from the co-introduction of North American crayfishes and their diseases.

Hybridization with Native Species

Introduction of nonindigenous species may result in hybridization with native species. Hybridization is a concern because it may adversely affect persistence of endangered species, jeopardize the legal status of these endangered species, or alter the ecological, behavioral, or genetic specialization of native species. Hybridization has contributed to 38 percent of native fish extinctions in North America over the past century. As introductions of species to lakes continue unabated, opportunities for hybridization should increase in the future.

In many cases, more than one factor is implicated in species extinctions. Hybridization can become an especially important factor when very small native populations interact with much larger populations of introduced species. For example, stocks of longjaw cisco *Coregonus alpenae*, deepwater cisco *C. johannae*, and blackfin cisco *C. nigripinnis* in lakes Michigan and Huron were severely depleted by overfishing, and, to a lesser extent, sea lamprey predation, following which remaining individuals are thought to have hybridized with common ciscoes. The last recorded finds of native individuals of these species were in 1967, 1951, and 1923, respectively.

While hybridization between introduced and native species poses the greatest conservation concern, hybridization involving multiple lineages within a species or between multiple nonindigenous species can also be a problem. For example, mitochondrial DNA analyses of common carp from Lake Biwa, Japan, uncovered an infusion of five separate European strains into the native population, jeopardizing the integrity of this ancestral population. In the Murray-Darling river system in Australia, hybrid carp became far more widely distributed than either of the introduced stock species from which it was formed. Two and possibly three feral tilapia (*Oreochromis*) species also form hybrids in parts of Australia.

SEE ALSO THE FOLLOWING ARTICLES

Carp, Common / Crayfish / Great Lakes: Invasions / Nile Perch / Ponto-Caspian: Invasions / Rivers / Water Hyacinth / Zebra Mussel

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LAMPREY

SEE SEA LAMPREY

LANDSCAPE PATTERNS OF PLANT INVASIONS

THOMAS J. STOHLGREN
U.S. Geological Survey

Natural landscapes can be viewed as microcosms of the global environment. At global scales, plant diversity is highest in warm-wet areas, with noticeable decreases in plant diversity in extreme environments: near the north and south poles, on cold mountaintops, and in deserts. Plant invasions generally follow the same predictable patterns at landscape scales. Many low-elevation meadows, riparian zones, and canopy gaps in zones of moderate climates contain the greatest native species richness and the greatest nonnative species richness. This "rich get richer" pattern of invasion often scales from landscapes to continents, as most species track favorable environmental conditions (e.g., high light, warm climates, ample precipitation, and high soil nutrients). Disturbances, such as fire, flooding, and insect outbreaks, often facilitate plant

invasions at landscape scales. Many exceptions occur in abiotically or biotically special environments: places where there is too much water or too much canopy cover, or where plant biomass is controlled by a few dominant native or nonnative species (e.g., dense stands of Arundo donax).

NATIVE SPECIES RICHNESS PATTERNS

There are generalities apparent in landscape patterns of native species richness and cover (abundance), although there are exceptions:

- High-productivity sites with high light, warm temperatures, ample precipitation, and adequate soil nutrients generally have higher native species richness than low-productivity (high-stress) sites. Likewise, low-elevation zones generally have higher species richness and cover than do high-elevation sites. Exceptions occur where a few species attain dominance on high-productivity sites (e.g., full-canopy tree species, sod-forming grasses, and monoculture sites).
- Heterogeneous areas generally have higher species richness than homogeneous areas. Heterogeneous areas are maintained by underlying patterns of soil, geology, grazing, disturbance, pathogens, diseases, and other factors.
- Areas of high environmental stress (e.g., severe drought conditions or anoxic conditions from standing water) usually contain fewer plant species.
- Areas with limiting resources such as low soil nutrients, water stress, or low light from shading by dominant species generally result in lower plant diversity and cover.
- Moderate disturbance areas and mid-successional areas generally support more species than immediate post-fire areas or late-successional forests. Frequent massive disturbances such as huge floods or frequent intense fires can decrease local plant diversity and cover.
- Later-age geological substrates (i.e., older surfaces) generally support more species than younger substrates.

The general patterns for native plant diversity often apply to other organisms. High-productivity sites attract or respond to areas of high numbers of soil organisms, pollinators, birds, small mammals, grazers, and all manner of pathogens and diseases. It is this palette of native species diversity that paves the way for invasive plant species.

INVASIVE SPECIES RICHNESS PATTERNS

Nonnative plant species often follow the same patterns as native species in many landscapes, assuming propagules are not limiting. Since every county in the United States contains invasive species, and since many invasive plant species are dispersed by wind, birds, small mammals, and insects, we can safely assume that some propagules have arrived (or will arrive) in most landscapes. Once the propagules arrive, they face the same suite of difficulties as native species propagules. They must find suitable habitat, including microsites with reduced competition, predators (herbivores), pathogens, and diseases.

Most field studies based on detailed vegetation plots strongly suggest that nonnative plant species are successfully establishing, growing, and reproducing in many landscapes. In fact, at landscape scales, hotspots of native species richness are often hotspots of invasion. Consider two examples of plant diversity patterns in mountains and deserts to understand typical invasion patterns. Species-accumulation curves (i.e., counting novel species encountered when adding more vegetation plots) illustrate the patterns.

In the mid-elevations of Rocky Mountain National Park (1800 m to 3200 m), native plant diversity is greatest in habitats with high light (little or no conifer canopy), high soil moisture, and warm temperatures (Fig. 1). Native plant species richness declines with increasing elevation and canopy cover. Native plant species accumulate quickly in stands of aspen (*Populus tremuloides*) along the edges of wet meadows. Such areas have high soil nitrogen and attract many species of birds, small mammals, and herbivores. Nonnative plant species have successfully invaded these same habitats. The dry meadow habitats have less soil moisture and nitrogen during the growing season, and thus have correspondingly fewer native and nonnative plant species.

Similar patterns can be found in the Grand Staircase-Escalante National Monument in southern Utah (Fig. 2). Riparian zones, with ample soil moisture, generally contain more native and nonnative species than xeric upland habitats. *Tamarix* sp. (salt cedar) has successfully invaded many riparian zones throughout the southwestern United States. However, fires in upland habitats can promote invasion of nonnative annual grasses (e.g., *Bromus tectorum* [cheatgrass]).

The prevailing pattern of invasion is "the rich get richer"—sites with high native species richness and cover are prone to invasion. However, there may be exceptions.

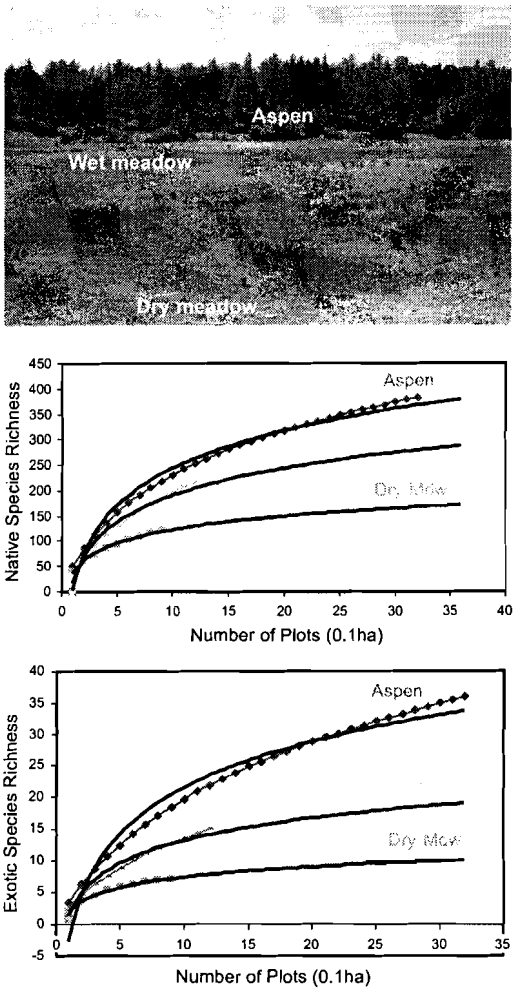

FIGURE 1 Species accumulation curves of native and nonnative species in Rocky Mountain National Park, Colorado. Curves were extrapolated from different numbers of sample plots.

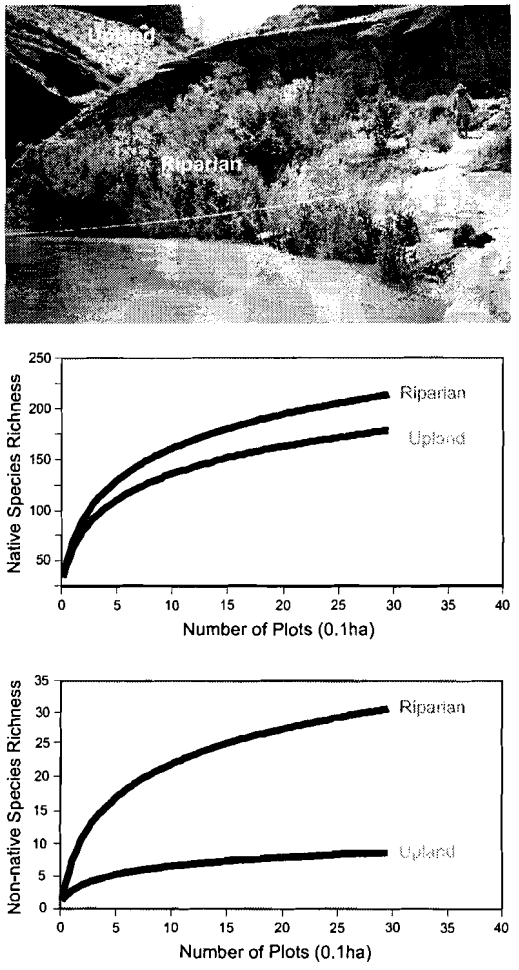

FIGURE 2 Species accumulation curves of native and nonnative species in Grand Staircase-Escalante National Monument, Utah.

ROLE OF COMPETITION AND OTHER FACTORS

Many additional factors are superimposed on these general patterns. Competition can play a role locally, where large, tall, high-biomass native species, such as large trees, preempt resources and inhibit invasion. Likewise, dominating species such as sod-forming grasses (*Poa pratensis* [Kentucky bluegrass]) and monoculture-producing species (*Arundo donax, Tamarix* sp.) can reduce the ability of native and other nonnative species to coexist locally.

The life history of species also plays a role. Early-succession habitats with highly variable precipitation and frequent disturbances such as fire, conducive to native annual plant species, are often conducive to nonnative annual plant species (e.g., *Avena fatua* grasslands in California). Likewise, nonnative perennial trees such as *Tamarix* and Norway maple (*Acer platanoides*) tend to invade habitats occupied by native perennial trees such as cottonwoods and eastern deciduous forest species, respectively.

Invading nonnative plant species may be one step ahead of their native pathogens and diseases. They may be exploiting unused resources or underused resources. Invaders might benefit from native pollinators and soil organisms. Thus, there are many potential factors influencing the establishment, growth, spread, and persistence of nonnative species in natural landscapes.

THE FUTURE LANDSCAPE

Landscape patterns of plant invasions are still unfolding. The invasion may be just under way in many areas. There is little sign of "saturation." Many microsites within landscapes may be filled by current invaders, or by new invaders assisted by trade and transportation. Current invaders, like native plant species, keep adapting to new environments. Large-scale effects of succession, land use change, climate change, fires, pollution, fertilization, insect outbreaks, floods, and hurricanes, and small-scale effects of grazing, diseases, and competition, provide for ever-changing patterns of plant invasions.

SEE ALSO THE FOLLOWING ARTICLES

Competition, Plant / Dispersal Ability, Plant / Invasibility, of Communities and Ecosystems / Protected Areas / Range Modeling / South Africa: Invasions / Tolerance Limits, Plant

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LAND USE

RICHARD J. HOBBS
University of Western Australia

Humans use ecosystems in many different ways and with differing degrees of transformation. Land uses range from conservation-related use, with relatively little intentional transformation, to the purposeful utilization of particular ecosystem components, as, for instance, in grazing systems, to the replacement of the original ecosystem with crops or plantations, and to the complete removal of virtually the entire ecosystem, as is the case in extractive uses such as mining. Possible changes include both ecosystem decline and recovery. A particular human activity may result in a sudden or a more gradual change in ecosystem properties. Such changes often result in conditions that lead to increased invasibility.

HUMAN LAND USE AND LAND USE CHANGE

The recent history of the world has been one of a dramatic increase in the incidence of human-induced disturbances, as humans utilize an increasing proportion of the Earth's surface in some way or another and appropriate an increasing amount of the Earth's productive capacity and natural resources. Increasing human modification of ecosystems has been noted for some time but has been reemphasized lately as a result of global assessments of the state of the world's ecosystems. Direct (e.g., land conversion) and indirect (e.g., long-range transport of pollutants) human influence takes many forms and is difficult to quantify in simple metrics, but global assessments using several available datasets have resulted in analyses which indicate that large proportions of the global land surface are significantly impacted by human activities. Prevailing trends include increasing urbanization, deforestation and ecosystem fragmentation, agricultural intensification in some areas, and abandonment of agricultural land in others. The areas involved in transformations such as deforestation are truly massive and are happening with considerable rapidity.

Land uses vary in their degree of modification of the existing ecosystem. Conservation-oriented use will tend to limit the extent of human-induced disturbance, either by design or by default (for instance in remote or harsh environments). Utilization of native ecosystems is a prevalent land use over large parts of the world and includes