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Natural and land-use history of the Northwest mountain ecoregions (USA) in relation to patterns of plant invasions

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Abstract

Although the Northwest currently has the least proportion of non-native invasive plant species relative to other regions of North America, invasions continue to increase into the mountainous areas of the region. Landscape structure, such as the variation found along the complex gradients of the Northwest mountain ecoregions, affects the expansion of invasive plant species and the invasibility of plant communities. Also, the history of land use and current use patterns affect the expansion of invasive plants, and many of the deteriorated environments in the region's mountains may invite and stabilize plant invasions. We examined the patterns of invasive plant diversity in Northwest mountain ecoregions, as derived from literature sources, to analyze which factors influence plant invasions. Our analysis found altered riparian systems and disturbed forests to be especially vulnerable to plant invasion. Conversely, alpine and wilderness areas are still relatively unaffected by invasive plants. Both riparian and alpine communities, while making up a relatively small area across Northwest mountain ecoregions, have significant ecological importance and deserve special protection from invasive plant introductions. Human settlement at low elevations and intense land use of upland forests will likely continue to enhance invasive plant introductions into Northwest mountain ecosystems. Knowledge of the relationships between biological and environmental factors, disturbance, and human land use will be critical for future management strategies that proactively locate, prevent, or contain plant invasions in the mountains of the Northwest.
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Keywords: Exotic plants; Invasive plant management; Landscape change; Mountain ecosystems; Pacific Northwest; Settlement history

Introduction

Plant invasions often occur across broad landscapes, but how spatial pattern affects the various stages of the invasion process is not well known (With, 2002). Landscape structure, such as found along the complex gradients of mountain ecoregions, will likely affect the future expansion of invasive plant species and the invasibility of plant communities. Thus, understanding the landscape patterns of non-native plant invasions in mountain ecoregions, especially as they interact with the

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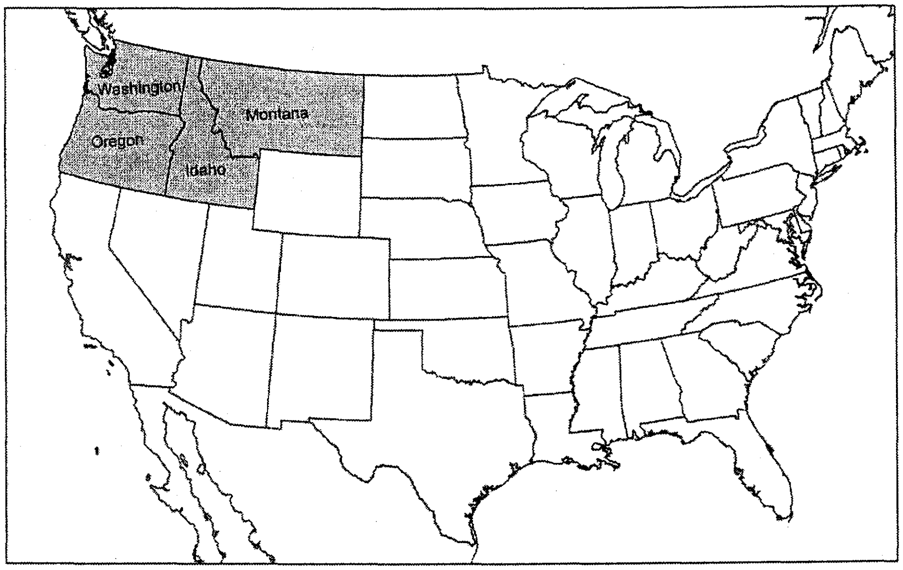

Fig. 1. Position of the Northwest in the conterminous US.

dynamics that follow local disturbance, affords new insights for managing plant invasions.

The states of Oregon, Washington, Idaho, and western Montana occupy the far northwest corner of the contiguous US and form the 'Northwest' (Fig. 1; Jackson and Kimerling, 2003). The Northwest is a region of shared history, wilderness, and natural areas that is exceptionally rich in agricultural, forest, and fishery resources. An increasing concern to land managers is the invasion and expansion of non-native plant species into the mountain ecoregions of the Northwest. We consider the mountainous ecoregions of the Northwest to be the Cascade Province (M242; Bailey, 1995), which includes the Pacific Coast, Cascade, and Olympic Mountain ranges; portions of the Sierran Steppe Province (M261) that encompasses the Klamath and Siskyou ranges in southern Oregon; all of the Middle Rocky Mountains Province (M332), which includes the Blue Mountains, Salmon River Mountains, and ranges of southwestern Montana; part of the Northern Rocky Mountain Province (M333); and the portion of the Southern Rocky Mountain Steppe Province (M331) that extends throughout the Greater Yellowstone Ecosystem (Fig. 2). Bailey (1995) provides detailed descriptions of the biogeoclimatic conditions of these provinces.

The specific goals of this paper are to (1) examine the geographic patterns of invasive plant diversity in Northwest mountain ecoregions, as derived from literature sources; (2) suggest apparent biogeographic factors that influence patterns of plant invasion; (3) examine the influence of disturbance on the distribution of invasive plants within the ecoregions; and (4) evaluate the susceptibility of native plant communities to plant invasions by spatially integrating plant distributions with elevation and land cover of the ecoregions.

This review focuses on the status of non-native plant invasions in Northwest mountain ecoregions. We also discuss how natural and land-use history influences plant invasion. We first present an overview of the settlement history and general land uses for the Northwest. We then introduce the general characteristics of the ecoregions and present important gradients across these areas as they relate to non-native plant invasions. Although the available literature is disproportionate among the ecoregions, we indicate plant species that are of particular concern under specific environmental conditions or management circumstances. With this background, we characterize each ecoregion emphasizing differences and commonalities among them and how these characteristics interact with local observations of plant invasions. In synthesis, we analyze the susceptibility of particular land-cover types, or habitats, to plant invasion, and discuss these findings with respect to landscape ecology and land uses. Areas are pointed out where additional research is needed to better understand the factors that affect plant invasions and their management in mountain ecoregions.

History, general land uses, and trends in non-native plant invasions

After the well-known Lewis and Clark expedition in 1805–1806 (Phillips, 2003), settlers of European origin from the eastern US began to occupy the Northwest. The arrival of railroads in the mid- to late-19th century

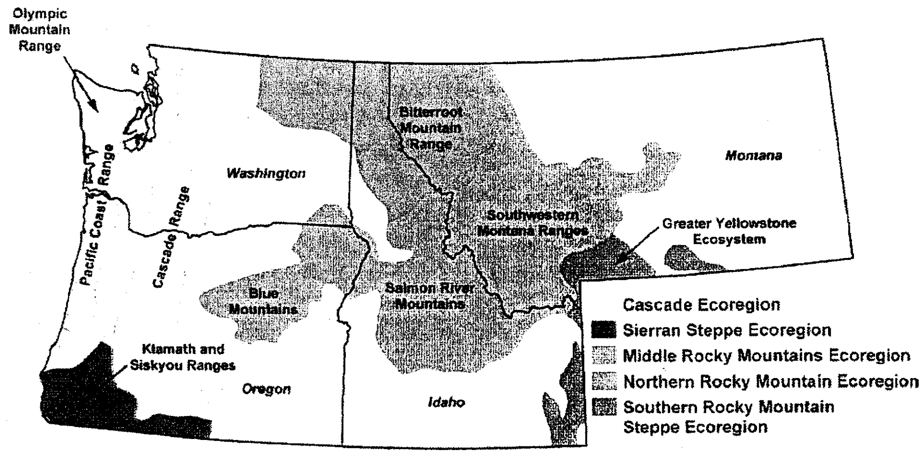

Fig. 2. A map of the mountainous ecoregions of the Pacific Northwest. The associated Bailey's ecoregion boundaries are shown (Bailey, 1995). Ecoregions included are: M242, Cascade; M261, Sierran; M332, Middle Rocky Mountains; M333, Northern Rocky Mountains; M331, Southern Rocky Mountains.

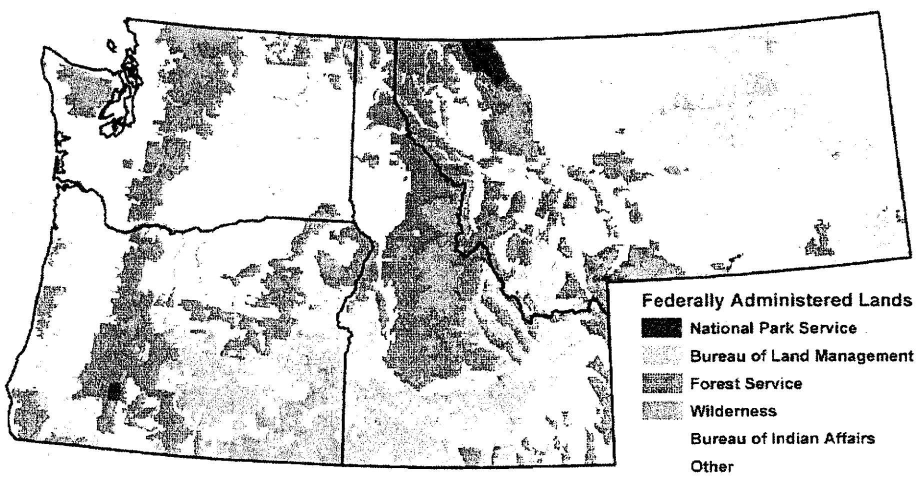

Fig. 3. Land under federal ownership in the Northwest.

made farming and industrial mining possible to satisfy the resource demands of the industrial revolution in Europe and the eastern US. The combined mining and agricultural boom drew an extremely diverse ethnic population to Northwest towns and cities. At about the same time, livestock-raising spread across the federal grasslands of the region, which foreshadowed high-plains cattle and sheep ranching, and the wheat farming industry. Timber was harvested as both an obstacle to agriculture and a natural resource that became an important industry in the Northwest (Franklin and Dyrness, 1988).

Land ownership still shapes the geographic, socio-economic, and environmental landscapes of the Northwest. Over 80% of the now 12 million people in the region live in metropolitan areas (US Census Bureau, 2000). People in these large population centers dominate politics in each state, especially concerns about environmental preservation and land-use planning. Rural land use and low human population density characterize areas that are predominately federal lands, which still have the traditional resource-based economy of agriculture, timber, livestock ranching, and mining. Federal government agencies manage much of the region as national forests, rangelands, parks, monuments, and wilderness (Fig. 3). Some smaller communities, particularly along the foothills of the mountains, have become attractive locations for new residents interested in retirement, recreation, and tourism. About 40% of federal lands provide primitive or semi-primitive recreational opportunities (Quigley and Arbelbide, 1997) to people who live in or visit the region.

The Northwest landscapes encountered 200 years ago by Lewis and Clark are vastly transformed by the trail of non-native plants that arrived, either accidentally or deliberately, with the people who settled the region. Many invasions of non-native plants established in the Northwest between 1850 and 1920 during the region's great influx of agrarian settlers. Port cites such as Portland, Oregon, and Seattle, Washington were notable entry points for foreign plants. Historically, trade vessels brought grain and livestock shipments contaminated with foreign seeds, while freighters dumped huge ore deposits and ship ballast laden with foreign plant material onto the shores and around docks of these cities (Kartesz, 1999). Timber production, livestock ranching, and farming activities throughout the region continue to provide endpoints for introduction and subsequent seed dispersal, as well as the environmental disturbance that enhances germination and establishment of non-native plant species (Mack, 1986; Wilcove, 1989; Toney et al., 1998; Saunders et al., 1991; Wooten and Morrison, 1995).

Rejmanek (2000) indicates that more than 21% of the 22000 vascular plant species found in North America are non-native. However, the proportion of non-native species is least in the mountain Northwest compared to other North American regions (Withers et al., 1999). Rice (2005) lists 183 non-native plants that occur in the Northwest that are considered noxious – species specified by law as being especially undesirable, troublesome, or difficult to control. Mountains, in general, have fewer non-native plant introductions relative to lowland areas in the region. The prevalent system of national parks and forests are believed to account for this paucity of non-native plant invasions relative to lowlands because early establishment of areas with low human impact probably restricted plant introductions. Nonetheless, plant invasions occur in the mountains, and land-use and land-cover change has undoubtedly been the underpinning for the successful establishment of these plant species.

Analysis

Knowing the susceptibility of different plant communities to plant invasion provides insight on non-native plant spread and can help design programs to manage non-native plants or restore native habitats. In Table 1, we explore the relationship between vegetation type, elevation, and disturbance on the presence of non-native plants in each ecoregion. The Invaders database (Rice and Rider, 1995; Rice, 2005), which contains nearly 10,000 records of invasive plant presence ranging over 76 plant communities across five Northwest states, was used in this analysis (Table 1). We combined these plant communities into six general vegetation cover types based on elevation (alpine to low upland forests and grasslands; Burns and Honkola, 1990), and proximity to water, i.e., riparian areas. A susceptibility rating for each vegetation type to the non-native plants listed in the database for each ecoregion was then made following Rice (2005) and Rice and Rider (1995). The susceptibility ratings are 'U' (uninvaded by non-native plant), 'I' (invasible without disturbance), or 'D' (invasible when the intact vegetation is disturbed).

We then calculated the floristic similarity of non-native plants listed in Table 1 among and within ecoregions using Sörensen's community similarity index. The Sörensen community similarity index is a measure of community similarity between two sites, or as is the case here, between two different elevation-based vegetation cover types. The Sörensen community similarity index was calculated using the equation: $2C/(N_1+N_2)$, where C is the number of non-native species in common between the communities, and N_1 and N_2 are the total number of non-native species of the two separate communities. To determine the similarity of non-native species among the different ecoregions, the Sörensen's index was calculated by comparing the species in common of each ecoregion at each of the six vegetation cover types. To determine the similarity of non-native species within an ecoregion, the index was calculated by comparing the similarity of non-native species occurring along the vegetation cover types with an individual ecoregion.

We then examined the susceptibility of plant communities more closely by integrating data from Rice (2005) and Rice and Rider (1995) with a land-cover map of Oregon (Northwest Habitat Institute, 1998). Thus, the susceptibility of particular land-cover types, or habitats, to invasion in the mountain ecoregions of Oregon was determined. Taxonomic information related to plants non-native to the Northwest that are referenced in this paper can be found on the National PLANTS Database (USDA, NRCS, 2005).

Climate and physiography, natural vegetation, land uses, and plant invasions of Northwest mountain ecoregions

Variation in climate, elevation, soils, and topography contributes to differences in vegetation that distinguish each ecoregion. A climatic gradient across the Northwest exists from west to east beginning at the Pacific Ocean. Climate is wettest and mildest at the Pacific Coast, which becomes drier and cooler toward the interior of the region (Fig. 4). Winter rain and snow provide most of the precipitation throughout the Northwest.

Conifers generally dominate Northwest mountains, except along rivers and streams where they are replaced by broadleaf species of *Populus* and *Alnus*. Dense, moist

Table 1. Land-cover susceptibility to non-native invasive plants in the Northwest

	Cascade						Sierran Steppe						Mid-Rocky Mountains						Rocky Mountains					
	A	S	H	M	L	R	A	S	H	M	L	R	A	S	H	M	L	R	A	S	H	M	L	R
Abutilon theophrasti	D	D	D	D	D	D		D	D	D	D	D		D	D	D	D	D	D	D	D	D	D	D
Acroptilon repens	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
*Agrostis gigantea**				I	I	I						I						I		I	I	I	I	I
*Ailanthus altissima**				I	I	I					I	I					I	I					I	I
Anchusa officinalis	D	D	D	D	D	D		D	D	D	D	D		D	D	D	D		D	D	D	D	D	D
Anthriscus sylvestris						D						D						D						D
Arctium minus	D	D	D	D	D	I		D	D	D	D	I	U	D	D	D	D	I	D	D	D	D	D	I
Artemisia absinthium	D	D	D	D	D	I		D	D	I	D	I	U	D	D	I	D	I	D	D	D	I	D	I
Azolla pinnata						D						D						D						D
*Bromus inermis**					D	D					D	D		D	D	D	D	D		D	D	D	D	D
*Bromus japonicus**					I	I				I	I	I				I	I	I				I	I	I
Bromus tectorum	D	I	D	D	I	D		I	D	I	I	D	D	I	D	I	I	D	D	I	D	I	I	D
Bryonia alba	D	D	D	D	D	D		D	D	D	U	D	U	D	D	D	D	D	D	D	D	D	D	D
Cardaria draba	D	D	D	D	D	D		D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D
Cardaria pubescens	D	D	D	D	D	D		D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D
Carduus acanthoides	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
Carduus nutans	D	I	D	I	I	I		I	D	I	I	I	D	I	D	I	I	D	D	I	D	I	I	I
Cenchrus longispinus	D	D	D	D	D	D		D	D	D	D	D		D	D	D	D	D	D	D	D	D	D	D
Centaurea biebersteinii	D	D	D	D	I	I		D	D	I	I	I	U	D	D	I	I	I	D	D	D	I	I	I
Centaurea debeauxii	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
Centaurea diffusa	D	D	D	D	I	D		D	D	D	D	D	U	D	D	D	I	D	D	D	D	D	I	D
Centaurea juncea x *nigra*	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D		D	D	D	D	D	D
Centaurea nigra	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D		D	D	D	D	D	D
Centaurea nigrescens						D						D						D						D
Centaurea solstitialis	D	D	D	D	D	I		D	D	D	D	I	D	D	D	D	D	I	D	D	D	D	D	I
Centaurea triumfettii	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
Chondrilla juncea	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	U	D	D	D	D	D	D
Cirsium arvense	D	I	I	I	I	I		I	D	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Cirsium vulgare	D	I	D	I	I	I		I	D	I	I	I	D	I	D	I	I	D	D	I	D	I	I	I
Conium maculatum	D	D	D	D	D	I		D	D	D	D	I	U	D	D	D	D	I	D	D	D	D	D	I
Convolvulus arvensis	D	D	D	D	D	I		D	D	D	D	I	U	D	D	D	D	I	D	D	D	D	D	I
Crupina vulgaris	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	U	D	D	D	D	D	D
Cuscuta approximata	U	U				D		U				D	U	U				D	U	U				D
Cuscuta spp.	U	U				D		U				D	U	U				D	U	U				D
Cynoglossum officinale	D	I	D	D	I	I		I	D	I	D	I	U	D	D	I	I	I	D	I	D	I	I	I
Cyperus esculentus						D						D						D						D
Cytisus scoparius	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
*Dactylis glomerata**			D	D	D	D				D	D	D					D	D					D	D
Daucus carota	D	D	D	D	D	I		D	D	D	D	I	U	D	D	D	D	I	D	D	D	D	D	I
Echium vulgare	D	D	D	D	D	D		D	D	D	D	D		D	D	D	D		D	D	D	D	D	D
Egeria densa	U	D	U	D	D	I		U	U	U	U	I	U	U	U	U	U	I	U	U	U	U	U	I
Eichhornia azurea						D						D						D						D
Elymus repens	D	I	D	D	D	I		I	D	I	D	I	D	I	D	I	D	I	D	I	D	I	D	I
Emex spinosa						D						D						D						D
Equisetum arvense	D	D	D	D	D	I		D	D	D	D	I	D	D	D	D	D	I	D	D	D	D	D	I
Equisetum telmateia					U	I						I					U	I					U	I
Euphorbia esula	U	D	D	D	I	I		D	D	D	I	I	U	D	D	D	I	D	U	D	D	D	I	I
Gypsophila paniculata	D	D	D	D	D	D		D	D	D	D	D		D	D	D	D		D	D	D	D	D	D
Halogeton glomeratus	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	U	D	D	D	D	D	D
Hemizonia pungens	D	D	D	D	D	D		D	D	D	D	D		D	D	D	D		D	D	D	D	D	D
Heracleum mantegazzianum						D						D						D						D
Hibiscus trionum	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D		D	D	D	D	D	D
Hieracium aurantiacum	D	D	D	D	D	I		D	D	D	U	I	D	D	D	D	U	I	D	D	D	D	U	I
Hieracium caespitosum	U	D	D	D	D	I		D	U	D	U	I	U	D	D	D	U	D	U	D	D	D	U	I
Hydrilla verticillata		D		D	D	I						I					U	I					U	I

Table 1 (*continued*)

	Cascade						Sierran Steppe						Mid-Rocky Mountains						Rocky Mountains					
	A	S	H	M	L	R	A	S	H	M	L	R	A	S	H	M	L	R	A	S	H	M	L	R
Hyoscyamus niger	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
Hypericum perforatum	D	I	D	I	I	I		D	D	I	D	I	U	D	D	I	I	I	D	D	D	I	I	I
Hypochaeris radicata	D	D	D	D	D	I		D	D	D	D	I	U	D	D	D	D	I	D	D	D	D	D	I
Isatis tinctoria	D	D	D	I	I	D		D	D	D	I	D	U	D	D	I	I	D	D	D	D	D	I	D
Kochia scoparia	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
Lagarosiphon major		D		D	D	I						I					U	I					U	I
Lepidium latifolium	D	D	D	D	D	I		D	D	D	D	I	U	D	D	D	D	D	D	D	D	D	D	I
Leptochloa chinensis						D						D						D						D
Leucanthemum vulgare	D	I	D	I	I	I		I	D	D	D	I	D	I	D	D	D	I	D	I	D	D	D	I
Limnophila sessiliflora						D						D						D						D
Linaria dalmatica	D	D	D	D	D	D		D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D
Linaria vulgaris	D	D	D	D	D	I		D	D	D	D	I	D	D	D	D	D	I	D	D	D	D	D	I
Lythrum salicaria	U	D	U	D	D	I		D	U	U	U	I	U	D	U	D	U	I	U	D	U	U	U	I
*Medicago lupulina**			D	D	D	D			D	D	D	D			D	D	D	D			D	D	D	D
*Melilotus officinalis**				D	D	D				D	D	D				D	D	D				D	D	D
Mirabilis nyctaginea	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D		D	D	D	D	D	D
Monochoria hastata						D						D						D						D
Monochoria vaginalis						D						D						D						D
Myriophyllum aquaticum	U	D	U	D	D	I		U	U	U	U	I	U	U	U	U	U	I	U	U	U	U	U	I
Myriophyllum spicatum	U	D	U	D	D	I		U	U	U	U	I	U	U	U	U	U	I	U	U	U	U	U	I
Nardus stricta						D						D						D						D
Onopordum acanthium	U	D	D	D	D	D		U	D	D	D	D	U	D	D	D	D	D	U	D	D	D	D	D
Opuntia aurantiaca	U	U		U	D	U		U				U	U	U			D	U	U	U			D	U
Orobanche spp.						D						D						D						D
Oryza longistaminata						I						I						I						I
Oryza punctata						I						I						I						I
Oryza rufipogon						I						I						I						I
Ottelia alismoides		D		D	D	I						I					U	I					U	I
Panicum miliaceum	D	D	D	D	D	D		D	D	D	D	D		D	D	D	D		D	D	D	D	D	D
Paspalum scrobiculatum						I						I						I						I
*Phleum pratense**					D	D					D	D			D	D	D	D			D	D	D	D
*Poa pratensis**			D	D	D	D			D	D	D	D			D	D	D	D		D	D	D	D	D
Polygonum cuspidatum	U	D	D	D	D	D		U	D	D	U	D	U	D	D	D	U	D	U	D	D	D	U	D
Potentilla recta	D	D	D	D	I	I		D	D	I	I	I	D	D	D	I	I	I	D	D	D	I	I	I
Proboscidea louisianica						D						D						D						D
Rorippa sylvestris		D		D	D	I					U	I					U	I					U	I
*Rubus discolor**						I						I						I						I
Rubus fruticosus agg.						D						D						D						D
Rubus moluccanus						D						D						D						D
Sagittaria sagittifolia	U	D	U	D	D	I		U	U	U	U	I	U	U	U	U	U	I	U	U	U	U	U	I
Secale cereale	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
Senecio jacobaea	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
Silene latifolia	D	D	D	D	D	D		D	D	I	D	D	U	D	D	I	D	D	D	D	D	I	D	D
Silybum marianum	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D		D	D	D	D	D	D
Solanum dulcamara	D	D	D	D	D	I		D	D	D	D	I	U	D	D	D	D	I	D	D	D	D	D	I
Solanum rostratum	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
Sonchus arvensis	D	D	D	D	D	I		D	D	D	D	I	D	D	D	D	D	I	D	D	D	D	D	I
Sorghum halepense	D	D	D	D	D	I		D	D	D	D	I	U	D	D	D	D	I	D	D	D	D	D	I
Sparganium erectum						D						D						D						D
Spartina anglica						D						D						D						D
Sphaerophysa salsula						D						D						D						D
Stratiotes aloides					U	D						D					U	D					U	D
Taeniatherum caput-medusae	D	D	D	D	D	D		D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D
*Tamarix ramosissima**						I						I						I						I
Tanacetum vulgare	D	D	D	D	D	I		D	D	D	D	I	U	D	D	D	D	I	D	D	D	D	D	I

Table 1 (*continued*)

	Cascade						Sierran Steppe						Mid-Rocky Mountains						Rocky Mountains					
	A	S	H	M	L	R	A	S	H	M	L	R	A	S	H	M	L	R	A	S	H	M	L	R
*Taraxacum laevigatum**	D	D	D	I	I	I		D	D	D	I	I	D	D	D	D	I	I	D	D	D	I	I	I
Taraxacum officinale agg. *	D	D	D	I	I	I		D	D	D	I	I	D	D	D	D	I	I	D	D	D	I	I	I
Tribulus terrestris	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
Tripleurospermum maritima	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
Ulex europaeus	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D
*Ventenata dubia**										D	D					D	D					D	D	
Verbascum thapsus	D	I	D	I	I	I		I	D	I	D	I	U	I	D	I	I	I	D	I	D	I	I	I
Xanthium spinosum	D	D	D	D	D	D		D	D	D	D	D	U	D	D	D	D	D	D	D	D	D	D	D

Ecoregions are Cascade, Sierran Steppe, Middle Rocky Mountains, and Northern and Southern Rocky Mountains combined. Vegetation types are composed from the plant communities listed in Rice (2005) and Rice and Rider (1995) and grouped according to elevation or proximity to water (Burns and Honkola, 1990). Vegetation types are alpine (A), subalpine (S), high (H), middle (M), or low (L) upland forests and grasslands, and riparian areas (R). Susceptibility categories of vegetation types are uninvaded by non-native plants (U), invasible without disturbance (I), and invasible with disturbance (D). Susceptibility ratings are identical to those found in Rice (2005) and Rice and Rider (1995) except in cases where an asterisk occurs after the plant name indicated the susceptibility rating were derived from USDA Forest Service Fire Effects Information System: http://www.fs.fed.us/database/feis/plants/weed/index.html. A blank in a column indicates that either no or insufficient information exists for that species and vegetation type.

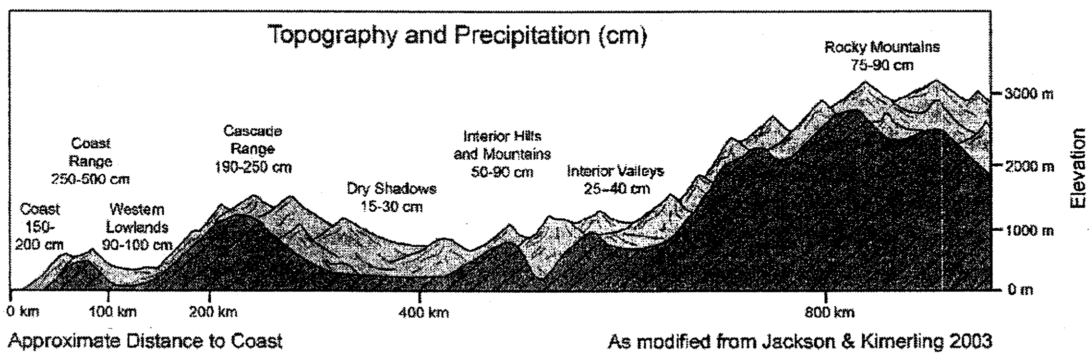

Fig. 4. A linear transect drawn about 1000 km from west to east along the 45th parallel includes climate types that range from the mild marine environments of the Pacific Coast to the continental climates of the Rocky Mountains. In between are found the Mediterranean-like climes, steppes and deserts.

forests of primarily *Tsuga heterophylla* and *Pseudotsuga menziesii* predominate the western edge of the Cascade Province. However, the Sierran Steppe Province supports a diverse mixture of drought-tolerant conifers and hardwoods, a result of lower precipitation and geological and ecological history. Moving eastward, increased aridity, and fire frequency promote open, park-like stands of *Pinus ponderosa*, *Pinus contorta*, and *Larix occidentalis* in the Northern and Middle Rocky Mountain Provinces and Greater Yellowstone Ecosystem.

Cascade Ecoregion

Climate and physiography

The Cascade Ecoregion (M242; Bailey, 1995; Fig. 2) is characterized by three steep, rugged mountain ranges that run north to south along the westernmost portion of the region. The Coast Range and Olympic Mountains rise 1500 m above sea level, with a local relief of 300–900 m. The more interior Cascade Range has mountains 2400–2700 m in altitude, dominated every 8–135 km by a volcano of much higher elevation. Mt. Rainier, in the Cascades, e.g., rises more than 4300 m above sea level. Areas throughout the three mountain ranges have been glaciated. Western Washington and Oregon (Fig. 4) are maritime in climate with mild temperatures and prolonged cloudy periods, wet mild winters and cool, dry summers, a long frost-free season, and heavy precipitation during the winter months, most of which falls as rain. Rainfall is heavy, 770–3800 mm/year, with a general decrease in precipitation from north to south. The mountain ranges create rain shadows to their leeward side. The climate of the eastern slope of the Cascade Range is more continental with cooler winters and hotter summers than its western slope. East slopes of the Cascades are also much drier than west slopes, accumulating less than 511 mm of precipitation per year, most of which falls as snow (Franklin and Dyrness, 1973).

Natural vegetation

Pacific Coast forests are productive and economically valuable forests (Noss, 1993). The coniferous forests of this ecoregion exceed other parts of the world for size and longevity of the dominant species with every conifer genus represented finding its largest (and often oldest) representative in the Pacific Coast and Cascade Mountains (Franklin and Dyrness, 1988). All but the highest peaks are covered by forest. Above timberline, there are alpine plant communities of shrubs and forbs. The temperate forests of the Olympic Mountains, Coast Range, and western slope of the Cascade Range are composed of *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata* at low elevations, and *Abies amabilis* and *Tsuga mertensiana* at higher elevations. *Picea sitchensis* are common along the coastal margin of the Coast Range and Olympic Mountains. The eastern Cascades are dominated by a mix of species, some represented on the western slope of the range while others are representative of the Rocky Mountains farther to the east. *Pinus ponderosa* is common at lower elevations and *Abies lasiocarpa* at higher elevations (Franklin and Dyrness, 1973).

Land uses

Forest management practices have shaped much of the Cascade Ecoregion. Initially, logging concentrated on lowlands, but gradually shifted to higher elevations. Past fires, extensive road building, land clearing, and over nearly a century of clearcut logging characterize the intensive forestry management of the Coast Range forests. The suitability of clearcuts for the invasion of non-native plants is well documented (Appleby, 1998). However, the resulting forest plantations form a landscape of young, even-aged, closed canopy stands. These young forest stands tend to have species-poor understories due to dense shading and intense competition. A somewhat different situation exists on the eastern slopes of the Cascades where a century of fire suppression has allowed dense understory vegetation to develop. These forests are now at risk to severe fire events. The common timber removal method in the eastern Cascades is selective tree harvest as opposed to the typical clearcutting used on western slopes of the Cascades, Olympics and throughout the Coast Range.

Plant invasions

In the Coast Range and western slopes of the Cascades (Table 1), non-native ruderal plant species are largely confined to early seral communities for 2–5 years following disturbance (DeFerrari, 1993; DeFerrari and Naiman, 1994; Planty-Tabacchi et al., 1996; Parendes, 1997). Although non-native plants are well represented in the seed bank of old-growth forests, these species are rarely present under the dominant vegetation (Ingersoll and Wilson, 1989). Size and intensity of disturbance are significant factors for invasion by grasses and forbs (Table 1). The proportion of non-native species is positively correlated with edge length of the disturbance, suggesting that larger disturbance gaps are more readily invaded than smaller gaps (Planty-Tabacchi et al., 1996). Clearcut logging is the most widespread disturbance in western mountains of the province (Morris, 1958; Dyrness, 1973; Kraemer, 1977; Stewart, 1978; Agee and Huff, 1980; Huff, 1984; Schoonmaker and McKee, 1988; Halpern, 1989; DeFerrari, 1993; Halpern et al., 1997), but non-native herbaceous or shrub species that dominate sites early are replaced by native shrubs or trees as succession progresses (Heckmann, 1999). Advancement of long-established invasive species (*Centaurea diffusa*, *C. debeauxii*, *C. solstitialis*, *Cytisus scoparius*, *Hypericum perforatum*, *Linaria dalmatica*, *Senecio jacobaea*, etc.) will probably continue into newly disturbed or clearcut areas (Toney et al., 1998).

While most non-native species are unable to persist in coniferous forest understories, there are a few exceptions. *Mycelis muralis* and *Mycelis serriola* are frequent along shaded abandoned roads and streams of the western Cascades (Parendes, 1997; Parendes and Jones, 2000), and have been observed in both young and mature conifer forests of the Olympic Range (DeFerrari, 1993; Halpern et al., 1999). *Brachypodium sylvaticum* and *Geranium robertianum* also invade mature *P. menziesii* and *T. heterophylla* forest stands.

Mature riparian forests contain a significantly greater number and cover of non-native species than coniferous upland forests. Flood and high flow events both disperse non-native propagules along riparian corridors and create new unvegetated floodplains for colonization (Thompson, 2001; Watterson, 2004). Though riparian areas are vulnerable to non-native species such as *Rubus discolor*, the patchiness of riparian habitats often allows coexistence of native and non-native species (Planty-Tabacchi et al., 1996). *Polygonum cuspidatum* is beginning to aggressively invade riparian areas of the Coast and Cascade ranges (Toney et al., 1998). In the steep and highly dissected mountain ranges of the Cascade Province, landslides are a common disturbance on both managed and unmanaged forests (Miles and Swanson, 1986), and upland sites may be important sources of non-native propagules for riparian corridors. In a study of *C. scoparius* and *Digitalis purpurea* in the western Oregon Cascades, Watterson (2004) concluded that seeds of these species move down the gradient from uplands to riparian areas via flood and debris flow events. Furthermore, human disturbances may accelerate the dispersal process from uplands to riparian areas (Parendes, 1997; Parendes and Jones, 2000). Although riparian areas serve as corridors for invasive species, they do not appear to be sources of propagules for upland sites (DeFerrari, 1993).

Natural disturbance gaps in alpine and many subalpine environments are largely free of non-native plants (Table 1). For example, high-elevation environments in the Cascades tend to have fewer non-native plants than lower elevation sites (DeFerrari, 1993; Parendes, 1997; Odion et al., 2005). Most non-native plants, particularly *C. scoparius*, *D. purpurea*, *R. discolor*, and *Cirsium arvense*, decrease in abundance with increased elevation (DeFerrari, 1993; Parendes, 1997). The fewest plant invasions are observed in mature forests located in high-elevation wilderness area of the Olympic Range (DeFerrari and Naiman, 1994). In general, an inverse relationship between non-native plant species and elevation exists in all of the mountain ranges of this ecoregion (Table 1; DeFerrari and Naiman, 1994; Parendes, 1997). Fire-effects studies conducted in wilderness and national parks located along the crest of the Cascades have not found non-native plant species (Douglas and Ballard, 1971; Miller and Miller, 1976; Hemstrom and Franklin, 1982); whether this absence is due to lack of seed source or to environmental barriers to establishment is unknown.

Heavily disturbed subalpine and alpine meadows may support persistent populations of non-natives. In an 8-year study of a closed parking lot located in an alpine meadow dominated by native *Festuca idahoensis*, Schreiner (1982) monitored established non-native species for persistence. Three non-native species were observed, *Poa pratensis*, *Phleum pretense*, and *Taraxacum officinale*. Of these, *T. officinale* had a negligible effect, *P. pratense* occurred only where there was no other vegetation, and *P. pratensis* excluded native colonizers for a short time. While there was no indication that *P. pratensis* would eventually be excluded from the area by native plants, there was also no indication that it could invade the undisturbed native meadow (Schreiner, 1982). However, there is concern that non-native plants that perform poorly under forest canopies, but are tolerant of a wide range of climatic and soil conditions, pose a threat to disturbed and therefore open subalpine and alpine environments (see Becker et al., 2005; McDougall et al., 2005). For example, *C. arvense* (Table 1), common in clearcuts, may spread to open alpine meadows of the Olympic Range (DeFerrari, 1993).

Sierran Steppe Ecoregion

Climate and physiography

In southwest Oregon between the Cascade Mountains and the Pacific Ocean is the northernmost portion of the Sierran Steppe Ecoregion (M261; Bailey, 1995; Fig. 2). These mountains form a unique topographic, geologic, and ecological transition zone with elevations from 600 to 2900 m. An important factor in the ecological makeup of the area is the east–west orientation of the Siskiyou Mountains, an unusual orientation for a large mountain range. The climate is warmer and drier than either the Coast or Cascade ranges (Fig. 4). Annual precipitation is between 600 and 1700 mm or more, depending on elevation and distance from the coast. Less than 20% falls during the growing season (Franklin and Dyrness, 1988). East slopes are much drier than west slopes.

Natural vegetation

The mountains are covered with steeply sloping forests crossed by valleys. The species composition of these forests is more native to California, such as *Pinus lambertiana*, *Calocedrus decurrens*, and *Lithocarpus densiflorus*. Thus, the forests of this ecoregion also represent the northernmost range of the mixed-conifer and mixed-sclerophyll forests typical of the Sierra Nevada and California Coast ranges. Forests and woodlands of the Klamath–Siskiyou are, in certain locations, more open than the conifer forests described in the previous section.

Land use

Primary land uses of the Klamath–Siskiyou Mountain ranges are timber harvest, wilderness recreation, and conservation. The ecoregion is highly valued for its high botanical diversity. Many endemic species occur in this area of the Northwest. The Siskiyous provide plant and animal species with critical connections between the Cascade Mountains and the wet forests of the western Coast Range. In addition, the Siskiyou and Klamath mountains were not heavily glaciated and served as a refuge for species whose former habitats disappeared during the last ice age. The World Conservation Union (IUCN) considers the Klamath–Siskiyou to be a place of global botanical significance, and the World Wildlife Fund included it in its global 2000 list of most valuable and threatened ecoregions of the world (Strittholt and DellaSala, 2001). Almost 13% of the region is protected as wilderness area, primarily at higher elevations (Strittholt and DellaSala, 2001).

Plant invasions

In an examination of non-native plant species in six national parks located within this ecoregion, Odion et al. (2005) found an inverse relationship between non-native species richness and elevation, and a weak relationship between soil surface disturbance and presence of non-native plant species. Since sampling took place near roads and trails where abundant sources of non-native seeds were present, the authors believe that a climatic barrier to establishment for many species may exist at high elevations. They also found an inverse relationship between non-native plant species richness and forest canopy cover, suggesting that non-native species may be more limited by light availability than seed source (Odion et al., 2005). Due to decades of fire suppression, closed canopies of trees are increasingly common in high-elevation forest environments of the Klamath–Siskiyou region, but moist, open meadow environments may be particularly vulnerable to non-native plant invasion (Odion et al., 2005).

Non-native plants are particularly abundant along streams and rivers in the Sierrian Steppe Ecoregion (Table 1). Low elevation riparian areas throughout the Klamath Park network are inhabited with dense thickets of *Rubus discolor* and other non-native species (Odion et al., 2005), which may be explained by frequent disturbance and abundant soil moisture. In the Klamath National Forest (KNF, 2004), riparian areas are vulnerable to non-native species invasions due to frequent flood events and high recreation use.

Non-native plant species that are especially problematic in the Klamath–Siskiyou Mountains include *Centaurea solstitialis*, *C. diffusa*, *C. biebersteinii*, and *Euphorbia esula* (Table 1). *Centaurea solstitialis* is abundant in the foothills of the Siskiyou Mountains (Arnold and Anthony, 2000; Roche and White, 2000). Although *C. solstitialis* most readily invades south slopes and disturbed sites, the species also will invade forest openings in the conifer transition zone above oak woodlands in the absence of competing perennial vegetation (Roche and White, 2000). State and national parks have high levels of non-native plants. For example, 25% of the flora in Redwood National Park is believed to be non-native (Odion et al., 2005). Chaparral and low elevation woodlands are invaded by *Ailanthus altissima*, *Genista monspessulana*, and *C. solstitialis*. Among the most widespread non-native plants in the Klamath Park network are *Hypericum perforatum* and *Hypochaeis radicata* (Odion et al., 2005). Coastal invaders are typically herbaceous perennials, such as *Cortaderia jubata* and *Anthoxanthum odoratum* (Sarr et al., 2003).

Middle Rocky Mountains Ecoregion

Climate and physiography

The Middle Rocky Mountains Ecoregion is comprised of the Blue Mountains, Salmon River Mountains, Bitterroot Mountains, Pioneer Mountains, Butte Highland Mountains, Tobaccoroot Mountains, and portions of the Madison and Gallatin Mountain ranges (M332; Bailey, 1995; Fig. 2). Most of central Idaho and the Salmon River mountains are formed by granitic intrusions that collectively make up the Idaho Batholith, with altitudes ranging from 900 to 2130 m. East of the Batholith is a basin-and-range area consisting of mountains with alluvial fans at their bases and floodplains along streams draining the valleys. To the west lie the Blue Mountains, which seldom exceed 2400 m, but has one peak 3050 m in height. The Snake River crosses the province at the bottom of Hells Canyon, the deepest river gorge in North America. Most high reaches have been glaciated.

Despite the northerly latitudes and high altitudes of this region, the climate remains relatively mild due to proximity to the Pacific Ocean and protection from Arctic cold fronts. Mean monthly temperatures in the valleys of the Blue Mountains in northeast Oregon range from just above freezing to 20 °C. In the mountain valleys of Montana, January temperatures average as much as 6 °C higher and summer temperatures 3–6 °C lower than on the Great Plains to the east. The average length of the growing season is about 120 days. Temperature and snowfall vary with altitude. Wind is generally from the west, with most moisture precipitated across the Cascade Ecoregion. Consequently, this portion of the Rocky Mountains is semi-arid; valleys receive less than 510 mm of precipitation each year with up to 1700 mm falling in the mountains mostly as snow (Fig. 4).

Natural vegetation

Low elevations (<1000 m) of the Middle Rocky Mountains are comprised mainly of arid grassland and shrub steppe vegetation, dominated by *Artemisia* spp. and perennial bunchgrass communities. Forest covers increase at mid-elevations (c. 1000–1600 m) and are dominated by *Pinus ponderosa* and *Pseudotsuga menziesii*. Higher elevation forests (up to approximately 1900 m) are dominated by *P. menziesii* and *Larix occidentalis*, with *Abies grandis* as an associate west of the continental divide, chiefly on west-facing slopes. *Picea engelmannii*, *Abies lasiocarpa* and *Pinus albicaulis* are the primary trees in subalpine areas (c. <2000 m). Due to aridity, forests directly east of the Salmon River Mountains are usually restricted to northern and eastern slopes. Although south- and west-facing slopes receive comparable precipitation, they are hotter and evaporation is higher as compared to northern and eastern slopes. Consequently, south- and west-facing slopes support few trees, and are covered by shrubs and grasses.

Land use

Over 40% of the land is federally owned, of which 17% is designated for recreation or wilderness management (Quigley and Arbelbide, 1997). Low- to mid-elevation sagebrush (*Artemisia* sp.) steppe and open *P. ponderosa* communities have been greatly impacted by current and past land use such as intensive livestock grazing, scattered small settlements, and wide-scale timber harvests.

Plant invasions

In common with the rest of the Northwest (Table 1), plant invasions in the Middle Rocky Mountains Ecoregion vary depending on elevation, past land use, and disturbance history. Lower elevation shrub steppe, grassland, and xeric *P. ponderosa* forest are most impacted by invasive plants. Particularly problematic non-native plants include annual grasses (*Bromus* spp., *Ventenata dubia*, *Taeniatherum caput-medusae*), rhizomatous perennial grasses (*Bromus inermis*, *Poa pratensis*), and perennial forbs (including species in the genus *Centaurea*, and *Hypericum perforatum*; Harrod, 2001). The knapweed complex is especially troublesome since more than 1.4 million ha of Oregon, Washington, Idaho, and Montana are covered with *Centaurea biebersteinii* alone (Langner and Flather, 1994; Wilson et al., 2003). It is estimated that 8% of the Payette and Salmon-Challis National forests are inhabited by *C. solstitialis*, *Euphorbia esula*, or *Carduus nutans* (Johnson, 2000).

Potentilla recta is a long-lived perennial that has become one of the most serious invaders of the Middle and Northern Rockies (Sheley and Petroff, 1999). *Potentilla recta* went unnoticed in many parts of its range because it is similar in appearance to native co-occurring congeners, particularly *Potentilla gracilis* (Aitken and Parks, 2004). Other invasive species found in the Blue Mountains are in limited areas or in low abundance. These species include *E. esula*, *Linaria dalmatica*, *L. vulgaris*, *Cardaria pubescens*, and *Chondrilla juncea* (Table 1). Other invasive species common throughout the Salmon River Range include *Cynoglossum officinale*, *Cirsium vulgare*, *Tribulus terrestris*, and *Crupina vulgaris*.

The majority of high-elevation uplands in the ecoregion are managed by the federal government where plant invasions are currently less pronounced and mostly restricted to early successional plant communities (Table 1). These areas are generally forested and dominated by mixed-conifer forests. *Cirsium vulgare* and *C. arvense* are often found following prescribed or wildfires, logging or heavy grazing. Additionally, reseeding programs to reduce soil erosion following timber harvest have resulted in wide distributions of many non-native grass species such as *Thinopyrum intermedium*, *B. inermus*, *P. pratensis*, and *Phleum pratense*. Past fire suppression has resulted in heavy fuel accumulations and high tree stand densities in many areas of the Middle Rocky Mountains, and have put these forests at risk to stand-destroying wildfires. In 2000, wildfires prevailed throughout the Middle Rocky Mountains and created optimal conditions for invasive plant establishment by decreasing tree, shrub and herbaceous cover and increasing light levels and nutrients (Table 1). Post-fire seeding of non-native grasses to stabilize soil, contributes to an increase in non-native plants at mid- and high-elevation. Over the last few years, controlled fires have been widely applied across the Middle Rockies to reduce forest fuel loads. Fuels reduction programs may enhance the spread of existing non-native species since sites are more susceptible to plant invasions after fire (Milberg and Lamont, 1995; D'Antonio, 2000; Goodwin and Sheley, 2001).

An important quality throughout the Middle Rocky Mountains is the expansive roadless wilderness areas that occupy the ecoregion's highest elevations. Non-native plants are less frequent in wilderness areas than in the other land-use categories. When they are found, the plants are mostly restricted to access trails, paths, trailheads, and campsites (Cole, 1982; Marion et al., 1986). *Centaurea biebersteinii*, *Chondrilla juncea*, and *P. recta* have been found in the Frank Church River of No-Return Wilderness, the largest wilderness area in the continental US (Wood and Lyman, 2004).

Hieracium caespitosum and *H. aurantiacum* are of concern in moist pastures and mid- to high-elevation meadows (Table 1). Extensive infestations of *H. caespitosum* have been discovered recently in the Wallowa Mountains of northeastern Oregon (Dwire and Parks, 2002). Non-native grasses and forbs were often seeded in montane meadows to increase forage value of the native vegetation, and several of these introduced species now persist as dominants even without livestock grazing (Crowe and Clausnitzer, 1997). *Euphorbia esula* is found along many rivers and streams, and appears to be spreading upstream to higher elevations. *Centaurea debeauxii* is a relatively new introduction to the Northwest (Roche and Roche, 1991). *Centaurea debeauxii* grows best on moist sites, including pastures and meadows along rivers, streams, and irrigation ditches, and in openings in forested areas. Seeds are carried in waterways. Infestations of *Tamarix ramosissima*, *Ailanthus altissima*, *Rubus discolor*, and *Polygonum cuspidatum* have been discovered in the upper reaches of the Snake River. Currently, alpine and subalpine areas have few non-native plants (Table 1), though there is concern about invasion by *Lythrum salicaria*, *H. caespitosum*, and *H. aurantiacum*.

Northern Rocky Mountain and Southern Rocky Mountain Steppe Ecoregions

Climate and physiography

The Northern Rocky Mountain Ecoregion (M333; Bailey, 1995; Fig. 2) consists of high, rugged mountains rising to more than 2700 m with local relief in excess of 900 m. Most of the ecoregion has been glaciated. Many valleys are nearly flat with some being several miles wide. Snowfall is heavy, but permanent snowfields and glaciers are small. The average temperature of the coldest month is below 0 °C, and the average temperature of the warmest month is below 22 °C. Summer days are often hot, but nights are cool. Precipitation averages 510–1020 mm/year and is concentrated in fall, winter and spring. Summers are usually dry (Fig. 4).

The Southern Rocky Mountains Province includes the Yellowstone Highlands, Bighorn Mountains, and Overthrust Mountains. The Yellowstone Highlands encompasses much of the Greater Yellowstone Ecosystem (M331; Bailey, 1995; Fig. 2). The Yellowstone Plateau was formed from two volcanic episodes. Other areas include high rugged mountains with ridges and cirques at higher elevations, and narrow to broad valleys. Much of this area has been glaciated, and moraines are common. Elevation ranges from 1800 to 4100 m in the mountains, and 763 to 1983 m in the basins and valleys. Precipitation ranges from 510 to 1140 mm annually; most occurs during fall, winter, and spring. Above 1800 m, precipitation falls mostly as snow. Rain is common during the growing season. Climate is cold, moist continental. The growing season lasts 25–120 days.

Natural vegetation

Well-marked elevation zones of vegetation are a striking feature of the Northern Rocky Mountain Ecoregion. In the uppermost alpine belt, trees are absent. The subalpine belt is dominated by *Picea engelmannii* and *Abies lasiocarpa*. In the Bitterroot Range, *Tsuga mertensiana* is the climax tree of the subalpine belt. *Thuja plicata* and *Tsuga heterophylla* are characteristic of the montane belt, along with *Pseudotsuga menziesii*, found throughout the ecoregion, along with *Pinus monticola*, *Larix occidentalis*, *Abies grandis*, and *Pinus ponderosa*, found in the south. In these forests, areas that have been burned or cut are regenerated first by *L. occidentalis*, a deciduous conifer. *Pinus monticola* crowds out the *L. occidentalis*, and then is replaced by *T. mertensiana*, *T. heterophylla*, *T. plicata*, and *Abies concolor*. Depending on latitude, the lower part of the montane belt may be interspersed with grass and sagebrush. Throughout the ecoregion, mixed-conifer-deciduous forest, such as *P. menziesii* and *T. plicata–T. mertensiana–P. menziesii* forests, predominate.

For the Southern Rocky Mountain Ecoregion, USDA Forest Service (1995) mapped potential vegetation as *Pseudoroegneria–Achnatherum*–shrub steppe in drier, lower elevation valleys (55%), and *P. menziesii–Picea–Abies* forest (45%) between 1667 and 2879 m. *Pinus contorta* is the common tree cover type, with an understory of *Vaccinium scoparium*, *Calamagrostis rubescens*, *Arnica cordifolia*, or *Mahonia repens*. Alpine vegetation, including *P. albicaulis* and *A. lasiocarpa*, occurs above 2878 m.

Intervals between fires typically range from 100 to 300 years (Romme and Knight, 1981). As evidenced by the extensive fires in the Yellowstone National Park in 1988, *Pinus contorta* forests are rejuvenated by crown fires that replace tree stands. Although *Populus tremuloides* stands generally cover less than 1% of the landscape (e.g., Rocky Mountain National Park, Grand Teton National Park), they are keystone plant communities for birds and mammals, and are especially important forage for deer and elk (Mueggler and Stewart, 1980).

Land use

An important quality of the Northern Rocky Mountain Ecoregion is the expansive roadless wilderness areas that are linked by minimally roaded submountain ranges. This ecoregion is important habitat for many animal species including large carnivores like the grizzly bear, wolf, and other animals reliant on large tracts of land (Ament and Craighead, 1998). The ecoregion is, however, becoming increasingly fragmented by roads (Noss, 1993), encroached upon by exurban development (Hansen et al., 2002), and intensively used for recreation (Johnson et al., 2003). Increasing numbers of elk may have an adverse effect on quality of the available winter forage (Knight, 1994) and also increase the occurrence of plant invasions.

Human-caused pressures in the Greater Yellowstone Ecosystem include commercial development, logging, exploitation of geothermal resources, and tourism. The park's visitation rate is about 3.2 million visitors/year (Knight, 1991) and increasing (Johnson et al., 2003). Although livestock allotment grazing intensity has decreased as in most of the Mountain West, livestock grazing is still permitted on about 40% of the Greater Yellowstone Ecosystem (Keiter and Boyce, 1991).

Plant invasions

There are 1251 vascular plant species in western Montana and 250 non-native species in the area (Whipple, 2001, modified from Rejmanek and Randall, 1994). In Glacier National Park, a total of 1131 plant species have been found of which 126 (11%) are non-native (Tyser and Worley, 1992). In Yellowstone National Park, 1265 plant species have been recorded and 187 (14.7%) are non-native species (Whipple, 2001). In a survey of non-native plant species adjacent to highways between Glacier National Park and Grand Teton National Park, Weaver et al. (2001) observed 29 non-native plant species. Most of the dominant plants are intentionally introduced grasses (*Agrostis gigantea*, *Bromus inermis*, *B. tectorum*, *B. japonicus*, *Dactylis glomerata*, and particularly *Poa pretense* and *Phleum pratensis*) and legumes such as *Melilotus officinalis*, *Medicago lupulina*, *Trifolium pratense*, and *Trifolium campestre*. Weaver et al. (2001) found non-native plant species in both grasslands and dry forests (Table 1).

Disturbed moist forests were similar in species richness to dry forests, but no non-native plants were recorded on undisturbed forest sites (Weaver et al., 2001).

A survey of 108 national forest districts in Montana, Idaho and western Wyoming in 1995–1996 provides more information about the most problematic non-native plants (Markin, 2004; Table 1). *Cirsium arvense* was most frequently mentioned and widely distributed species, followed by *Carduus nutans* and *Hypericum perforatum*. These three plants have been present in the region for the longest time. Species that have arrived more recently, but believed to be spreading rapidly are *Centaurea biebersteinii* and *Ephorbia esula. Linaria vulgaris, L. dalmatica, Potentilla recta*, and *Centaurea solstitialis* are more limited in distribution, but are also increasing (Markin, 2004).

Several studies address the impact of wildfire on the presence and abundance of invasive plants. A study of succession after wildfire in *P. ponderosa* and *Juniperus scopulorum* in central Montana found that high severity fires result in increased *B. japonicus* and other non-native species, particularly *C. arvense* (Cooper and Jean, 2001). Merrill et al. (1980) found significant differences between annual grass (primarily *B. tectorum*) yield on unburned and burned sites the first growing season following fire in the Selway-Bitterroot Wilderness, Idaho. This response lasted several years. No consistent pattern in non-native plant responses to wildfire in natural areas were discernable from the few studies conducted in either *A. lasiocarpa–Picea* or *P. contorta* forests (Stickney, 1980; Turner et al., 1997; Doyle et al., 1998). Fire-line disturbances create suitable conditions for many non-native species to become established.

Wildlife habitat improvement efforts starting in the 1920s and continuing into the 1960s included widespread planting of non-native grass seed and their common contaminants (e.g., *C. arvense, Carduus nutans, Thlaspi arvense*, etc.; Cook, 2002). Wildlife species, particularly ungulates and birds, now spread non-native plants into backcountry areas even though these improvement practices have stopped. Post-wildfire planting for soil stabilization and protection against weed establishment ironically has encouraged the introduction of non-native plants because seed sources of native species are rare and expensive. Even if the seed source is certified weed-free, some low level of seed impurity is allowed by law. These native seed contaminants can be aggressive invasive plants.

Silviculture and other forest management practices are also perceived to increase the risk of non-native plant invasions, but only a few studies have addressed the effect of forest management practices in this ecoregion. Selmants and Knight (2003) evaluated the effect of site preparation treatments on previously clearcut and slash sites in the Snowy Range of southeastern Wyoming. Non-native plant cover was generally less than 1% in the clearcut sites, but was essentially absent from the uncut forest. Species observed in the harvested stands included *C. arvense, L. vulgaris, Poa compressa, P. palustris, P. pratensis, Taraxacum laevigatum*, and *T. officinale* (Selmants and Knight, 2003).

Hay hauled into wilderness areas to support horses and mules for hunting or pack trips is a major source of noxious weed seed. Dale and Weaver (1973) found non-native plants distributed along trails in wilderness areas, but their distribution decreased sharply within a few meters of trails. Marcus et al. (1998) found similar results in the Selway-Bitterroot Wilderness where *C. biebersteinii* decreased to no occurrences within 1.2 km of trailheads and decreased to no occurrences within 5 m perpendicular to the trails. In addition, out of 36 active hunting horse camps that have been used for the past 30 years, *C. biebersteinii* was found in only six camps and the number of plants totaled less than 20. Wilderness Area management now requires certified weed-free hay. Unfortunately, weed-free hay often includes hay meadow grass species that are some of the most invasive alien monocots (e.g., *P. pratense, B. inermis, P. pratensis*), as well as *Trifolium* spp.

Susceptibility of Northwest mountain habitats to non-native plants

This analysis highlights the overwhelming importance of disturbance in facilitating the establishment of non-native plants in the mountainous ecoregions of the Northwest. Well over half of the non-native plants in any of the land-cover types examined are disturbance-dependent (Table 1). Many of these non-native plants are 'generalists' and are not limited by the environmental gradients that influence the distribution of native species. However, alpine and some subalpine plant communities appear to be uninvaded by non-native plants (Table 1), while riparian areas are invasible by certain non-native plants either with or without human disturbance (Table 1). Floristically, the non-native plants found throughout the mountain ecoregions of the Northwest are generally similar for specific vegetation types. When comparisons were made for specific vegetation types among all Northwest mountain ecoregions (Table 1) they exhibit a Sörensen community similarity coefficient (0 = total dissimilarity, 100 = identical) of 93–99 for subalpine (S), 98–99 for high (H), 91–99 for middle (M), 90–99 for low (L) upland forests and grasslands, and 94–100 for riparian areas (R). Within ecoregions non-native plant similarity is somewhat lower with different plants occurring along an elevational gradient, differences are most pronounced between riparian and upland vegetation types (Table 2).

Table 2. Floristic similarity of non-native plants within vegetation types of Northwest mountain ecoregions using data from Table 1

	Vegetation types					
	Alpine	Subalpine	High forest	Middle forest	Low forest	Riparian
Cascade						
Alpine	—					
Subalpine	91	—				
High forest	95	92	—			
Middle forest	87	96	92	—		
Low forest	85	94	90	98	—	
Riparian	72	80	77	84	85	—
Sierran Steppe						
Alpine	—					
Subalpine	[a]	—				
High forest	[a]	96	—			
Middle forest	[a]	94	97	—		
Low forest	[a]	90	93	95	—	
Riparian	[a]	74	75	77	77	—
Mid-Rocky Mountains						
Alpine	—					
Subalpine	40	—				
High forest	40	97	—			
Middle forest	38	96	97	—		
Low forest	36	91	94	95	—	
Riparian	30	67	68	70	68	—
Rocky Mountains						
Alpine	—					
Subalpine	94	—				
High forest	94	98	—			
Middle forest	92	96	98	—		
Low forest	90	92	94	96	—	
Riparian	72	77	78	79	78	—

Numbers are percent similarity of the non-native flora, calculated using the Sörensen index the equation: $2C/(N_1 + N_2)$, where C is the number of species in common between the communities, and N_1 and N_2 are species richness of the two separate communities.

[a]No or insufficient information exists for species in vegetation type.

We confirmed (Fig. 5) that different land-cover types are susceptible to invasive species, but the range of invasive species richness plants among the habitats is considerable (Fig. 6). Drier climates, such as that of the Middle Rocky Mountain Ecoregion and the eastern portions of the Cascade and Sierra Steppe ecoregions are at greater risk to invasive species than the more mesic western portions of the Cascade Ecoregion (Fig. 5). In Oregon, xeric grasslands comprised mostly of perennial bunchgrass communities, upland shrub communities, and riparian areas are susceptible to the most non-native plant species, while subalpine meadows and salt-desert shrub are susceptible to the fewest invasive plant species (Fig. 6). Using the data from Fig. 6 a calculation of the percentage of land area in susceptible plant communities in each ecoregion (Table 3) indicates the overall level of risk for mountains in Oregon. Specific areas of risk are also indicated, e.g., the Cascade ecoregion has less land cover in the invasive species-rich xeric grassland category but twice the amount of land cover in the riparian category than the other Oregon mountain ecoregions.

Discussion

The mountain ecoregions of the Northwest have fewer non-native invasive plants than other regions of the US because of (1) climate factors including a short growing season at high elevations and lack of moisture during the growing season, (2) a limited settlement history, (3) relatively low frequency of seed sources, and (4) widespread forested areas with closed canopy conifers that limit light and acidify the forest floor with needle litter. Thus, compared to more invaded forest

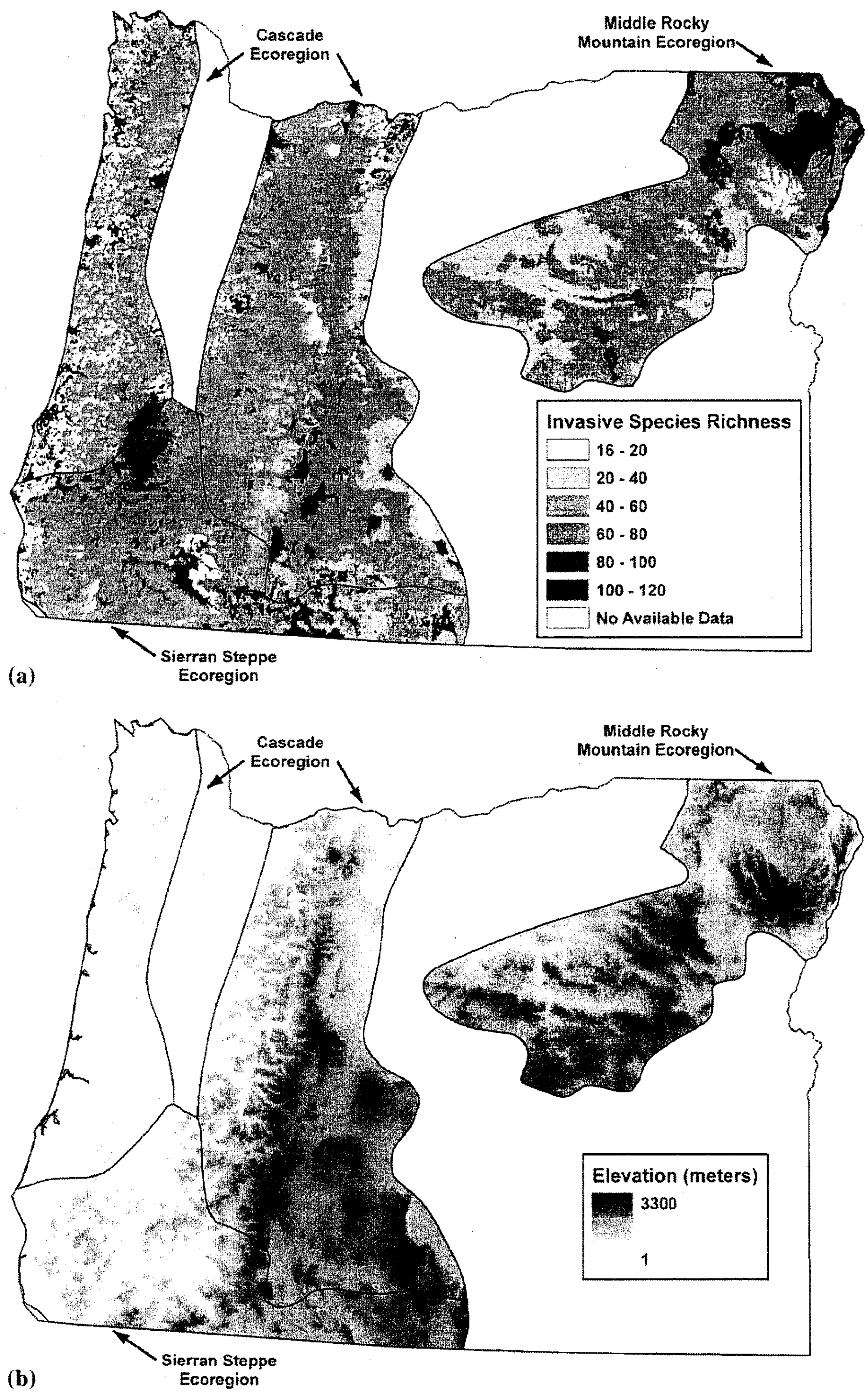

Fig. 5. (a) Numbers of non-native invasive plants to which mountain ecoregions of Oregon are susceptible and (b) elevation gradients of mountain ecoregions in Oregon.

steppe grasslands, high-elevation Northwest forests experience limited invasion by non-native plant species, except where modified by natural or human-mediated disturbance (Table 1, Figs. 5 and 6).

Non-native plant invasions within and among Northwest mountain ecoregions vary according to climate, elevation, soils, and topography that contributes to differences in vegetation that distinguish each ecoregion.

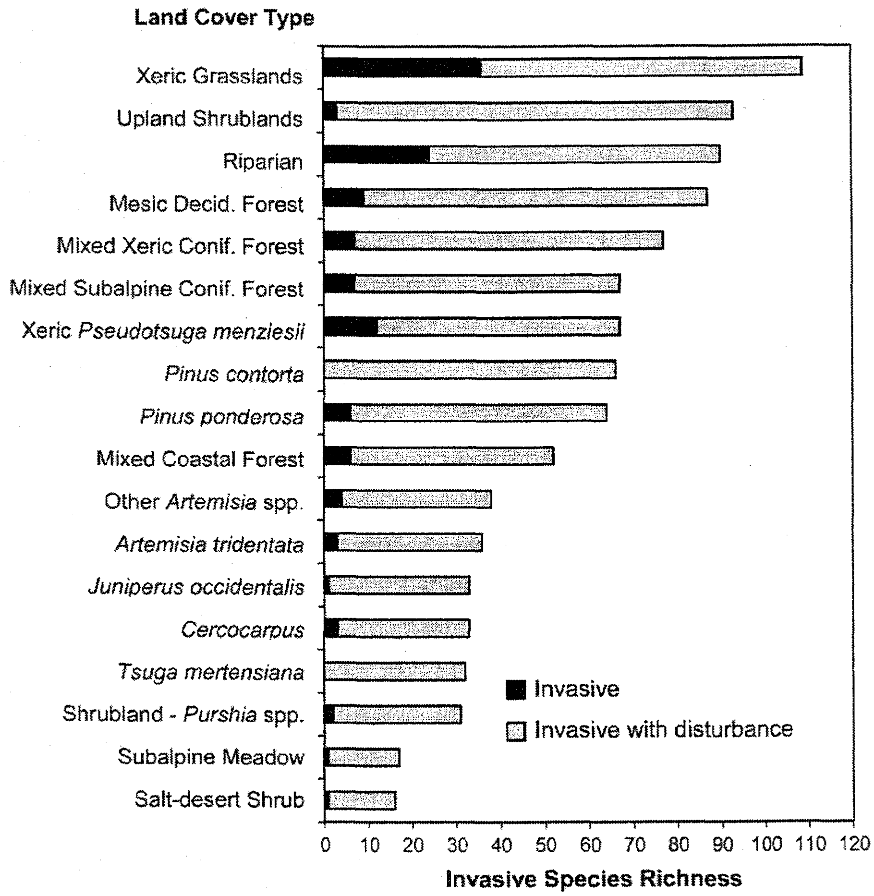

Fig. 6. The number of non-native plant species, listed as noxious by the state of Oregon that can potentially invade different land-cover types in the mountain ecoregions of Oregon. A species is categorized as 'invasive' if the species can obtain dominance or co-dominance in the absence of intense or frequent disturbance events. 'Invasive with disturbance' refers to non-native species that require disturbance that impacts the soil surface or vegetation layer to establish.

Thus, the western slopes of the Cascade ecoregion (Fig. 2), influenced by a maritime climate, support dense conifer forests with a subcanopy of trees and many understory shrubs, ferns, herbs, brophytes, and lichens (Franklin and Dyrness, 1973). Similar vegetation extends inland, on west-facing slopes, to the Middle Rocky Mountains as a peninsula created by storm tracks that extend as far southeast as Yellowstone National Park in the Southern Rocky Mountains ecoregion (Brouillet and Whetstone, 1993). Therefore, the most mesic sites of the Rocky Mountains ecoregions and the Sierran Steppe Ecoregion in Oregon have vegetation remarkably similar to those of parts of the Cascade ecoregion in western Oregon and Washington (Brouillet and Whetstone, 1993). The eastern mountain slopes of the Cascade ecoregion, however, and the southern and eastern edges of the Sierran Steppe Ecoregion, are characterized by a drier continental climate with cold winters and hot summers similar to much of the Middle Rocky ecoregion that exhibit a more open vegetation complex that proceeds through zones of *Juniperus occidentalis–Artemisia* savanna, and *Pinus ponderosa* forest, to a mesic *Abies lasiocarpa* or *Tsuga mertensiana* forest above 1500 m elevation (Brouillet and Whetstone, 1993). Throughout the Northwest, climate, physiography, and vegetation define the plant invaders that are shared among the ecoregions. For example, coastal invaders are typically herbaceous perennials, such as *Cortaderia jubata* and *Anthoxanthum odoratum*, whereas drier interior areas are invaded by Eurasian annuals. Across the Northwest mountain ecoregions the mid- and lower-elevation valleys of grasslands and shrublands have a number of Great Basin attributes and associated species, such as *Bromus tectorum*. We found little evidence in the literature to suggest that non-native plant species that are shared among ecoregions behave differently in the different ecoregions.

Land-use and land-cover change has undoubtedly been the underpinning for the successful introduction and establishment of non-native plants in the Northwest mountains. Current and historic land use is

Table 3. Percentage of area in the three mountain ecoregions of Oregon in each land-cover category presented in Fig. 6

Vegetation types	Ecoregion		
	Cascade	Sierran Steppe	Middle Rocky
Xeric Grasslands	7.1	8.1	8.3
Upland Shrublands	<0.1	0.7	<0.1
Riparian	2.6	1.3	1.2
Mesic Deciduous Forest	0.8	3.0	<0.1
Mixed xeric coniferous forest	12.3	2.0	32.2
Mixed Subalp. Coniferous Forest	1.4	<0.1	5.1
Xeric *Pseudotsuga menziesii*	6.0	23.6	<0.1
Pinus contorta	1.6	0	<0.1
Pinus ponderosa	5.3	8.0	23.8
Mixed Coastal Forest	44.5	30.9	<0.1
Other *Artemisia* spp.	0.4	0	0
Artemisia tridentata	4.4	3.2	6.9
Juniperus occidentalis	2.6	2.9	13.5
Cercocarpus	0	0	0
Tsuga mertensiana	1.9	0.2	0
Shrubland – *Purshia* spp.	0.2	0	<0.1
Subalpine Meadow	0.7	0.2	2.1
Salt-desert Shrub	0.6	0	0

an important factor in non-native invasive plant management, particularly as it relates to grazing, forest management, fire and fuels management, urban development, and recreation. The ecoregions of concern in this paper fall into three general land-use categories – anthropogenic systems, human impacted natural systems, and wilderness areas and some national parks (Williams, 1997) – that are spatially interwoven, though often discernable by elevation and terrain. Because the human use patterns are different for each of these categories, the threat of non-native plant invasions to them also differs.

The first category of land use is anthropic systems, which have a high degree of human use and impact. These systems are often at low- to mid-elevations and include farms, forests near towns, roads, rights-of-way, homesites, and managed parks and campsites. Human settlement and intense land development will likely continue to transfer non-native plant species into these areas, but they will probably be concentrated in the mountain foothills because of extensive federally owned lands and rugged topography at higher elevations. Roads and riparian areas are the major conduits for dispersal of non-native species in this land-use category, with the degree of penetration of non-native plant species into associated natural areas depending on the level of disturbance to them.

The second category of land use, human impacted natural systems, encompasses areas that have experienced intense or prolonged anthropogenic animal grazing, logging, an altered fire regime, or old fields from past farming activity. Roads create significant pathways for plant introductions, and forests in this land-use category are extensively logged. In such areas, herbaceous non-native species can be locally abundant depending on the degree of disturbance, rate succession to native shrubs and trees, and amount of connecting roads. Recently, large tracts of lands in the region have experienced stand-replacing wildfire. However, the role of wildfire on the introduction and establishment of alien plants remains unclear, except for their association with the soil disturbance of roads and road building. Non-native plant invasions in severely grazed meadows and old fields are often the object of local site restoration.

Wilderness areas and some national parks comprise the third category of land at risk to non-native plant invasion. These are areas designated for limited human use, preservation of natural biota, and maintenance of ecological integrity. The intact vegetation common in such areas commonly limits the intrusion of non-native plants to within a few meters of trails. Riparian areas within wilderness often have the highest occurrence of non-native plant invasions because they experience the most human use, while wilderness alpine areas remain relatively free of plant invasions.

Our analysis found altered riparian systems to be especially vulnerable to plant invasions. Studies show that species-rich riparian communities that receive an intermediate level of disturbance (fire, flood, herbivory) have more resources available for invading species (Planty-Tabacchi et al., 1996; Stohlgren et al., 1999a, b). Riparian habitats, while making up a relatively small area across the mountain ecoregions of the Northwest, have significant ecological, cultural, and economic importance. For example, an estimated 80% of wildlife species depend at some time during the year on this limited area for habitat (Thomas, 1979; Knight, 1994). Alpine and subalpine areas of the Northwest are still relatively unimpacted by invasive plant species. These communities make a critical contribution to overall biodiversity and deserve special protection from threats caused by increased human activity, including invasive plant introductions (Raphael et al., 2002).

Wilderness areas and national parks, in general, may be at particular risk to new plant invasions. MacDonald et al. (1989) observed significant correlations between the number of visitors to natural areas and the number of non-native invasive plants in those reserves. Positive correlation between visitor numbers and invasive plant richness suggests that visitors are either increasing accidental introductions or that more visitors cause more disturbances that facilitates invasive plant establishment, or both (Lonsdale, 1999). This indicates that the larger Northwest parks that can hold more visitors, e.g., Yellowstone National Park, are potentially at higher risk than smaller parks to plant invasions at all elevations. Wilderness areas and parks that are contiguous to one of the other land-use categories, human impacted systems or anthropic systems, are also likely to be at higher risk to plant invasions than wilderness areas and parks that are continuous.

As pointed out by Lonsdale (1999), to simply determine which ecosystems have more invasive species does not answer the question of which ecosystems are intrinsically more invasible. In an analysis of native and non-native plants along the latitudinal gradient in the US, Stohlgren et al. (2005) conclude that humans facilitate the initial establishment of non-native plants, but the spread and subsequent distributions of non-native plants are controlled by biotic and environmental factors. For example, a biotic factor limiting invasion of common non-native plants into alpine zones may be growth rate. Most alpine plants exhibit relatively low growth rates and exhibit vegetative developmental patterns that limit their growth capacity, including preformation of buds 2–4 years in advance of emergence and reduced cell numbers relative to lowland congeners (Bowman and Damm, 2002). However, since some species, including grasses and some herbs, can produce vegetative shoots in the same growing season in which they emerge, their likelihood of becoming a successful plant invader into alpine ecosystems may be increased over non-native plants without this ability.

Clearly, the interaction among suitable habitat, dispersal potential, propagule production, and absence of biotic and abiotic hazards determines the relative success of a non-native plant introduction (Lonsdale, 1999). However, little quantitative data on these factors, other than the largely descriptive information reported in this paper, is available to determine the risk of different plant communities to non-native plant invasions or to project their rates of spread. Thus, land managers in the region now must consider every non-native plant invasion that occurs in any habitat a risk and attempt to eradicate the plants, rather than systematically locate plant invasions or to prevent their occurrences in particularly risky habitats. Shafii et al. (2003) and Rew et al. (2005) propose methodologies to determine habitat risk and rates of expansion of non-native plant species. Radosevich et al. (2005) describe an approach to project invasive plant expansion that relies on proximity of non-native species to susceptible habitats, empirical information on non-native plant species population dynamics, and their dispersal distances. Reliable and consistent spatial databases among land management agencies to document non-native plant presence in disturbed and undisturbed plant communities will be required for managers to proactively prevent or contain invasive plant species in the mountains of the Northwest.

Several global processes, including climate, economic globalization, and alteration of nutrient cycles are predicted to contribute to escalating rates of species invasions and impacts (Chornesky et al., 2005). How will mountain ecoregions respond to these processes? Mountain ecoregions have a unique complex landscape structure, land-use history, and current land-use patterns that influence their susceptibility to non-native plant invasions. Understanding the landscape patterns of non-native plant invasions in mountain ecoregions, especially as they interact with the dynamics that follow local disturbance, affords new insights for managing plant invasions. Accomplishing these management objectives, however, will require a new level of cooperation among international, national, and local government agencies, private landowners, and general citizens.

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