Rainbow smelts, white perch, zebra mussels, and a handful of other invaders in the Great Lakes have not halted their advance at the southern shores of Lake Michigan. Instead they have pressed on, taking advantage of a series of canals to infest the Mississippi River drainage. By contrast, other established invaders in Lake Michigan, such as the sea lamprey, round goby, and spiny water flea, have not succeeded in reaching the river. The still-open question for biologists is, why? More important, what sorts of human-driven changes in these aquatic systems might alter the fortunes of these laggard species and send a new wave of invaders from the lake through the canals and into the Mississippi?

Although biologists have worked for several decades to figure out what makes some plants and animals good "weeds," and what makes some habitats more vulnerable to weedy invasions than others, there are no consistent answers. But the need for answers is becoming more urgent as scientists are being called on to project how native species and ecosystems will respond to a bevy of disturbances, such as fire; rapid growth in world trade and travel; and the accelerating loss of native biodiversity.

In addition, the increasing pace of species invasions is itself considered a key aspect of global change—one more visible in most regions than the extinction crisis. "Exotic invasions are the number-two threat to native biodiversity [behind habitat destruction], but that just doesn't say it all," Stanford University ecologist Harold Mooney told his colleagues at a meeting near Stanford, California, last spring. "Invasions are the number-one component of biotic change in the world today. The number of extinctions pales beside the number and impact of biological additions, at least for the present."

Spurred by the Convention on Biological Diversity and growing international concern, a number of agencies and groups around the world are developing strategies to curb new invasions and prevent further damage by established invaders in wild as well as managed landscapes (BioScience 46: 732–736). That task is complicated, however, by continuing shifts in climate, land use, avenues for invasion, and other factors that affect the fate of potential invaders. Furthermore, invasions that alter the biological landscape feed back to drive new changes in the atmosphere, climate, and natural disturbance patterns.

At the Stanford meeting, two dozen scientists led by Mooney gathered to take a preliminary look at the direction in which various global changes are likely to drive the fate of would-be invaders, including exotic species, such as the sea lamprey and spiny water flea, that already lurk like time bombs at the edges of many systems. The workshop was sponsored by the Global Invasive Species Program (GISP), part of an international program on the science of biodiversity known as DIVERSITAS. GISP is coordinated by the Scientific Committee on Problems of the Environment.

The general consensus of the workshop participants was evident from the start: "Without question, global change is going to exacerbate the invasives problem," Mooney said. But not all types of change have equally strong or unambiguous impacts. Workshop participants found that two global trends consistently and strongly encourage invasions: land-use change and the proliferation of vectors that promote species movement, especially those created by the growth in world trade. A number of other global changes, they concluded, have less consistent impacts but still play a role in influencing invasions.

How land-use changes promote invasions

Changes in land use have long been known to provide opportunities for invading species, Richard Hobbs, of Australia’s Commonwealth Scientific and Industrial Research Organization (CSIRO) Division of Wildlife and Ecology, pointed out. As natural forests are cut or burned, meadows plowed or paved, wetlands drained or filled, and roads cut through formerly wild ecosystems, environmental conditions change, providing new opportunities for both native generalists (species that tolerate a wide range of conditions) and weedy invaders. Often these land-use changes are accompanied by the deliberate im-
A series of canals connected by locks, such as this one in Chicago, have enabled some invasive species to spread from Lake Michigan into the Mississippi River drainage. University of Notre Dame biologist David Lodge and graduate student Cindy Kolar are studying the factors that favor expansion by certain native and exotic species from Lake Michigan, through the canals, and into the Illinois River, a tributary of the Mississippi. Photo: Cindy Kolar.

Invasive grasses have fostered the spread of fire in a variety of landscapes around the world. On the island of Hawaii, introduced grasses such as broomsedge and molasses grass have fueled fires in seasonally dry woodland habitat such as this burned area in Hawaii Volcanoes National Park (upper right). The fires killed the dominant native tree, ohia, and most of the understory shrubs. In California, the giant reed, Arundo donax, imported from Asia and grown in plantations for use in making clarinet reeds, has escaped cultivation and invaded river courses in coastal California, such as the Sonoma creek (lower right; a large clump of Arundo can be seen in the left middle ground). This invasive species changes riparian areas from barriers that prevent the spread of fire into wicks that carry fire into housing developments. Photos: Carla D'Antonio (top) and Tom Dudley (bottom).
Although the team has only preliminary results, Lodge said that some of the traits found among "winning" fishes are consistent with traditional anecdotal descriptions of the traits of successful invaders—higher fecundity, less parental care, and greater silt tolerance. But in another comparison between established invaders and native species in the Great Lakes, one of the team's findings is surprising: The successful invaders seem to have more parasites than native species. "This is inconsistent with the idea reported in the past that invaders can become abundant and succeed because they escape from the parasites and predators that kept them in check in their native range," Lodge said. He noted that so far, the only clue to explain this observation is that many of the exotics have large native ranges and may thus be exposed to more potential parasites. If so, then a higher parasite load may simply be a byproduct of range size and not a causal factor in invasion success.

Changing environmental conditions influence more than just the initial spread of invaders. Evolutionary biologist Spencer Barrett, of the University of Toronto, said that changing conditions may also favor rapid adaptive responses by invaders that will speed the evolution of forms adapted to local conditions and make the newcomers more difficult to control.

The water hyacinth, for instance, reproduces sexually in the fluctuating water levels of its native Amazonia because seeds can germinate on exposed mud. By contrast, when it invades waterways that have constant high water levels, it spreads only by clonal growth and its sexual reproduction is inhibited. Thus, Barrett said, this aquatic weed is highly uniform genetically in many parts of its introduced range. Attempts to control water hyacinth using a variety of insects and pathogens have met with mixed success in various parts of the world. If global changes cause water levels to fluctuate, the result may be "bursts of sexuality" and increasing genetic variation, including development of some genotypes with resistance to pathogens or parasites that could make biological control of water hyacinth even more difficult.

### The impact of global trade

A second global trend that consistently favors invaders is the accelerating pace of world trade, a phenomenon that connects the remotest regions to global markets by truck, train, ship, and airplane. All of these conveyances serve as avenues for the movement of plants, pests, pathogens, disease vectors, and other organisms.

Global trade creates a particularly severe problem for aquatic systems because ships transport 80 percent of the world's trade volume and altogether carry along in their ballast water tanks an estimated 3000 species of protists, animals, and plants on any given day. It was ballast water discharges, for example, that brought the European zebra mussel, a "poster child" for noxious aquatic invaders, to the Great Lakes and that let loose the exotic comb jellyfish _Mnemiopsis leidyi_ that has devastated fisheries and food webs in the Black Sea, said James Carlton, director of the Williams College Maritime Studies Program in Mystic Seaport, Connecticut.

The problem doesn't end with international shipping. The proliferating pathways for movement of aquatic species operate at all scales, from local and regional to global. These include the import of species for the pet trade and aquaculture, deliberate stocking of non-native game fish into rivers and lakes, release of exotics into garden ponds (from which they can be flushed by rains and flooding into surface waters), use of exotic plants in marsh restoration projects, dumping of live bait into waterways by fishermen at the end of the day, and trailer of boats from one waterway to another with aquatic plants and other organisms clinging to the trailers and boat hulls. As the United States and other nations move to impose tighter regulations on discharge of ballast water by ships, and even to devise electronic barriers to block fish movements through canals, and as state and federal fisheries agencies move away from intentional stocking of exotics, the importance of most other invasion pathways—especially "bait bucket introductions" by fishermen—is increasing, Lodge said.

### The role of temperature change and large-scale disturbances

Other global changes are less consistent in their effects on the fate of invaders than land-use change and increasing trade. But two human-driven phenomena—predicted global temperature changes and related shifts in the frequency of large-scale disturbances such as fire—do appear to promote invasions in a large proportion of known cases.

Carlton pointed out that changes in water temperature can have myriad impacts, from shifts in primary productivity that alter both water quality and food webs to shifts in the length or timing of reproductive or growing seasons. Any of these changes may favor particular exotics over native species. One potential problem, for example, is "sea ranching" of non-native species. Some sea ranching, such as commercial cultivation of Japanese red algae in the Gulf of Maine, is currently restricted to areas where water temperatures allow the exotic species to grow but prevent their reproduction. (Propagation is done in isolated tanks). However, shifts in water temperature might allow exotics like the Japanese red algae to proliferate and invade.

Temperature changes might also allow range expansions by invaders that have established in neighboring waters. Indeed, there is a possibility that warming of the Pacific Ocean along the west coast of the United States is already allowing some marine invaders to expand northward,
Carlton said. For instance, a Korean stalked sea squirt (Styela clava), which arrived in San Francisco Bay during the 1940s clinging to the hull of a ship, appeared in Oregon, Washington, and British Columbia waters in the 1990s. A New Zealand boring isopod (Sphaeroma quoyanum) made it to San Francisco Bay by the 1890s, either on or bored into the hulls of wooden sailing ships. It was found in Humboldt Bay in Northern California by the 1930s and then appeared in Coos Bay, Oregon, around 1995.

But are these invaders really moving north, and if so, is their migration a reflection of warming waters? Carlton cautioned that at least a half dozen alternative hypotheses might explain these and a handful of other new northward sightings, although none of the new sightings can be linked to El Niño events. For example, the sightings could reflect new introductions, perhaps as a result of new ship traffic or other pathways, rather than range expansions. Or they might represent range expansions that reflect the slow evolution of new cold-adapted genotypes rather than gradually warming waters. In addition, Carlton pointed out that field data on invaders is notoriously sparse and that this isopod and sea squirt might have previously gone unnoticed in more northern locations. In fact, he said, so few marine biologists actually spend time along the nation’s shorelines anymore that most invasions are first spotted and reported by non-scientists.

Pest and disease specialists also see an alarming potential for shifts in range and abundance among both native and invasive terrestrial species in response to changing air temperature and moisture. Hosts, pests, and disease vectors, as well as the environment itself, will all respond in different ways to climatic and other global changes.

To project potential changes in the distribution and relative abundance of pests under various climate regimes, Australian scientists have developed a computer model called CLIMEX. One concern, according to CSIRO entomologist Robert Sutherst, one of the CLIMEX developers, is that certain agricultural exports now considered a low risk for introducing agricultural pests will, with climate change, pose a much higher risk. For instance, “area freedom” provisions of the World Trade Organization permit export of citrus fruit from South Australia to the United States based on the current assessment that the Queensland fruit fly is highly unlikely to contaminate the fruit and invade the United States. But climate change could alter the risk of invasion by making the citrus growing area in Australia more favorable for the development and persistence of fruit fly populations. Sutherst said that modeling potential risks using CLIMEX can provide policymakers with information needed to adjust quarantines and take other preventive measures.

Interactions among human pathogens, disease vectors, and the envi-
environment are also complex. Epidemiologist Anthony McMichael, of the London School of Hygiene and Tropical Medicine, predicted that, thanks to global change, we are entering "the fourth great transition in human disease history." The first transition began 10,000 years ago, with the advent of agricultural settlements and the rise of endemic diseases such as measles and smallpox; the second came 3000 years ago, when the classical civilizations of Europe and Asia met and great plagues consequently swept through Europe; the third came when European contact with the Americas provoked massive epidemics and population die-offs in the New World. In the fourth period, McMichael believes, ecological changes rather than population contacts are "greatly altering the landscape of infectious diseases within human populations."

A 1991 cholera outbreak in Peru illustrates the complex interplay of global changes that make precise predictions about tomorrow's disease landscape difficult, McMichael said. An Asian strain of *Vibrio cholerae* was transported to the coastal waters of Peru in the ballast water from a freighter and quickly spread along hundreds of miles of coastline. The introduction occurred in the midst of an algal bloom, which was quickly followed by a bloom of zooplankton, which serve as a reservoir for the cholera bacterium. McMichael noted that this and other massive algal blooms off the Peruvian coast have been variously linked to El Niño events or to a range of human-related causes, from warming of coastal waters or increased nutrient flows to overfishing of algae-eaters. The cholera bacteria spread through the marine environment, contaminating fish, shellfish, and drinking water; it eventually sickened 300,000 people in Peru (about 1 percent of the victims died) and cost the nation hundreds of millions of dollars in seafood exports.

Like climate change, shifts in the frequency and intensity of major natural disturbances such as fire—a projected consequence of climate change in some regions—also appear to promote invaders more often than not. In turn, invaders often promote further shifts in fire patterns. Carla D'Antonio, of the University of California–Berkeley, examined 35 examples in the scientific literature and found that in 27 cases fire-promoted invasions, in 6 cases it slowed invasions, and in 2 cases it had no effect. Conversely, in looking at how invaders affect fire, she found that in 23 of 28 cases, ranging from the South African fynbos, to the Sonoran Desert of Mexico, to the coastal sage scrub of California, invaders enhanced fire by altering such factors as the amount, distribution, and rate of accumulation of fuel. For example, D'Antonio noted that before cheatgrass invaded the shrublands of the Great Basin (a 200,000-square-mile swath of the inland West that stretches from the Sierra Nevada east to the Wasatch Mountains of Utah), the region burned every 60–110 years. Now, because of the higher fine fuel load, fires burn there every three to five years.

### Some less clear-cut cases

The workshop participants concluded that three other global trends—rising atmospheric carbon dioxide levels, heavy nitrogen deposition resulting from air pollution and fertilizer use, and potential rainfall changes—are likely to be more variable in their impacts on invasions, with the effects differing with the setting and circumstances. For instance, a number of North America's worst weeds, including kudzu, cheatgrass, and yellow star thistle, have been shown to respond positively to elevated carbon dioxide levels when they are grown in monoculture. But Stanford University researcher Jeff Dukes pointed out that few of these plants have been studied extensively in natural settings, where they are in competition with native plants.

The complex interactions among rising carbon dioxide, nitrogen deposition, shifting climate, and other global changes help to confuse predictions about future invasions. Yet it is clear that the need for management of invasive species is on the rise, as is the cost of that management, said Jeff Waage of the International Institute of Biological Control, at Silwood Park in the United Kingdom. For example, the World Bank already devotes $45 million a year to combating aquatic weeds in its irrigation, hydropower, and other projects; such costs will escalate as more land is converted to food production to feed a growing human population. By contrast, little money is currently spent on biological control of invaders in natural areas. Demand for such management will undoubtedly increase along with concerns about conserving biodiversity. In the end, the success of efforts to combat invaders will provide a yardstick for monitoring how well humans are maintaining the vitality of the Earth's ecosystems. As McMichael pointed out, "Invaders are grand integrators that provide signals about the integrity of systems in the face of global changes."