There is no assurance of course that even more destructive alien species could arrive , either accidentally or through some deliberate plant introduction .

Restoration of these grasslands has been an object of concern for more than 100 years. By 1904, some observers deemed the destruction of the native range species as already irreversible (Cotton, 1904) and attempts have followed to find non-native species that could tolerate the region s physical environment and the new biotic/physical environment imposed by ranching and farming. The purported solutions have ironically also drawn on Eurasian species, such as *A gropyron desortorum*, which have been deemed satisfactory for livestock forage (Asay et al., 2003; Huber-Sannwald and Pyke, 2005). Widespread sowing of these species has been problematic at best. Quite aside from their value as forage, some of these species have not been persistent where sown, thereby requiring costly and recurring re-sowing. Alternatively, they have elsewhere spread beyond the area for which they were intended. More fundamentally, these are non-native species introduced and fostered to take up roles on sites than long supported native steppe. Still missing is an informed public discussion of the fate of these regional grasslands. Should they be restored to some resemblance of their native composition and structure? Or will they ultimately become simply artificial ecosystems in which any species community membership is decided by strictly anthropocentric values (sustained , low cost livestock production , minimal fire risk , fragmentation of land parcels for diverse human use , and no attention to the conservation of native plants and animals) ?

These are not questions unique to the Intermountain West. Each temperate grassland, whether in the Great Plains of North America, the steppe in Patagonia, or even the now changing steppe in Mongolia, will be viewed in the context of highly varied human values and aspirations for land use. These grasslands are universally viewed as essential to humans because of their roles in food production. The question will be whether society in the broadest sense will have the wisdom and will to view native steppe as more than simply the one-time place-holders for highly restricted communities that serve only humans immediate interests.

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