Disruption of ecosystem processes in western North America by invasive species

Alteración de procesos en ecosistemas en el oeste de Norteamérica producidos por especies invasoras

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ABSTRACT

Many ecosystems of western North America have been dramatically changed by non-native species. Here, we review ecological impacts of 56 plant, animal, fungus, and protist species that were brought to this region by humans. We discuss characteristics of invasive species that can lead to major ecosystem impacts, and explore how invasive species alter many different attributes of ecosystems. Specifically, we include examples of invasive species that affect geomorphology, fire regimes, hydrology, microclimate, atmospheric composition, nutrient cycling, and productivity. Finally, we review the direct consequences of biological invasions for some native species. We summarize examples from this paper in Appendix 1. Our examples illustrate how, as invasive species have become dominant across large areas of western North America's grassland, shrubland, dune, riparian, and estuarine ecosystems, the properties and functioning of these systems have changed. To date, some systems in this region, such as its forests, remain relatively unaffected by invasive species. However, recent attacks of forest pathogens highlight the potential vulnerability of these ecosystems.

Key words: biological invasions, ecosystem functioning, community structure, exotic species, impact.

RESUMEN

Muchos ecosistemas de Norteamérica occidental han cambiado dramáticamente a causa del efecto producido por especies no autóctonas. Aquí se muestra una revisión del impacto ecológico producido por 56 especies diferentes de plantas, animales y hongos, y especies de protistas que fueron traídos a esta región por humanos. Discutimos las características de las especies invasoras que pueden producir un gran impacto en el ecosistema, y exploramos cómo las especies invasoras pueden alterar de forma muy diferente los atributos de un ecosistema. Específicamente, incluimos ejemplos de especies invasoras que afectan a la geomorfología, a los regímenes del fuego, a la hidrología, al microclima, a la composición atmosférica, al ciclo de nutrientes, y a la productividad. Finalmente, revisamos las consecuencias directas de invasiones biológicas de algunas especies autóctonas. Resumimos los ejemplos de este artículo en el Anexo 1. Nuestros ejemplos ilustran cómo, a medida que la especie invasora llega a ser dominante a lo largo de áreas extensas de ecosistemas como los prados del oeste de Norteamérica occidental, en zonas arbustivas, dunas, cauces de ríos y estuarios, las propiedades y el funcionamiento de estos ecosistemas han cambiado. Hasta ahora, algunos ecosistemas en esta región, como los bosques, permanecen relativamente intactos por efecto de la especies invasoras. Sin embargo, ataques recientes de patógenos a los bosques ponen de manifiesto la vulnerabilidad potencial de estos ecosistemas.

Palabras clave: invasiones biológicas, funcionamiento ecosistémico, estructura de comunidades, especies exóticas, impacto.

INTRODUCTION

As global transport becomes faster and cheaper, the distant corners of our planet become increasingly connected. People and their products, traveling from continent to continent, provide opportunities for thousands of plant and animal species to be transported, or even to hitchhike along. Most of the hitchhiking species do not survive in their new environment. However, some thrive, and some of those that thrive cause great ecological or economic harm. Many alien species attack or outcompete native species, and a small

percentage cause major changes in the appearance and operation of ecosystems (Vitousek et al. 1997, Sala et al. 1999). Invasive species (those aliens that thrive and increase their ranges) have already done great economic harm in countries around the world, either by depressing growth or populations of more valuable species, or by directly impeding human activity (e.g., Pimentel et al. 2000). The acceleration of international trade is likely to increase the number of propagules that are transported out of their home ranges each day. Thus, unless measures are taken to prevent propagules from hitching rides, the ongoing expansion of global commerce is likely to exacerbate the problem of biological invasions.

Here, we examine some of the ecological impacts of a variety of alien species, including several invasives. First, we examine characteristics of species that can lead to large ecosystem impacts after their introduction. Then, we explore how alien species are altering many different attributes of ecosystems, such as geomorphology, fire regime, hydrology, microclimate, atmospheric composition, nutrient cycling, and productivity. Finally, we review the direct consequences of biological invasions for some native species. Where possible we use examples of invasive species in western North American ecosystems. These examples are summarized in Appendix 1.

Invasive species that affect ecosystem processes may indirectly impact populations of native species. A simplified conceptual model of direct and indirect interactions among native and alien species is shown in Fig. 1.

We must emphasize that the ecological impacts of many of western North America's invasive species have not been studied, and so this review should not be viewed as comprehensive. We have simply attempted to compile a survey of some invaders' impacts (and potential impacts) in this region.

WHICH BIOLOGICAL INVADERS ARE MOST LIKELY TO ALTER ECOSYSTEMS?

Much of western North America's current biota is non-native. For instance, the latest surveys show that 1,109 of California's 8,274 catalogued species (13.4 %) were introduced from elsewhere (Hobbs & Mooney 1998). Which of the invaders have the potential to disrupt ecosystems? Invasive species that differ from natives in some trait, behavior, or function increasingly alter ecosystem properties and processes as their populations expand. Such species can be grouped into two categories: discrete trait invaders and continuous trait invaders. Discrete trait invaders add a new function to the invaded ecosystem, such as nitrogen fixation, hydraulic lift, or predation on a particular trophic level. Continuous trait invaders differ from natives only in traits that are continuously distributed among species such as litter quality or relative growth rate. Chapin et al. (1996) argue that discrete trait invaders are more likely than continuous trait invaders to have large ecosystem effects, and a recent meta-analysis of invaders' effects on disturbance regimes supports this argument (D'Antonio et al. 1999). However, continuous trait invaders can also alter ecosystem structure and functioning, especially if they constitute a large proportion of the ecosystem's biomass at one trophic level.

The conceptual model in Fig. 2 illustrates how an invader that replaces other species in its trophic level can alter properties of an ecosystem such as water use, flammability, or isoprene emission. In this example, the invading species has a higher inherent value for the hypothetical ecosystem function than the native species (although this value could just as easily be lower than that of the native). In an uninvaded ecosystem, the value of the ecosystem function may vary over time due to shifts in species dominance. As an invasion progresses, the invader makes up an increasing proportion of biomass at its trophic level. This forces the value of the function toward the inherent value of the invader. If the function crosses some threshold (increased water use draws down water tables below a certain level, increased flammability accelerates the fire cycle, increased predation on an herbivore reduces vegetation disturbance, among others), the species composition of the region may change, either as a result of the local elimination of a native species that required the pre-invasion conditions for survival or due to an increase in the susceptibility of the system to invasion by other species. Species composition change could further displace the ecosystem function or trait from its initial value. However, competition with native species may prevent the invader from achieving a great enough dominance to force the value of the ecosystem function across a threshold.
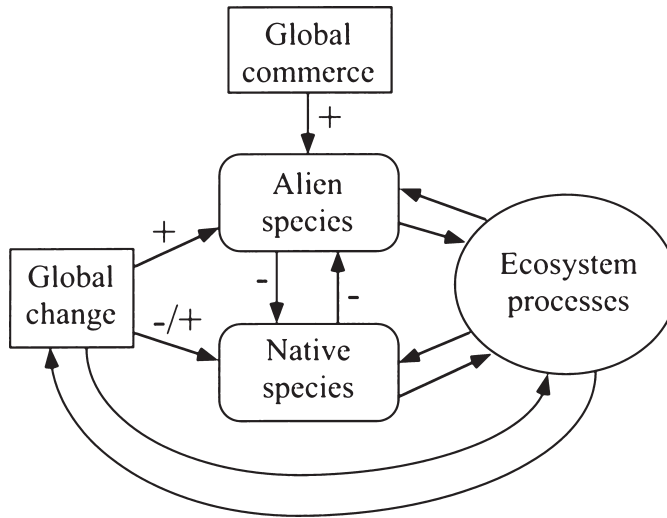
Fig. 1: Conceptual model of interactions among biological invaders, native species, ecosystem processes, global commerce, and global change. Arrows show directions of influence, and symbols next to arrows (in descending order: +, -/+, -) indicate whether a given influence is generally thought to be positive or negative. Because "ecosystem processes" encompasses several independent elements that are not easily generalized, arrows from this compartment are left blank. Global transport has brought invasive species to new regions, where some of these species suppress native populations. Together, native and alien species modulate ecosystem processes. Elements of global change such as nitrogen deposition, habitat fragmentation, and global change affect both ecosystem processes and the balance between native and alien species (Dukes & Mooney 1999).

Modelo conceptual de interacciones entre invasores biológicos, especies nativas, procesos ecosistémicos, comercio global y cambio global. Las flechas indican dirección de las interacciones, y los símbolos al lado (en orden ascendente o descendente +,-/+, -) indican si una influencia dada es en general interpretada como positiva o negativa. Debido a que el concepto de "procesos ecosistémicos" abarca varios elementos independientes que no son fácilmente generalizables, las flechas desde este compartimiento se dejan en blanco. El transporte global ha llevado especies invasoras a nuevas regiones, donde algunas de estas especies suprimen a las poblaciones de especies nativas. En conjunto, las especies nativas y foráneas modulan los procesos ecosistémicos. Elementos del cambio global tales como la deposición de nitrógeno, fragmentación de hábitat, y cambio global afectan tanto los procesos y el balance entre las especies nativas y foráneas (Dukes & Mooney 1999).

IMPACTS OF NON-NATIVE SPECIES

Geomorphology and soil disturbance regimes

Introduced animals and plants have altered geomorphic processes in many of western North America's ecosystems. Beaver (*Castor canadensis*) are native to some parts of the west, but have been introduced in areas beyond their original range (Johnson & Harris 1990). By building dams, beaver directly modify the morphology and hydrology of streams. Dams create ponds, slow the stream current, increase sediment retention, alter seasonal stream discharge regimes, and expand the influence of the water table (Naiman et al. 1988). Decomposition, nutrient cycling, and water quality are also altered by beaver ponds (Naiman et al. 1986). These effects can influence the composition of downstream plant and animal communities (Pollock et al. 1995).

Although the introduction of beaver can substantially alter stream geomorphology, the extent of these changes is limited by the number of suitable sites for beaver ponds (Johnston & Naiman 1990).

Just as beaver dams trap substrate and increase sedimentation in an area, other introduced animals cause soil to be lost. Many species contribute to erosion by disturbing the soil or overgrazing vegetation. Studies of these phenomena on California's Channel Islands led to the implementation of new land management practices. For instance, feral goats (*Capra hircus*) and sheep (*Ovis aries*) were removed or exterminated on some islands once their impacts on geomorphology and vegetation were understood (Schuyler 1987, Keegan et al. 1994, Laughrin et al. 1994). Before their eradication in 1987, sheep compacted the soils of Santa Cruz Island and overgrazed the plants. These activities suppressed woody species regeneration (Wehtje 1994),
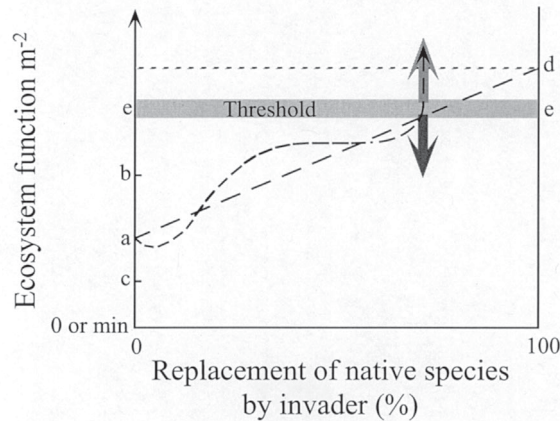
Fig. 2: Conceptual model of the impact of a plant invader on a given ecosystem function (such as flammability, water use, or isoprene emission) over the course of an invasion. Point (a) represents the average initial value of the function across the area of study. The individual species within the system have characteristic values on the y axis that lie between (b) and (c); thus the value for the initial system as a whole can vary between (b) and (c) depending on the species composition at a given time. In this scenario, the hypothetical invader has a characteristic value of ecosystem function that is considerably higher than the original species, represented by (d). As the invasion progresses, the composite value for the function of the area varies, as is represented by the dashed lines. If the invader were to replace all species at equal rates, then the average value might progress along the straight dashed line from (a) to (d). However, if the invader preferentially replaces certain species before others, the composite value will vary from line a-d, as is represented by the crooked dashed line. With some ecosystem functions there exists a threshold (e), at which point the variation from the initial average value may cause irreversible changes in the system (cf. Laycock 1991). If the function is flammability, for instance, the area might experience increased fire frequencies once the threshold was passed, which could lead to rapid changes in community composition. If these changes involve further invasion by other species, the average value of ecosystem function m^{-2} could change again, and in some cases might move outside the limits defined by the initial species or even by the invader (see arrows and crooked dashed line).

Modelo conceptual del impacto de una planta invasora sobre una función ecosistémica dada (tal como la inflamabilidad, uso de agua, o emisión de isoprenos) sobre el curso de una invasión. La especie individual dentro del sistema tiene valores característicos en el eje y que están entre (b) y (c); por lo tanto el valor para el sistema inicial como un todo puede variar entre (b) y (c) dependiendo de la composición de especies en un momento dado. En este escenario, el invasor hipotético tiene un valor característico de función ecosistémica que es considerablemente más alto que la especie original representada por (d). A medida que progresa la invasión, el valor compuesto para la función del área varía, lo que se representa por la línea en trazos. Si el invasor reemplazara a todas las especies a la misma tasa, entonces el valor promedio podría variar a lo largo de la línea recta en trazos desde (a) a (d). Sin embargo, si el invasor reemplazara preferencialmente a ciertas especies más que a otras, el valor competitivo variará desde la línea a-d, tal como lo representa la línea en trazos curvos. En algunas funciones ecosistémicas existe un umbral (e), punto en el cual la variación desde el valor promedio inicial puede causar cambios irreversibles en el sistema (cf. Laycock 1991). Si la función es la inflamabilidad, por ejemplo, el área podría experimentar un incremento en las frecuencias de fuegos una vez que el umbral ha sido cruzado, lo cual puede llevar a rápidos cambios en la composición comunitaria. Si estos cambios involucran la invasión adicional de otras especies, el valor promedio de la función ecosistémica m^{-2} podría cambiar nuevamente, en algunos casos podría moverse fuera de los límites definidos por las especies iniciales o incluso el invasor (véase las flechas y las líneas de trazos curvos).

reduced the amount of herbaceous cover (Klinger et al. 1994), and contributed to the development of deep hillslope gullies (Brumbaugh 1980). Feral goats on Santa Catalina Island (Coblentz 1980) and European rabbits (*Oryctolagus cuniculus*) on Santa Barbara Island (Halvorson personal communication) accelerated erosion by similar means. Herbaceous cover rebounded on these islands after the animals were removed (Klinger et al. 1994, Laughrin et al. 1994). Disturbance by feral pigs (*Sus scrofa*) may still contribute to erosion on the Channel Islands. Feral pig activity hampers regeneration of woody species such as the native oak *Quercus agrifolia* (coast live oak) on Santa Cruz Island (Peart et al. 1994).

On the California mainland, the range and population size of pigs has expanded since the 1950s (Waithman et al. 1999). Feral pigs are now the primary agents of soil disturbance in some California grasslands. Kotanen (1995)

found that pigs overturned 7.4 % of the surface of five Californian coastal meadows annually, changing the species composition and richness of the grubbed areas. Pigs may increase siltation of streams by turning up soil along streambanks and wallowing in the channel (Ray 1988, Peart et al. 1994).

Mountain goats (*Oreamnos americanus*), which are native to some parts of Washington, were transported outside of their range to that state's Olympic Mountains in the 1920s. The goats caused serious damage to native vegetation and increased erosion in alpine areas of Olympic National Park, leading to the development of a goat population management plan (Carlquist 1990).

We found no research on the effects of alien invertebrates on the geomorphology of western ecosystems. It seems likely that some burrowing invertebrate invaders have affected the movement of the substrate in which they live. For instance, since at least 1893, San Francisco Bay's terraces and margins have been under attack from the isopod *Sphaeroma quoyanum*. This native of Australia and New Zealand riddles sediments and structures with half-centimeter-wide burrows. Such burrows may increase erosion at the Bay's edge (Cohen & Carlton 1995).

Plant invaders can affect geomorphology by altering the stability of the substrate in which they live. For instance, two species of introduced beachgrass have slowed dune movement on the west coast of United States. The most widespread of these, *Ammophila arenaria* (European beachgrass), was imported from northern Europe around 1869 to stabilize dunes in San Francisco's Golden Gate Park (Lamb 1898). Three factors may have contributed to *A. arenaria*'s subsequent colonization of the majority of dunes on the United States' Pacific coast. First, widespread planting of *A. arenaria* continued for a period of 100 years (Wiedemann & Pickart 1996). Second, lateral growth of rhizomes allowed the grass to spread rapidly. Finally, living rhizome fragments may have washed down the shore to colonize new sites (Wallén 1980).

Ammophila arenaria collects sand more effectively than the previously dominant native grass *Leymus mollis* (native dune grass; Barbour et al. 1985, Barbour & Johnson 1988), and its invasion has caused the rapid development of steep, continuous foredunes along the coast. In some locations, foredunes have grown to a height of 10 m (Wiedemann & Pickart 1996). These large foredunes, which border the upper beach above the mean high tide line, may starve active inland dune systems of sand, causing them to become more static and allowing

vegetation to become established (Wiedemann & Pickart 1996). This phenomenon, in combination with the rapid spread of *A. arenaria* on the dunes themselves, has reduced the area of open dunes on the coast (Wiedemann 1984). In addition, the changes in foredune characteristics have led to a new alignment of some inland dunes. The dunes and swales inland of *Leymus* foredunes were oriented roughly perpendicular to the shore, but those inland of *A. arenaria* foredunes tend to run parallel to the coast (Barbour & Johnson 1988).

Wiedemann & Pickart (1996) argue that the Pacific northwest coast has experienced periods of slow foredune stabilization followed by strong erosion events for thousands of years, and suggest that although *A. arenaria* has accelerated sand stabilization, native plants would also eventually cause the formation of an unbroken foredune. However, a native-dominated foredune might not attain the height or strength of *A. arenaria* foredunes, and might be more rapidly eroded by waves during storms.

Another introduced species of beachgrass now dominates the foredunes of southern Washington, and alternates with *A. arenaria* as the dominant foredune species in the northern part of the state (Seabloom & Wiedemann 1994). This species is *Ammophila brevigulata* (American beachgrass), a native of the east coast and Great Lakes regions of North America. Both *Ammophila* species cause the formation of long, unbroken foredunes, but those formed by *A. brevigulata* are lower than those formed by *A. arenaria* (Seabloom & Wiedemann 1994).

As introduced beachgrasses reshape the west coast's dunes, introduced cordgrass species (*Spartina* spp.) stabilize sediments in its estuaries. The most widespread alien cordgrass is *Spartina alterniflora* (smooth cordgrass). This native of North America's east coast now grows in San Francisco Bay, Suislaw Estuary in Oregon, and in two locations in Washington (Daehler & Strong 1996). *Spartina alterniflora* outcompetes the native cordgrass *Spartina foliosa* in parts of San Francisco Bay where the two species co-occur (Callaway & Josselyn 1992). The upper boundaries of these two perennials are roughly the same, but *S. alterniflora* can colonize areas 9 to 20 cm below the lower limit of the native (Callaway & Josselyn 1992). This encroachment into lower tidal areas extends the marshlands and reduces mudflat area. The denser growth and thicker stems of *S. alterniflora* slow the tidal flow more effectively, causing suspended sediment to precipitate and become trapped in the alien's thick network of roots and rhizomes (Daehler &

Strong 1996). In a study of a New Zealand estuary, Bascand (1970) found that areas colonized by *S. alterniflora* accumulated up to 5 cm of sediment per year, while open mud flats trapped little or no sediment. Sayce (1991)[1], who has studied *S. alterniflora* in Washington, asserts that the invader can trap as much as 15 cm of material annually. As sediment accumulates in formerly open areas, these areas may rise above the intertidal zone. In some estuaries, sediment accretion and growth of *S. alterniflora* has restricted tidal channels and waterways (Asher 1991). For example, the invader colonized and threatened the flow capacity of a major flood control channel in San Francisco Bay, leading to the initiation of an eradication program (Daehler 1996).

Three other introduced cordgrass species, *S. anglica*, *S. densiflora*, and *S. patens*, now grow in estuarine ecosystems of the Pacific coast (Daehler & Strong 1996), and may cause similar changes to those driven by *S. alterniflora*. *Spartina anglica*, which has invaded Puget Sound in Washington, is particularly well known for its ability to rapidly colonize mudflats and accrete sediment in European marshlands (Thompson 1991, Daehler & Strong 1996).

Exotic invaders also affect riparian geomorphology. Shrubs of the genus *Tamarix* have caused the most widespread changes. Recent estimates suggest that *Tamarix* spp. (tamarisk, salt cedar) has invaded approximately 4,700 km^2 of western United States floodplain (Zavaleta 2000). Blackburn et al. (1982) studied the impact of *Tamarix* spp. invasion on sedimentation processes in the Brazos River in Texas. As the phreatophytic shrub encroached onto formerly unoccupied sandbanks along the river, it stabilized sediments and slowed water velocity. As water slowed, sediment deposition increased and the river channel narrowed. When channel sizes are reduced, flooding frequencies and flood levels increase. *Tamarix* has caused similar changes to the geomorphology of the Green River in Canyonlands National Park, Utah (Graf 1978).

Other exotic plant species may also increase sediment deposition, although the evidence is less solid. *Arundo donax* (arundo, giant reed) has invaded many waterways of southern and central coastal California (Hickman 1993, Dudley & Collins 1995). This tall perennial reed purportedly traps and stabilizes more

sediment than native vegetation, thus decreasing channel sizes (Frandsen & Jackson 1993). *Arundo* is also said to grow densely enough to substantially reduce the carrying capacity of small waterways (Robbins et al. 1951). However, no data have been published to support these observations. In larger streams and rivers, rafts of the reed can lodge against natural obstructions, bridges, or culverts, forming debris dams (Frandsen & Jackson 1993). *Arundo* clogging is suspected to have played a role in the bursting of a levee on the Santa Margarita river, which caused $12.5 million dollars in damage to the Camp Pendleton military base (La Rue 1996). Mats of *Senecio mikanoides* (German ivy) may also form debris dams in some California waterways, redirecting water out of its channel (Chippin personal communication).

Another exotic plant species stabilizes sediment in some Arizona streams. During floods, mats of *Cynodon dactylon* (bermudagrass) protect streambanks from erosion and shelter the basal fragments of native aquatic macrophytes. Recovery of the aquatic macrophyte communities proceeds more rapidly in these stabilized sites than in areas without *C. dactylon* (Dudley & Grimm 1994).

Since its introduction for landscaping purposes, *Cortaderia jubata* (pampas grass) has colonized disturbed areas such as eroding banks, dry washes, cliffs, and logged redwood forests throughout coastal California (Kerbavaz 1985). Dense stands of the perennial must alter erosion rates from invaded areas, but no studies have quantified these changes.

Invading plants can also increase rates of erosion. The biennial forb *Centaurea maculosa* (spotted knapweed) is replacing native bunchgrasses throughout many rangelands of western North America (Roché & Roché 1988, Tyser & Key 1988, Lindquist et al. 1996). Lacey et al. (1989) found greater losses of sediment and greater runoff from areas dominated by *C. maculosa* than from bunchgrass communities. The *C. maculosa* community's larger fraction of bare ground may explain these differences.

From the above examples it is clear that in the case of both plants and animals, some invaders accelerate the process of erosion, and others stabilize substrates or trap sediments. Of the invasive plants that affect geomorphology, most slow erosion. Of the nonindigenous animals, most accelerate erosion, especially on islands. In addition to the types of species mentioned above, some biological invaders influence geomorphic processes through their

[1] SAYCE K (1991) Species displaced by *Spartina* in the Pacific Northwest. In: Mumford TF Jr, P Peyton, JR Sayce & S Harbell (eds) *Spartina* workshop record: 26-27. Washington Sea Grant Program, Seattle, Washington, USA.

effects on disturbance regimes. For instance, alien plants that alter the fire frequency or intensity in an area also affect erosion because fire reduces plant and litter cover (Swanson 1981). We discuss invaders that alter fire regimes in the next section.

Fire regimes

Exotic grasses have replaced or currently threaten vast regions of western deserts and shrublands through their influence on fire regimes (D'Antonio & Vitousek 1992). The invading grasses occupy gaps between native plants in these sparsely vegetated systems, creating a continuous path of fine fuel that promotes the spread of fire. The grass populations tend to rebound quickly after fires, but many of the native perennials recover slowly. Short fire-return intervals decimate populations of many shrubs and desert perennials. Thus, by accelerating fire frequencies, grass invaders can reduce the density of widely spaced perennials, turning shrublands to annual grasslands.

The most dramatic conversion of this kind is occurring in the mixed-shrub steppe of Nevada, western Utah, southern Idaho, eastern Oregon, and eastern Washington. Many areas formerly dominated by *Artemisia tridentata* (big sagebrush) and other shrubs are today covered with exotic annual grasses, primarily *Bromus tectorum* (cheatgrass; Young & Evans 1978, Whisenant 1990, Billings 1994, Pellant & Hall 1994) and *Taeniatherum caput-medusae* (medusahead, Young 1992). Mack (1981) chronicled the invasion of *B. tectorum* into the region, and Whisenant (1990) documented the accompanying change in fire-return intervals. Pinyon-juniper woodland ecosystems of the Great Basin region have undergone a similar metamorphosis due to anthropogenic disturbance of native vegetation and the spread of *B. tectorum* (Billings 1994).

Introduced grasses and forbs also threaten to accelerate fire cycles in portions of the Mojave and Sonora deserts. The most prevalent exotic annuals in these deserts are *Bromus madritensis* ssp. *rubens* (red brome, syn. *Bromus rubens*) and *B. tectorum,* but *B. trinii* (Chilean chess), *Schismus barbatus* (Mediterranean grass), and *Erodium cicutarium* (redstem filaree) are also common in some areas (Brown & Minnich 1986, Hunter 1991, Rundel & Gibson 1996, Brooks 1999). Hunter (1991) studied populations of brome grasses in the transition zone between the Mojave and Great Basin deserts, and found that a series of wet years allowed *B. madritensis* to become quite dense. At its peak in 1988, *B. madritensis* produced 34 g m^{-2}, which was 97 % of that year's total biomass production. Although exotic annuals are the most prolific invaders of North America's deserts, perennial species also pose a threat to the Sonoran desert. *Cenchrus ciliaris* (Buffel grass, syn. *Pennisetum ciliare*) has been widely planted in northern Mexico as a forage species for cattle, and was planted in the southwestern United States by the Soil Conservation Service and the Arizona Department of Transportation (Pater personal communication). This southern African perennial can survive in a wide variety of Sonora desert microenvironments, and has spread into many undisturbed areas (Burgess et al. 1991, Búrquez & Quintana 1994). Lehmann lovegrass (*Eragrostis lehmanniana*), another African perennial that was once recommended by the Soil Conservation Service, has also spread from planted areas and become dominant in some areas of Arizona's Sonora desert (Anable et al. 1992). Grass litter decomposes slowly in dry desert climates, maintaining a continuous fuel load through years of low biomass production. Fires carried by grass litter threaten populations of native annuals (Hunter 1991) or long-lived perennials (Brown & Minnich 1986, Búrquez & Quintana 1994) in at least three types of North American deserts.

Deliberate post-fire seeding and accidental invasion of non-native annuals into chaparral and coastal sage scrub may facilitate an increase in fire frequencies in some areas of southern California. Planted annuals such as the grasses *Lolium multiflorum* (Italian ryegrass) and *Vulpia myuros* (rattail fescue) and the mustard *Hirschfeldia incana*, and invaders such as *Bromus madritensis* and *B. diandrus* (ripgut brome) have recently increased in dominance in these ecosystems (Keeley 1995, Minnich & Dezzani 1998). These exotics persist through frequent fires more successfully than native shrubs such as *Adenostoma fasciculatum* (chamise), *Ceanothus oliganthus*, and *Salvia mellifera* (black sage; Zedler et al. 1983, Keeley 1995). A combination of increased fire frequencies, competition from introduced annuals, and other anthropogenic factors may drive the replacement of chaparral and coastal sage scrub ecosystems by grassland in many areas of southern California (Keeley 1995, Minnich & Dezzani 1998).

Fire-promoting exotic grasses also threaten riparian ecosystems. *Arundo donax* (arundo, giant reed) has invaded many waterways of southern and central coastal California. The tall perennial reed quickly colonizes areas left bare

from flooding, achieving dominance along riverbanks and even in some estuaries (Dudley & Collins 1995). *Arundo* increases the fuel load in riparian zones and provides an unbroken fuel corridor along which fire can spread (Jackson 1993, Scott 1993). Increased fire frequencies may prevent recovery of native plant species and purportedly changes the successional cycle of the cottonwood-willow riparian system, converting the vegetation to an *Arundo* monoculture (Bell 1993).

In western North America, most of the invasive species that affect fire regimes are grasses, and most of these species decrease fire-return intervals. Many native species, especially longer-lived plants in arid regions, cannot tolerate these frequent fires. Of all the ways that invasive species modify ecosystems in western North America, this impact on fire regime may have the most widespread repercussions for native species.

Hydrology

The invasion of exotic plants into North American ecosystems has altered the hydrology of vast areas of western North America. Invasions of *Tamarix* spp. have lowered water tables in many riparian zones of the southwestern United States (e.g., Neill 1983, Weeks et al. 1987). On a per-unit-leaf-area basis, water loss of *Tamarix* is comparable to that of native phreatophytes (Sala et al. 1996, Cleverly et al. 1997), so what characteristics of *Tamarix* lead to such great water loss? Two mechanisms have been proposed. First, monospecific stands of the invasive shrub may develop a higher leaf area index (LAI) than would be found in native stands. Second, *Tamarix* stands tend to occupy a wider cross-section of the riparian zone than native stands (Sala et al. 1996).

Spanish colonists began altering the composition and hydrology of California grasslands around 1769 when they introduced plants from Mediterranean Europe (Frenkel 1970). Until that time, perennial grasses such as *Nassella pulchra* (purple needlegrass) probably dominated most California grasslands (Heady 1988; but see Mooney et al. 1986). Under conditions of heavy grazing and possibly drought, introduced annuals outcompeted most of the original species (Hendry 1931, Mack 1989, Rejmánek et al. 1991). The annual grasses such as *Avena* spp. and *Bromus* spp. that now dominate extensive areas use less of the available deep water over the course of a growing season than do native perennial grasses, probably because they senesce earlier and have shallower roots (Holmes & Rice 1996, Gerlach 2000). The excess water left by annual grasses may have created favorable conditions for *Centaurea solstitialis* (yellow starthistle, Dyer & Rice 1999), a more recent invader of these grasslands (Maddox & Mayfield 1985). *Centaurea* is a late-season annual that now draws deep soil moisture down to levels found under native perennial grasses (Gerlach 2000). Borman et al. (1992) observed similar soil moisture dynamics among introduced annual and native perennial grasses and *C. solstitialis* in southwestern Oregon. Hydrologic changes caused by grassland invaders may affect the establishment of native woody perennials (Da Silva & Bartolome 1984, Gordon & Rice 1993).

The replacement of native and naturalized systems by *Eucalyptus* spp. forests (Boyd 1985, Bulman 1988, Westman 1990) may have altered the hydrology of large tracts of California, although no studies have quantitatively documented these changes. *Eucalyptus* (primarily *Eucalyptus globulus*, blue gum) forests have replaced many different ecosystem types in California. These forests probably altered hydrology most drastically where they replaced grassland. *Eucalyptus* roots grow much deeper than those of grassland species (Canadell et al. 1996), and extract water from lower in the soil profile. *Eucalyptus globulus* is the only widespread woody alien known to transport deep soil moisture to shallower layers through hydraulic lift (Dawson personal communication). It is not known whether this process eases drought stress for nearby shallow-rooted plants, as occurs around other hydraulic lifters (Dawson 1993). Evergreen eucalypts transpire year-round, but California's grasslands are mostly dormant in the summer. Although *Eucalyptus* forests probably transpire more water than grasslands on an annual, per-area basis, the forests have greater surface roughness and deeper litter layers than grasslands (Poore & Fries 1985, Robles & Chapin 1995), and may lose less water to surface evaporation. On balance, eucalypt forests probably extract more water from the ground than California grasslands. Such a difference has been observed in South Africa, where Van Lill et al. (1980) documented a dramatic reduction in runoff from a grassland after its conversion to an *E. grandis* plantation. In areas where *Eucalyptus* forests have replaced native forests or woodlands, alterations to local hydrology were probably less drastic.

Replacement of native perennial vegetation by *Bromus tectorum* in western shrublands (see above) reduced rooting depths and shortened the period when plants in these systems are photosynthetically active. As a consequence, annual evapotranspiration has declined in some of these systems (Cline et al. 1977, Kremer & Running 1996).

Although relatively few studies have compared the hydrology of invaded and pristine plant communities in western North America, these few studies have examined changes caused by some of the most widespread species that are likely to have effects. Two alien genera, *Tamarix* and *Eucalyptus*, probably increase water use rates beyond what the invaded ecosystems experienced previously. The invasion of California's alien-dominated annual grasslands by *Centaurea solstitialis* may move the hydrological cycle closer to a pre-European settlement dynamic. In some parts of western North America, the invasion of annual grasses has reduced plant water use, primarily by reducing the abundance of deeply rooted species.

Climate and microclimate

Biological invasions have altered moisture transport and land surface characteristics of a large portion of western North America (see above). However, the extent and implications of these changes are poorly understood. Recent studies have indicated that changes in vegetation types can alter local or regional climatic patterns (Lean & Warrilow 1989, Shukla et al. 1990, Chase et al. 1999, Hoffman & Jackson 2000). While it seems possible that some invaders of western North America, particularly the annual grasses, have altered the land surface characteristics and hydrology of sufficient area to affect the regional climate, this hypothesis has not yet been tested.

Plant invaders can also alter the microclimate of invaded areas. For instance, dense stands of *Ammophila arenaria* sharply reduce temperatures and available light at the underlying surface of the Pacific coast's dunes relative to stands of the native grass *Leymus mollis* (Barbour et al. 1985). *Spartina alterniflora* may similarly reduce light levels under the plant canopy of marshes, which could depress estuarine algal production (Callaway & Josselyn 1992). Soil temperature, soil moisture, and light conditions under the plant canopy affect the germination and establishment success of plants (Evans & Young 1970, Evans & Young 1972), and the suitability of habitat for animals.

Invasive species have undoubtedly altered microclimates in many other ecosystems, but we did not find studies that documented these changes.

Composition of the atmosphere

Biological invaders can alter the flux of gases between the land surface and the atmosphere. In the United States, annual emissions of volatile organic compounds (VOCs) from vegetation equal or exceed anthropogenic emissions (Guenther 1997), although the biogenic output is more evenly distributed across the landscape. Because vegetation contributes such a great proportion of atmospheric VOCs, and because plant species vary widely in their rate of VOC emission (Evans et al. 1982, Winer et al. 1992, Arey et al. 1995), regional atmospheric VOC pools depend largely on the species composition of local plants. Invasive species that overrun large areas can alter regional VOC emissions and atmospheric composition (Monson et al. 1995), with important consequences for atmospheric chemistry and air quality (Mooney et al. 1987). Air quality of the west coast may have been adversely affected by the introduction of *Eucalyptus globulus* and *Arundo donax*, which emit high levels of isoprene relative to many native species (Evans et al. 1982, Hewitt et al. 1990, Arey et al. 1995).

The invasion of plants of one growth form into a region dominated by another may alter the local rate of CO_2 uptake and storage. For instance, the replacement of shrublands and pinyon-juniper woodlands by annual grasslands probably reduces long-term carbon storage in biotic pools. Conversely, replacement of grassland with *Eucalyptus globulus* or other woody species may increase both biotic carbon storage and net primary productivity (NPP, Robles & Chapin 1995).

Invaders may also alter the emission of NO_x, N_2O, NH_3, and CH_4 from the landscape. Chatigny et al. (1996) found evidence that the species composition of a plant community affects local rates of nitrification and denitrification, which in turn moderate the emission of nitrogenous gases by the microbial community (Schlesinger 1991). By creating ponds, beaver (*Castor canadensis*) can substantially increase methane emissions from an area (Yavitt et al. 1992). Naiman et al. (1991) estimated that North America's expanding beaver population has contributed 1 % of the recent rise in atmospheric methane. Methane release rates from wetlands also

depend on the biomass and structural properties of the inhabitant vascular plants (Sebacher et al. 1985, Schimel 1995, Verville et al. 1998). Invaders such as *Lepidium latifolium* (perennial pepperweed) and *Lythrum salicaria* (purple loosestrife) change the amount and composition of wetland vegetation in western North America, and may alter regional methane emission, although this remains unstudied.

Plant invaders can also affect atmospheric composition by altering fire frequencies. During fires, carbon, nitrogen and other elements enter the atmosphere through gasification, volatilization, and convection (Christensen 1994). However, the contribution of exotic grass-fueled fires to changes in atmospheric composition is estimated to be small (D'Antonio & Vitousek 1992).

The effects of biological invaders on the composition of the atmosphere remain largely unstudied. Although these effects are probably small at the global and regional scales, they may in some cases (such as near large eucalypt forests, in the case of VOCs) be locally important.

Nutrient cycling and soil chemistry

Non-native plants and animals can alter ecosystem nutrient cycling and soil chemistry through a number of mechanisms. Nitrogen-fixing invaders increase the rate of N input to a system when they replace non- or less-efficiently fixing plants, and when they colonize open areas. Vitousek & Walker (1989) and Vitousek et al. (1987) found that the invasion of an N-fixing plant into a young ecosystem in Hawaii increased the rate of ecosystem N accumulation more than fourfold.

Horticulturists have introduced many species of leguminous European shrubs to the western United States, including gorse *Ulex europaea*, and the brooms *Cytisus scoparius*, *Genista monspessulana* and *Spartium junceum*. The nitrogen-fixing capacity of brooms has stimulated research into their potential as yield enhancing understory shrubs in commercial *Pseudotsuga menziesii* (Douglas-fir) plantations. Studies have focused on *C. scoparius*, which fixes nitrogen year-round under mild conditions, albeit at relatively low levels (Wheeler et al. 1979, Wheeler et al. 1987). Helgerson et al. (1979) integrated a year's worth of nitrogenase activity measurements on a young stand of broom in Oregon, and estimated an annual fixation rate of 35 kg N ha^{-1} year^{-1}. This value itself represents a substantial input, but because this method of estimation is imprecise, the actual fixation rate could be twice as high (Wheeler et al. 1987). In addition to the brooms and gorse, several leguminous annual and perennial herbs such as *Medicago polymorpha* (burr medic), *Melilotus alba* (white sweetclover), and *Trifolium hirtum* (rose clover) have invaded Western ecosystems (Hickman 1993). It is not known whether all of the invasive legumes actively fix N.

Nitrogen inputs to a system from N-fixing alien plants may be constrained by the compatibility of the plants with local symbionts. Absence of a compatible *Rhizobium* strain could explain the low nodulation on *C. scoparius* roots observed by Wheeler et al. (1987) in Oregon and Scotland, although acidic soil conditions or other factors could also have limited nodulation.

Some plant invaders may decrease nitrogen inputs in their vicinity by leaching chemicals that reduce the ability of other species to fix N (Rice 1992). In glasshouse and pasture studies in New Zealand, Wardle et al. (1994) found evidence that decomposing leaves of the invasive thistle *Carduus nutans* inhibit nitrogen fixation by *Trifolium repens*. *Carduus nutans* has invaded many areas of western North America, but no published studies have examined whether this thistle adversely affects growth and nitrogen fixation of native legumes.

Both N-fixing and non-fixing plants directly affect the nutrient retention of ecosystems by moderating erosion of nutrient-rich topsoil, and by sequestering available soil nutrients, thus reducing leaching losses. Gholz et al. (1985) found that the invasive annual *Senecio sylvaticus* took up a large fraction of the nutrients released from unburned clear-cut stands of old-growth Douglas-fir in Oregon. Invaders can also indirectly modulate N losses by influencing soil moisture and nitrate levels, which can constrain denitrification rates. We found no studies of invasive plants that examined indirect effects on nutrient retention.

Although fires increase short-term N-availability in a system, frequent fires generally cause long-term loss of N (Ojima et al. 1994), depending on grazing practices (Hobbs et al. 1991). Alien species that accelerate fire cycles (such as those mentioned above) could eventually increase N losses from ecosystems.

Plant species strongly influence the rate at which nutrients cycle within an ecosystem through litter-quality feedbacks (Wedin & Tilman 1996, Evans et al. 2001; for review see Hobbie 1992). The invasion of a species with rapidly decomposing litter into an ecosystem

dominated by plants with slow-decomposing litter will accelerate net nutrient mineralization in the system (Van Vuuren et al. 1992, Van Vuuren & Berendse 1993, Van Vuuren et al. 1993). For instance, leaves of the notorious wetland invader *Lythrum salicaria* (purple loosestrife) have higher phosphorus (P) concentrations and decompose more quickly than shoots of native *Typha* spp. (Emery & Perry 1996). These characteristics will force changes in the nutrient dynamics of invaded wetlands that may accelerate eutrophication of downstream water bodies.

Introduced detritivores also alter ecosystems' internal nitrogen cycling. In Kansas' tallgrass prairie, James (1991) observed that the invasion of European earthworms has decreased nutrient mineralization and soil turnover rates. At least 45 species of exotic earthworms have been introduced to North America north of Mexico (Reynolds 1995). These species have been particularly successful in disturbed habitats, and also dominate some wildland habitats including southern California chaparral and riparian zones (Kalisz & Wood 1995). It is unclear how detritivore invasions have affected these ecosystems.

A few of western North America's most invasive plants release compounds that alter the soil's nutrient availability or suitability for other species of plants. For instance, the ubiquitous tumbleweed *Salsola tragus* (syn. *S. iberica*) releases oxalate in leachate from its canopy and litter (Cannon et al. 1995). The leached oxalic acid increases phosphorus (P) availability in the soil by solubilizing it from the pool of inorganic-bound soil P. Other western invaders such as *Halogeton glomeratus* and some plants in the Oxalidaceae probably affect P availability similarly, as they also produce high concentrations of oxalic acid (Kingsbury 1964, Whitson et al. 1996).

The iceplant *Mesembryanthemum crystallinum* exploits its high salt tolerance to outcompete native species in coastal areas of California. This South African annual stockpiles salts in living tissue. Once the tissue has senesced, rainfall and fog drip leach the salts out and deposit them on the soil surface. The high concentrations of salt that accumulate around populations of this grassland invader exclude competitors through osmotic interference (Vivrette & Muller 1977).

Another iceplant that plagues California's coastal plant communities, *Carpobrotus edulis*, modifies soil in a different way. This rapidly spreading succulent acidifies the soil around its roots (D'Antonio 1990), through an as yet unstudied mechanism. Investigations in England suggest that the common west coast invader *Ulex europaea* may affect soils similarly (Grubb et al. 1969, Grubb & Suter 1971). Changes in soil pH can influence the dominance of different plant species in old fields (Tilman & Olff 1991) and montane forests (Goldberg 1985).

Other introduced species release compounds that can inhibit their own growth, as well as that of competitors. Phytotoxic chemicals that leach from the leaves and litter of eucalypts during rainfall and fog drip events can directly inhibit germination and retard seedling growth of grasses, as well as of the eucalypts themselves (del Moral & Muller 1969, del Moral & Muller 1970).

Nutrient cycles and soil properties are subject to change by many of western North America's invasive species. The most widespread change may be an increase in N inputs from nonindigenous legumes. However, few researchers have studied the amount of atmospheric N fixed by these species. Exotic earthworms may also have caused important and widespread changes in nutrient cycles, but these changes remain unstudied.

Productivity and decomposition

An ecosystem's live biomass (LB) and NPP may respond to the addition of a species with novel traits. For instance, invaders that access or use existing resources more completely or efficiently than native plant species, or that produce more readily mineralizable litter than native species, may cause increases in LB and NPP. Examples of exotic species that access previously untapped water and nutrient stores can be found in previous sections (see sections on hydrology and nutrient cycling). Invaders that represent a new life form or that eliminate a prominent life form may also alter an area's LB and NPP. Unfortunately, relatively few studies of invaders in western North America have included data on these basic ecosystem properties.

Along the edges of San Francisco Bay, invading *Spartina alterniflora* produces six to seven times as much aboveground biomass per unit area as the native cordgrass *Spartina foliosa*, and 1.6 to 3.2 times as much belowground biomass (Callaway & Josselyn 1992). The great aboveground production of *S. densiflora*, deposited as wrack on the upper marsh in Humbolt Bay, California, smothers native marsh species, opening space for further

S. densiflora invasion (Daehler & Strong 1996).

Along the California coast, *Ammophila arenaria*-dominated beach communities have up to three times as much standing biomass as native-dominated communities (Barbour & Robichaux 1976, Pavlik 1983a). The difference in aboveground biomass of stands of *A. arenaria* and the native perennial grass *Leymus mollis* stems from *A. arenaria*'s higher nitrogen use efficiency, greater allocation of nitrogen and photosynthetic assimilate to leaf blades, different architecture, and slower leaf senescence (Pavlik 1983a, 1983b, 1983c).

Robles & Chapin (1995) compared adjacent exotic-dominated annual grassland and eucalypt-covered sites in the San Francisco Bay area. Annual aboveground production of *Eucalyptus globulus* forests was more than twice that of grassland, and the layer of slow-decomposing *E. globulus* litter had grown nine times thicker than the litter layer of the grassland.

Growth and decomposition rates of primary producers can be affected by organisms on other trophic levels. Plant pathogens that attack one of the dominant species in an ecosystem can, at least temporarily, lower the system's productivity and live biomass. At least three exotic fungi are causing widespread damage to western trees, and must have temporarily lowered the productivity of some forests. The fungal pathogen *Fusarium subglutinans* f. sp. *pini*, endemic to the southeastern United States, causes pitch canker disease in a number of coniferous tree species (Storer et al. 1994). The disease appeared in California in 1986 (McCain et al. 1987), and spread rapidly, killing off *Pinus radiata* stands along much of the coast. The disease has now reached all three of California's relictual *P. radiata* stands (Gordon et al. 1997), and may eventually infect as many as 85 % of the trees in these stands (Wood personal communication). Pitch canker has also been found in a native *Pinus attenuata* stand near Mendocino (Storer et al. 1994).

The fungus *Cronartium ribicola*, which causes white pine blister rust, has infected pines in the Cascades, Rocky Mountains, and the Sierra Nevada (Kinloch & Dulitz 1990). Growth of the pathogen can rapidly girdle and kill shoots of pines in the subgenus *Strobus* (white pines), or lead to their attack by *Dioryctria* spp. larvae. White pine blister rust epidemics generally lead to the loss of all infected seedlings and saplings, and the death of many adult trees (Kinloch & Dulitz 1990, Tomback et al. 1995).

A third imported fungus has attacked the roots of Port-Orford-cedar (*Chamaecyparis lawsoniana*) throughout its native range in southwestern Oregon and northwestern California. This fungus, *Phytophthora lateralis*, probably arrived from Asia on ornamental plants sometime in the 1920s. A field survey of three infested drainages found 46 % mortality of Port-Orford-cedar and 10 % mortality of another native, Pacific yew (*Taxus brevifolia*, Murray & Hansen 1997).

The recent invasion of Asian clams (*Potamocorbula amurensis*) has probably increased consumption rates of bacterioplankton and phytoplankton in San Francisco Bay. These clams, which can reach densities as high as 10,000 individuals m^{-2} (Carlton et al. 1990), filter the water column more than once per day in deep waters, and as much as 13 times per day in shallow waters (Werner & Hollibaugh 1993). This rapid filtration equals or exceeds planktonic growth rates, and may affect the standing crop of plankton and intensity of the annual spring algal blooms in San Francisco Bay.

Although relatively few studies have compared the productivity of invaded and uninvaded communities in western North America, it seems likely that most invasive plants have increased resource use of invaded communities, and also increased ecosystem-level productivity. Invasive species that alter disturbance regimes or otherwise eliminate other life forms from the community may be the most common exceptions to this trend. The effects of invasive animals on primary productivity are rarely examined, and we can only speculate that these species have had relatively little effect on the productivity of most ecosystems, excepting the case of Asian clams in San Francisco Bay.

Native species

Although biological invaders add to the species richness of an area upon their arrival, some can eventually cause the decline or even extinction of native species through predation, competition, disease, or replacement of resource species. In fact, the spread of biological invaders is generally regarded to be the second greatest agent of species endangerment and extinction after habitat destruction (Wilcove et al. 1998). As a general rule, native populations are more likely to be impacted by invaders if they are in isolated systems such as on islands, in lakes or in streams than if they are on the mainland (D'Antonio & Dudley 1995).

Introduced fish and amphibians have suppressed native fish and amphibian populations in the majority of lakes and rivers in western North America. Non-native bullfrogs (*Rana catesbeiana*) prey on and compete with yellow-legged frogs (*Rana boylii*) (Moyle 1973, Kupferberg 1997), and introduced predatory fish appear to be a factor in the decline of mountain yellow-legged frogs (*Rana pipiens*) in Yosemite National Park (Drost & Fellers 1996). Bullfrogs and exotic fish both may have contributed to the decline in red-legged frog (*Rana aurora*) populations (Kiesecker & Blaustein 1998, Adams 2000).

Nonindigenous fish species are dominant through most of the San Joaquin river drainage, and the entire Colorado river drainage, where most of the native fish species are listed as threatened or endangered (Moyle 1986). The exotic protozoan *Myxobolus cerebralis*, the causative agent of whirling disease, is likely responsible for recent declines in populations of the rainbow trout (*Oncorhynchus mykiss*) (Nehring & Walker 1996, Bergersen & Anderson 1997). However, in many other cases, the decline of native fish can be directly attributed to competition with or predation by fish species that were introduced for sportfishing. Such is the case with the endangered razorback sucker (*Xyrauchen texanus*) in the Colorado river basin (Minckley et al. 1991). There, heavy predation by introduced fish on larval razorback suckers prevents the regrowth of native populations. Some suspect that the thicktail chub (*Gila crassicauda*), a native fish species that once populated the Sacramento-San Joaquin delta, was extirpated by the predation of introduced largemouth bass (*Micropterus salmoides*) and striped bass (*Morone saxatilis*, Cohen & Carlton 1995). Although non-native fish species have depressed populations of native fauna in many western rivers, global extinctions such as that of the thicktail chub are rare (Moyle & Light 1996).

Just downstream from the thicktail chub's former habitat lies one of the world's most biologically polluted ecosystems, the San Francisco Bay estuary (Cohen & Carlton 1998). Invaders have relegated native species to obscurity in much of this isolated system. The most abundant invader is probably the Asian clam (*Potamocorbula amurensis*). This small bivalve blankets sediments in many regions of the bay (see above), precluding the establishment of other benthic organisms (Carlton et al. 1990, Cohen & Carlton 1995). Another invader, the mudsnail *Ilyanassa obseleta*, has usurped much of the former habitat of *Cerithidea californica*, relegating the native mudsnail to the estuary's highly saline margins (Race 1982). Advancing across the mudflats, *Spartina alterniflora* has reduced feeding habitat for many species of shorebirds (Callaway & Josselyn 1992). In creeks that feed into San Francisco Bay, two species of introduced crayfish (*Orconectes virilis* and *Pacifastacus leniusculus*) may have contributed to the extinction of the native sooty crayfish (*Pacifastacus nigrescens*). These invaders may now be factors in the decline of the Shasta crayfish (*Pacifasctacus fortis*) in other regions of California (Light et al. 1995).

At one time, 17 of 19 threatened or endangered plant species on California's Channel Islands were imperiled by exotic species, primarily feral animals (D'Antonio & Dudley 1995). Feral animal disturbance also lowered soil mite diversity (Bennett 1987). Removal of livestock and feral fauna may have allowed regrowth of threatened populations on some of these islands, but *Foeniculum vulgare* (fennel) and other invasive plants have also benefited from the reduction in herbivory (Beatty & Licari 1992, Brenton & Klinger 1994). Persistent alien plants may now pose the greatest risk to some of the Channel Islands' beleaguered native plant populations.

Although native populations in isolated systems are at the greatest risk from biological invaders, native species in mainland terrestrial ecosystems can also be affected. Some dramatic instances have been mentioned in the above sections (e.g., displacement of western shrublands and California's native grassland community by introduced annual grasses, attack of California's relictual *Pinus radiata* stands by the pitch canker fungus *Fusarium subglutinans*, among others); we add and expand on a few examples here.

Argentine ants (*Linepithema humile*) have been introduced to every continent except Antarctica (Hölldobler & Wilson 1990), and have spread to much of western North America, including California, Arizona, southern Nevada, and Mexico (Wheeler & Wheeler 1986). The invaders displace native ant colonies in California (e.g., Ward 1987, Human & Gordon 1996, Human & Gordon 1997), and possibly throughout the zone of invasion. The displacement of native seed-burying ants by Argentine ants has reduced the establishment of some native shrubs in South Africa (Bond & Slingsby 1984, Slingsby & Bond 1985), and may affect plant species distributions in California grasslands as well (Human 1996).

Argentine ants are known to tend aphids and scale insects; the ecological consequences of this behavior have yet to be investigated (Human 1996).

Non-native eastern gray (*Sciurus carolinensis*) and fox (*S. niger*) squirrels have developed large populations in and around California's suburban environments, particularly in the San Francisco Bay area. Native western gray squirrels (*S. griseus*) have been displaced from some areas where they overlapped with the introduced species, but they maintain dominance in xeric sites (Byrne 1979).

Physical disturbance by feral burros (*Equus asinus*) once caused contamination of water sources and local elimination of native plant species in Death Valley, California. These burros may have once contributed to the decline of native bighorn sheep (*Ovis Canadensis*, McMichael 1964 as cited by Woodward 1976), but the population of burros has now been effectively controlled (Loope et al. 1988).

According to Vuilleumier (1991), most of Mediterranean California's non-native bird species have only small populations or are restricted to urban environments, and are unlikely to adversely impact native species. However, some of the state's most abundant bird species were introduced from elsewhere, including the European starling (*Sturnus vulgaris*), house sparrow (*Passer domesticus*), and rock dove (*Columbia livia*). Starlings are thought to have the most negative impact on native bird species, as they occupy the nest sites of other cavity-nesting birds. This behavior may be contributing to the decline of the purple martin (*Progne subis*) in California (Small 1994).

Exotic plant invasions can also reduce the amount of habitat available for native birds. An invasion of *Tamarix* spp. at Eagle Borax Spring in Death Valley, California, caused a large marsh to dry up, reducing habitat for migratory birds (Neill 1983). Subsequent removal of the invader led to the return of surface water and wildlife. Along western North American rivers, stands of *Tamarix* spp. (Cohan et al. 1978, Hunter et al. 1988) and *Elaeagnus angustifolia* (Russian-olive, Knopf & Olson 1984) support a more depauperate avian fauna than do native stands. Government-subsidized replacement of cottonwood-dominated riparian vegetation with invasive Russian-olive may have reduced habitat for cavity-nesting birds (Olson & Knopf 1986). Invasions of *Lythrum salicaria* (purple loosestrife) are thought to have degraded wetland habitat for waterfowl and other wildlife throughout much of North America (Thompson 1987) although many claims for damage wrought by this species are as yet unsubstantiated (Anderson 1995, Hager & McCoy 1998). In the Sonora desert, areas dominated by the introduced perennial grass *Eragrostis lehmanniana* provide undesirable habitat for scaled quail (*Callipepla squamata*, Medina 1988).

In addition to providing poor foraging for quail, *Eragrostis*-dominated desert supports a more depauperate faunal community than native-dominated areas (Bock et al. 1986). Similarly, Pacific coast dunes dominated by the introduced beachgrass *Ammophila arenaria* support fewer species of arthropods (Slobodchikoff & Doyen 1977) and plants (Barbour et al. 1976, Boyd 1992) than native-dominated dunes. The Eurasian perennial herb *Euphorbia esula* (leafy spurge), which as of 1997 infested more than 110 km^2 in the United States and Canada (including parts of Idaho, Montana, Wyoming, and Colorado, Lajeunesse et al. 1999), decreases habitat quality for bison (*Bos bison*) and deer (*Odocoileus* spp.) in Theodore Roosevelt National Park, North Dakota (Trammell & Butler 1995).

Invasive exotic plants can threaten populations of rare native plant species, but few cases have been documented. Some findings: on Montana rangeland, introduced *Centaurea maculosa* can reduce recruitment and population growth of the rare native *Arabis fecunda* (Lesica & Shelly 1996). *Phalaris arundinacea* (reed canarygrass), which has genotypes native to both northern North America and northern Europe, appears to have displaced the endangered aquatic annual *Howellia aquatilis* (Lesica 1997) from parts of two Montana marshes. In central New Mexico, habitat for the endemic thistle *Cirsium vinaceum*, a federally listed threatened species, is being taken over by the Eurasian biennial *Dipsacus fullonum* (teasel). Studies by Huenneke & Thompson (1995) suggest that the native thistle could decline if the *Dipsacus* invasion continues unchecked.

Plant invaders can also depress fungal communities. Allen et al. (1995) report lower fungal diversity and colony numbers under introduced annual grasses and forbs compared with neighboring coastal sage habitat. In the intermountain west, most native plant species are mycorrhizal, whereas some invaders are not. When nonmycorrhizal species such as *Salsola tragus* invade rangeland in this region, populations of vesicular-arbuscular mycorrhizae decline (Goodwin 1992).

Although we found many reports of declines of native biodiversity following invasions, we also found some cases where native species preferentially made use of habitat created by introduced species. In these cases the introduced species were generally replacing habitat that had formerly been provided by native species. For instance, monarch butterflies (*Danaus plexippus*) that overwinter on the west coast of United States most commonly roost in groves of *Eucalyptus globulus*. For the monarchs, this introduced species probably replaces habitat that was lost when groves of native trees were logged in the late 1800s (Lane 1993). However, the eucalypts may not provide suitable replacement habitat for all the species that had used the native groves.

It is clear from the above examples that invasive species pose significant threats to native populations. A handful of the most successful invasive species has contributed to declines in populations of several native species through competition, predation, and habitat alteration. Native populations on islands or in isolated systems such as creeks and estuaries seem much more likely to be impacted by invasive species than mainland populations. Considering the number of alien species that have become established in mainland systems, it seems that a minority of these invaders has widespread and adverse impacts on native species. However, effects of the vast majority of mainland invaders remain unstudied.

CONCLUSIONS

A small number of biological invaders have drastically changed the structure and functioning of ecosystems in western North America, and thousands of other invaders have wrought more subtle changes. The ecological disruption caused by invasive species, in combination with other factors (including land development and elements of global change such as N deposition, climate change, among others), threatens to drive species extinctions and to reduce the dominance of natives in many ecosystems, altering the character of much of western North America (Fig. 1).

Many of western North America's grassland, shrubland, dune, riparian, and estuarine ecosystems are already dominated, probably irreversibly, by non-native species. Some of California's remaining coastal scrub is undergoing annual grass invasion, and some of the state's chaparral faces threats from

management practices that encourage annual grass dominance. The forests of the west coast have escaped threats from biological invaders more successfully than other systems. However, the current declines of Port-Orford-cedar, relictual stands of *Pinus radiata*, and five-needled pines in the Sierra Nevada, all due to introduced fungi, highlight the potential vulnerability of these ecosystems.

We know very little about the impacts of most biological invaders on native species and on ecosystem functioning (Levine et al. 2003). Even some potentially dramatic impacts of the most widespread invasions have yet to be studied. For example, the large-scale replacement of mixed-shrub steppe with annual grasslands must have affected the energy and water balance of the intermountain west, and thus may have affected regional weather patterns. Transformations such as this would have important ecological and economic consequences, and should be examined. We do know that some invaders are causing important ecological changes. If we observe and quantify these changes, and we identify viable ecosystem restoration strategies, then our society (and its land managers) will be better able to make informed decisions about which of these invaders are noxious enough to merit large-scale eradication campaigns.

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APPENDIX 1

Some western North American ecosystem disruptors and their effects

Algunos disruptores ecosistémicos del oeste de Norteamérica y sus efectos

Invasive species	Areas affected[1]	Disruption	Evidence[2]	Reference
PLANTS[3] (life form[4])				
Ammophila arenaria (PG)	Pacific coast dunes	Alters dune morphology	**O-R**	Barbour & Johnson (1988)
		- Open dune area	**O-R**	Wiedemann & Pickart (1996)
		- Plant diversity	**O**	Wiedemann (1984)
		- Arthropod diversity	**OD-R**	Barbour et al. (1976)
		+ Productivity	**OD-R**	Slobodchikoff & Doyen (1977)
		Excludes native plants	OD-R	Pavlik (1983a)
		Alters microclimate	O-R	Barbour at al. (1985)
			OD-R	Barbour et al. (1985)
Ammophila brevigulata (PG)	Pacific northwest dunes	Alters dune morphology	**OD-R**	Seabloom & Wiedemann (1994)
Arundo donax (PG)	California riparian zones	+ Fire frequency	O/S	Bell (1993), Jackson (1993)
		Alters flood regimes	O/S	Frandsen & Jackson (1993)
		- Plant diversity	O/S	Bell (1993)
		+ VOC emissions	**OD-R**	Based on Hewitt et al. (1990)
Bromus diandrus (AG)	Pacific states, British Columbia to Mexico	Alters hydrology	**EM-R**	Holmes & Rice (1996)
Bromus madritensis ssp. *rubens* (AG)	Pacific states, British Columbia to Mexico	+ Fire frequency	**SD-R**	Brown & Minnich (1986)
				Hunter (1991)
			OD & EM-R	Brooks (1999)
Bromus tectorum (AG)	Western North America	+ Fire frequency	**OD-R**	Whisenant (1990)
		Alters N cycling	**OD-R**	Evans et al. (2001)
		- Evapotranspiration	**OD-R**	Cline et al. (1977), Kremer & Running (1996)
Carduus nutans (BF)	Widespread in United States and Canada	- N inputs	**EM-R**	Wardle et al. (1994)
Carpobrotus edulis (S/V)	Coastal regions northern California to Mexico; usually on sand	- Soil pH	**OD**	D'Antonio (1990)
Centaurea maculosa (BF)	Western rangelands	+ Erosion	**EM-R**	Lacey et al. (1989)
Centaurea solstitialis (AF)	California, Oregon, Washington grasslands, patchy in Idaho	Alters hydrology	**OD**	Borman et al. (1992), Gerlach (2000)

Invasive species	Areas affected[1]	Disruption	Evidence[2]	Reference
Cynodon dactylon (PG)	California, Arizona, southern United States	Stabilizes streambanks	**OD-R**	Dudley & Grimm (1994)
Cytisus scoparius (S)	Pacific coastal range of United States, patches in Sierran foothills	+ N inputs to system	**OD-R** **OO-R**	Wheeler et al. (1987) Dancer et al. (1977)
Dipsacus fullonum (BF)	Widespread in North America	Threatens native plants	**EM-R**	Huenneke & Thompson (1995)
Elaeagnus angustifolia (S/T)	Western desert riparian zones	Alters wildlife habitat	S	Olson & Knopf (1986)
Eucalyptus spp. (T)	California riparian zones, California grasslands	+ Productivity + Litter layer + VOC emissions Alters hydrology + Allelopathic chemicals	**OD-R** **OD-R** **OD-R** **OO-R** **EM-R**	Robles & Chapin (1995) Robles & Chapin (1995) Evans et al. (1982), Arey et al. (1995) Van Lill et al. (1980) Del Moral & Muller (1969, 1970)
Euphorbia esula (PF)	Northern United States, southern Canada	- Habitat quality	**OD-R**	Trammell & Butler (1995)
Festuca arundinacea (AG)	Widespread in North America	+ Erosion	S	Cheater (1992)
Lythrum salicaria (S)	Widespread in North America, esp. n. United States	- Wildlife habitat Alters P cycling	**O** **OD-R**	Thompson et al. (1987) Emery & Perry (1996)
Mesembryanthemum crystallinum (AF)	Coastal bluffs, cliffs, northern California to Mexico, Arizona	+ Salinity of topsoil	**OD&EM-R**	Vivrette & Muller (1977)
Salsola tragus (AF)	Disturbed inland areas	+ P availability Alters fungal community	**EM-R** O-R	Cannon et al. (1995) Goodwin (1992)
Schismus spp. (AG)	Southwestern United States	+ Fire frequency	**OD & EM-R**	Brooks (1999)
Senecio mikanioides (V)	Coastal northern California	Alters streamflow	S	D. Chipping (personal communication)
Senecio sylvaticus (AF)	Northern California to British Columbia	- Nutrient loss from clearcuts	**OD-R**	Gholz et al. (1985)

Invasive species	Areas affected[1]	Disruption	Evidence[2]	Reference
Spartina alterniflora (PG)	San Francisco Bay California; Suislaw estuary, Oregon; Willapa bay, Washington; Puget Sound, Washington	Colonizes bare mud flats + Sedimentation + Productivity	**OD-R** **OD-R** **OD-R**	Callaway & Josselyn (1992) Bascand (1970) Callaway & Josselyn (1992)
Taeniatherum caput-medusae (AG)	Widespread in western United States, especially Pacific northwest	+ Fire frequency	O-R	Young (1992)
Tamarix spp. (S/T)	Southwestern United States & Baja California riparian zones	+ Water use + Sedimentation - Bird habitat	**O** **OD-R** **OD-R** **OD**	Neill (1983), Weeks et al. (1987) Blackburn et al. (1992), Graf (1978) Hunter et al. (1988) Cohan et al. (1978)
Tribulus terrestris (AF)	Patchy throughout North America	+ Allelopathic chemicals	**OO-R**	El-Ghareeb (1991)
Ulex europaea (S)	Coastal areas from central California to Baja California, patches in lower cascades and sierras	+ N input to system + Production - Soil pH	**OO-R** **OO-R** **OO-R**	Egunjobi (1969) Egunjobi (1971) Grubb et al. (1969), Grubb & Suter (1971)
FUNGI *Cronartium ribicola* (causes white pine blister rust)	Cascade Range, Rocky Mountains, Sierra Nevada forests	Kills native white pines	**OD**	Kinloch & Dulitz (1990)
Fusarium subglutinans (causes pitch canker)	Pinus radiata stands in central and southern California	Kills native trees	**OD-R**	Correll et al. (1991), Storer et al. (1994)
Phytophthora lateralis	Southwest Oregon, Northwest California	Kills Port-Orford-cedar	**OD-R**	Murray & Hansen (1997)
INVERTEBRATES *Aporrectodea caliginosa* (earthworm)		- Soil turnover - Nutrient mineralization	**OD&EM-R** **OD&EM-R**	James (1991) James (1991)

Invasive species	Areas affected[1]	Disruption	Evidence[2]	Reference
Batillaria attramentaria (mudsnail)	Northern California bays	Displaces native mudsnail	**EM-R**	Byers (2000)
Carcinus maenas (green crab)	Pacific coast: central California to central Washington	- Invertebrate abundance Mixes sediments	**OD & EM-R** O-R	Grosholz et al. (2000) Cohen et al. (1995)
Ilyanasia obseltis (mudsnail)	San Francisco Bay	Displaces native mudsnail	**OD&EM-R**	Race (1982)
Linepithema humile (Argentine ant)	California, Arizona, southern Nevada, México	Replaces native ants Alters native community -Horned lizard growth	**OD&EM-R** **OD-R** **EM-R** **OD-R** **OD&EM-R**	Human & Gordon (1996) Ward (1987), Wetterer et al. (2001) Holway (1999) Sanders et al. (2003) Suarez & Case (2002)
Octolasion cyaneum (earthworm)		- Soil turnover - Nutrient mineralization	**OD&EM-R**	James (1991)
Orconectes virilis (virile crayfish)	San Francisco Bay Delta, northern California irrigation ditches	Displaces native crayfish	O	Cohen & Carlton (1995)
Pacifastacus leniusculus (signal crayfish)	San Francisco Bay	Displaces native crayfish	O	Cohen & Carlton (1995)
Potamocorbula amurensis (Asian clam)	San Francisco Bay	+ Filtration rate of water Alters sediment characteristics	**EM/OD-R** **O-R**	Werner & Hollibaugh (1993) Carlton et al. (1990)
Sphaeroma quoyanum (isopod)	San Francisco Bay	+ Erosion	O/S	Cohen & Carlton (1995)
VERTEBRATES *Capra hircus* (goat)	California Channel Islands	+ Erosion	**O**	Coblentz (1980)
Castor canadensis (beaver)	Widespread in United States and Canada, excluding deserts (native to most of this region)	Alters regional geomorphology, hydrology + Methane emission	**OD-R** **OD-R**	Naiman et al. (1986), Naiman et al. (1988) Naiman et al. (1991), Yavitt et al. (1992)
Equus asinus (burro)	California (Death valley)	Kills native vegetation	**O**	Loope et al. (1988)
Lepomis macrochirus (bluegill)	Widespread in California (native to eastern and central North America)	Preys on/competes with native species	O	Cohen & Carlton (1995)

Invasive species	Areas affected[1]	Disruption	Evidence[2]	Reference
Lepomis cyanellus (green sunfish)	Widespread in western United States (native to eastern and central North America)	Preys on/competes with native species	O	Cohen & Carlton (1995)
Micropterus salmoides (largemouth bass)	Widespread in California (native to eastern and central North America)	Preys on/competes with native species	O	Cohen & Carlton (1995)
Morone saxatilis (striped bass)	Widespread in western rivers and bays (native to Atlantic coast)	Preys on/competes with native species	O	Cohen & Carlton (1995)
Oreamnos americanus (mountain goat)	Washington (Olympic mountains)	+ Erosion	O	Carlquist (1990), Bratton (1982)
Ovus aries (sheep)	California Channel Islands	+ Erosion	**O**	Brumbaugh (1980)
Rana catesbeiana (bullfrog)	Widespread in western United States (native to eastern and central North America)	Preys on/competes with native species	**OD-R** **OD&EM-R**	Moyle (1973) Kupferberg (1997)
Rattus norvegicus (Norway rat)	Coastal and central California	Preys on native species	O	Cohen & Carlton (1995)
Sturnus vulgaris (European starling)	Widespread in North America	Displaces native cavity-nesting birds	**O**	Small (1994)
Sus scrofa (pig)	Widespread in California	Disturbs soils	**OD-R**	Kotanen (1995)
Vulpes vulpes (red fox)	Widespread in California	Preys on native species	O	Cohen & Carlton (1995)
PROTIST *Myxobolus cerebralis*	Pacific states, northern United States	Kills rainbow & brown trout by causing whirling disease	OD	Nehring & Walker (1996), Bergersen & Anderson (1997) (range data)

[1] Information in "areas affected" is largely derived from Hickman (1993) and Whitson et al. (1996), or from the cited references.
[2] Key to evidence column: experimental manipulation, EM; observation with data, OD; observation without data, O; observation outside of western North America, OO; speculation with data, SD; speculation, S. Boldface is used to denote primary references. The suffix -R denotes evidence published in peer-reviewed scientific literature.
[3] Plant nomenclature from Hickman (1993).
[4] Key to plant life forms: tree, T; shrub, S; vine, V; annual grass, AG; perennial grass, PG; annual forb, AF; perennial forb, PF