Understanding Regional Change: A Comparison of Two Lake Districts

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We compared long-term change in two lake districts, one in a forested rural setting and the other in an urbanizing agricultural region, using lakes as sentinel ecosystems. Human population growth and land-use change are important drivers of ecosystem change in both regions. Biotic changes such as habitat loss, species invasions, and poorer fishing were prevalent in the rural region, and lake hydrology and biogeochemistry responded to climate trends and landscape position. Similar biotic changes occurred in the urbanizing agricultural region, where human-caused changes in hydrology and biogeochemistry had conspicuous effects. Feedbacks among ecosystem dynamics, human uses, economics, social dynamics, and policy and practice are fundamental to understanding change in these lake districts. Sustained support for interdisciplinary collaboration is essential to build understanding of regional change.

Keywords: interdisciplinary research, lake, landscape, long-term change, regionalization

Environmental changes are often regional in scope, involving multiple kinds of ecosystems and social systems in a changing mosaic (MA 2005). Urbanization is expanding globally (MA 2005) and, in the United States, is spurring rural residential development and the prominence of the urban–rural interface (Hansen et al. 2005). Land-use changes are altering the composition and spatial arrangement of habitats, and introducing new habitats (Foley et al. 2005, MA 2005). Introductions of nonnative species, and reintroductions of native species, are altering terrestrial and aquatic communities over extensive areas (MA 2005). Biogeochemical processes are responding to the addition and redistribution of nutrients (Bennett et al. 2001, Foley et al. 2005, MA 2005). Projected trends in climate also have implications for regional biota and ecosystem processes, through modification of temperature, precipitation, and disturbance regimes (MA 2005). All of these trends not only influence contemporary ecosystems but also bestow persistent legacies (Foster et al. 2003). Thus, understanding regional ecological change has emerged as a key goal for ecologists and other scientists. However, progress is difficult because of four fundamental features of regional change.

Regions are inherently social and ecological systems, and understanding change therefore requires the perspectives of many disciplines. Although the importance of interdisciplinary studies is widely recognized, such studies are hard to organize and sustain (Turner and Carpenter 1999, Lélé and Norgaard 2005, Carpenter and Folke 2006). Disciplines such as ecology, economics, and sociology are separated by different lexicons and cultures of scholarship, types of data, and modes of analysis; the questions deemed most interesting for research

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vary among the disciplines as well. Overcoming these differences requires substantial investments to build teams and nurture a culture of collaboration.

Regional changes result from multiple causes that interact in complex ways, not from simple cause-and-effect mechanisms. Assessments of natural resources must consider changing climate, economic trends, intensifying land use, changing habitat, shifting biotic composition, and a growing human population with changing expectations of, and behavior toward, nature. The outcomes of such processes are fundamentally uncertain. Dynamics are nonlinear and are likely to produce surprises that cannot be anticipated from single-factor, small-scale studies. Instead, scientists must rely on long-term observation, regional perturbations (such as droughts), large-scale experiments, comparative case studies, and models.

Causes, patterns, and consequences of regional change typically encompass multiple spatial scales. Causes may be distant in space from effects. For example, transboundary pollution, human migration, species invasions, and global market trends connect distant systems. The practical difficulties of obtaining empirical data and developing spatial models for regional analyses are daunting. Despite conceptual progress in landscape ecology and further progress in understanding scales of variability for some key drivers, we are a long way from understanding how effects transfer and interact across spatial scales (Miller et al. 2004).

Regional changes reflect variations that occur over a range of temporal scales. Key processes range from nutrient turnover rates measured in minutes to soil development measured in centuries. Events can have long-lasting legacies, such as historical land-use effects on soil nutrients and plant communities (Bennett et al. 2001, Foster et al. 2003). Ecological and social systems can exhibit rapid changes that are hard to anticipate. Gradual changes can be difficult to perceive against a background of natural variation and can be missed unless research adopts a long-term perspective.

Understanding complex systems, and managing them, requires complex approaches. The development of those approaches for understanding regional change, which presents significant though not intractable problems, is under way in many parts of the world. For more than a decade, the North Temperate Lakes Long Term Ecological Research program has been comparing two lake districts in Wisconsin, using a combination of long-term, comparative, experimental, and modeling approaches (*http://lter.limnology.wisc.edu;* Magnuson et al. 2006). This article presents a perspective on regional change that is emerging from these studies. First, we describe the lake districts and sketch changes in the regions over the past 150 years. We focus on the responses of lakes as sentinel ecosystems embedded in spatially complex regions. The comparison of the two regions suggests a common framework for understanding regional change.

Lake districts

There are distinct lake districts—that is, extensive regions with high densities of lakes—in the northern and southern parts of Wisconsin, each lying in formerly glaciated terrain: the Northern Highland Lake District (NHLD) and the Yahara River Lake District (YRLD; figure 1). Lakes are the focal landforms of both regions, providing unique habitats, ecosystem services, and centers of human activity. At present, Dane County (where the YRLD is located) and Vilas County (the center of the multicounty NHLD) are the two Wisconsin counties with the highest per capita rates of population growth. Ecological research began in the YRLD in the 1880s and in the NHLD in the 1920s (Kitchell 1992, Magnuson et al. 2006).

Despite these similarities, the two lake districts differ in many ways. The NHLD, one of the most lake-rich regions of the world, is largely forested and sparsely settled. Outdoor recreation centered on the 7600 lakes of the region is a mainstay of the economy, along with forest products. In contrast, the YRLD is an agricultural, but urbanizing, landscape with scattered remnants of presettlement ecosystems. The diverse economy involves agriculture, some light industry, service industries, emerging technologies, state government, and the state's flagship university.

A bird's-eye view of the present-day NHLD reveals a landscape made up of relatively intact second-growth forest (figure 1). About a third of the NHLD consists of lakes and wetlands, and the remainder is mostly forested, with a few small urban centers (Peterson et al. 2003, Vano 2005). A closer look at lakeshore riparian areas, however, reveals rapid lakeshore residential development (figure 2; Riera et al. 2001, Schnaiberg et al. 2002). Comparison of 1940 and 2000 census data for private land in Vilas County shows a 4.6-fold increase in housing density over this period (from 3.7 housing units per square kilometer [km^2] to 17.2 units per km^2). Second-home development has been the major driver of this trend, and lakeshores are a nexus for residential development in the region (Schnaiberg et al. 2002, Jorgensen et al. 2006, Marburg et al. 2006).

In contrast to the NHLD, the YRLD is obviously a human-dominated landscape (figure 3). Most of the land is agricultural, urban, or suburban. The YRLD has undergone two major waves of landscape change since 1800 (Carpenter et al. 2006). The first was the conversion of prairies, savannas, forests, and wetlands for agriculture during 1840–1870. The second is the expansion of urban land uses into formerly agricultural land. At present, about 65% of the watershed is agricultural, about 20% is urban, and the remainder is forest, wetland, or open water.

Development and biotic change in the Northern Highlands

Trends in the Northern Highlands provide a unique opportunity to examine the consequences of lakeshore development for lake ecosystems (figure 4). Old-growth forests were exploited for timber in the late 19th and early 20th centuries.

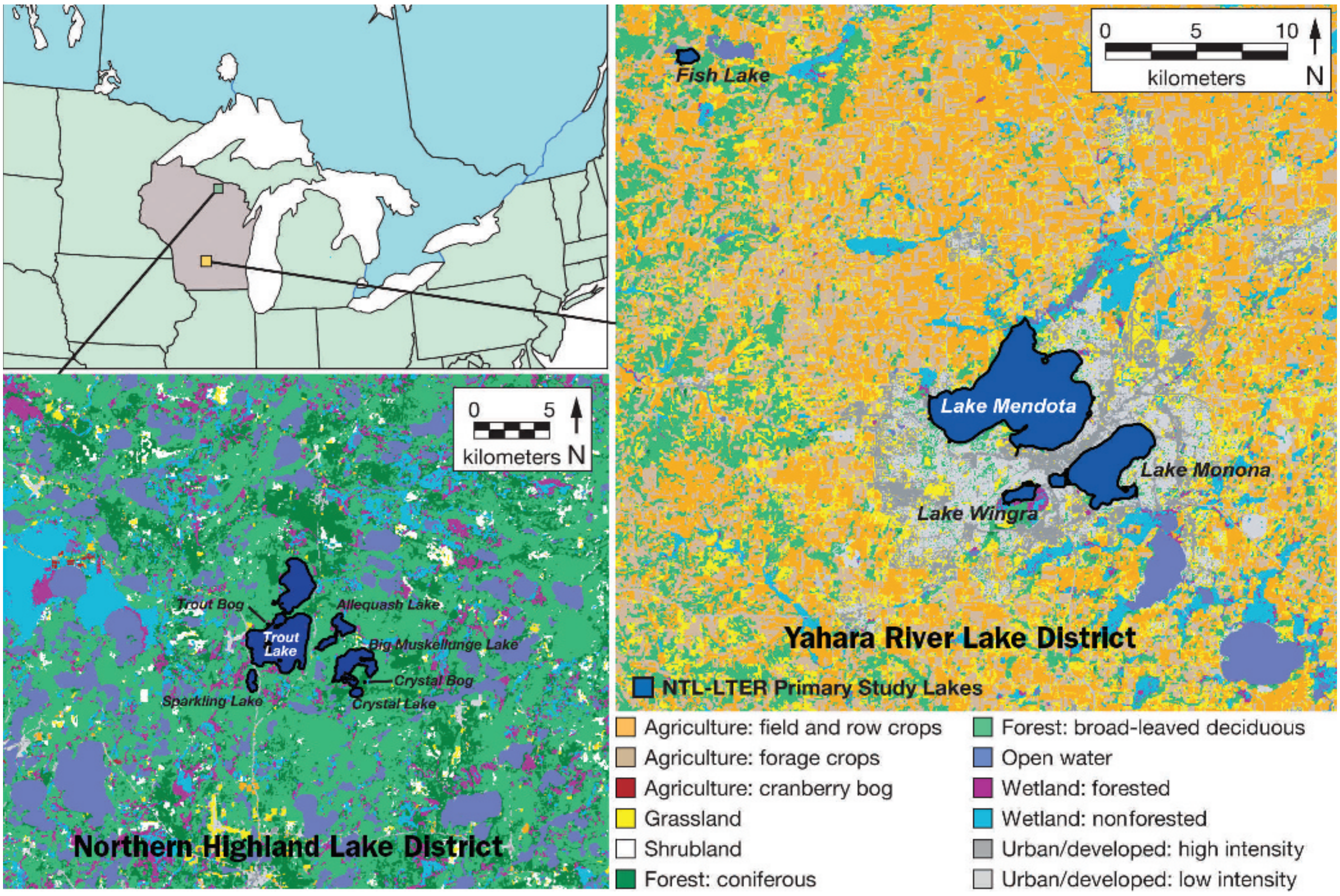

Figure 1. Maps showing locations within Wisconsin of the Northern Highland and Yahara River lake districts (top left), and land use and land cover within each lake district. Abbreviation: NTL-LTER, North Temperate Lakes Long Term Ecological Research.

Poor soil and cold climate limited the development of agriculture in the region, and forests have been allowed to recover, a trend that continues to the present day. After the logging era, the region was impoverished and sparsely populated (Jorgensen et al. 2006). By about 1950, development was accelerating, particularly around the lakes. By the 1980s, small cabins were being replaced by large homes around many lakes, a trend that has intensified to the present. Lawn fertilizers, septic fields, and erosion from construction activity raise concerns about eutrophication. Ecological changes such as the loss of lakeshore habitat, species invasions, and poorer fishing are noticed by the public and by lake managers. In response to these issues, more property owners are forming lake associations for the governance of resources shared by all property owners around a lake.

Long-term research has documented changes in hydrology and lake biogeochemistry driven by climate trends and events such as droughts (Magnuson et al. 2006). Landscape position, the location of a lake relative to other lakes within the hydrologic flow system, is associated with physical, chemical, and biotic differences among lakes and also explains different responses of lakes to regional climate (Kratz et al. 2006). As one example of a multiscale pattern in lake chemistry, Hanson and colleagues (2006) compared controls of dissolved oxygen (O_2) and carbon dioxide (CO_2) concentrations averaged over timescales of a day to a decade in lakes of different landscape position. At daily to monthly timescales, both gases were controlled by ecosystem production and respiration. At annual to decadal timescales, geochemical factors became the dominant control of CO_2, while temperature trends became the dominant control of O_2.

Residential development is the most conspicuous human impact in the NHLD. Simulations suggest that the effects of climate on hydrology and carbon flow are stronger than the effects of development (Vano 2005). However, on the basis of extensive studies of the link between residential development and lake eutrophication, we anticipated that water quality would decline more in developed lakes than in undeveloped lakes (Carpenter et al. 1998). Marburg (2006) compared present-day and historical (1930s; Juday and Birge 1933) limnological data along a lake development gradient. Surprisingly, Secchi depth, a measure of water clarity, did not change notably over time in either developed or undeveloped lakes (figure 5a). However, historical data were not available for chlorophyll, phosphorus, periphyton, or other indicators that might be more sensitive than Secchi depth. Models suggest that many lakes in the NHLD are vulnerable

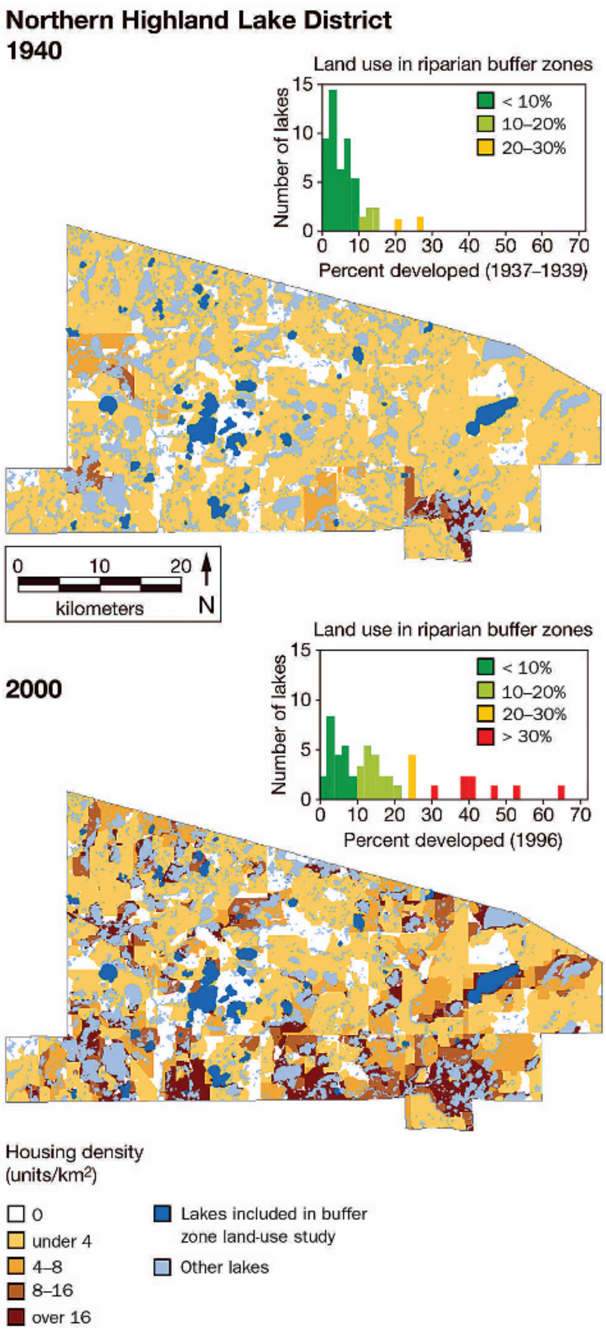

Figure 2. Changes in housing density in the Northern Highland Lake District, 1940–2000. Inset histograms show increases in residential development within 100 meters of the lakeshore between 1939 and 1996 for 50 lakes in Vilas County.

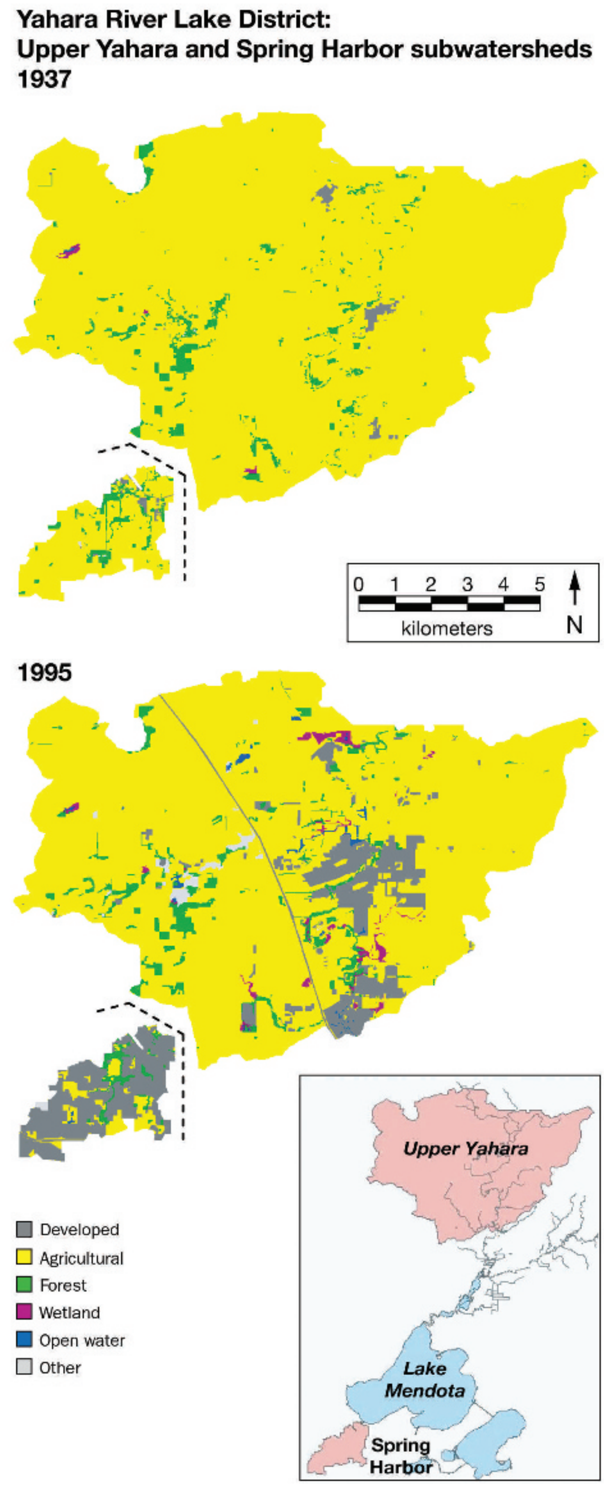

Figure 3. Changes in land use and land cover in two subwatersheds of Lake Mendota in the Yahara River Lake District, 1937–1995. Maps show the Upper Yahara subwatershed (larger image) and the Spring Harbor subwatershed (smaller image) at the same scale, separated by a dashed line, in 1937 (above) and 1995 (below). The inset shows the actual locations of these subwatersheds.

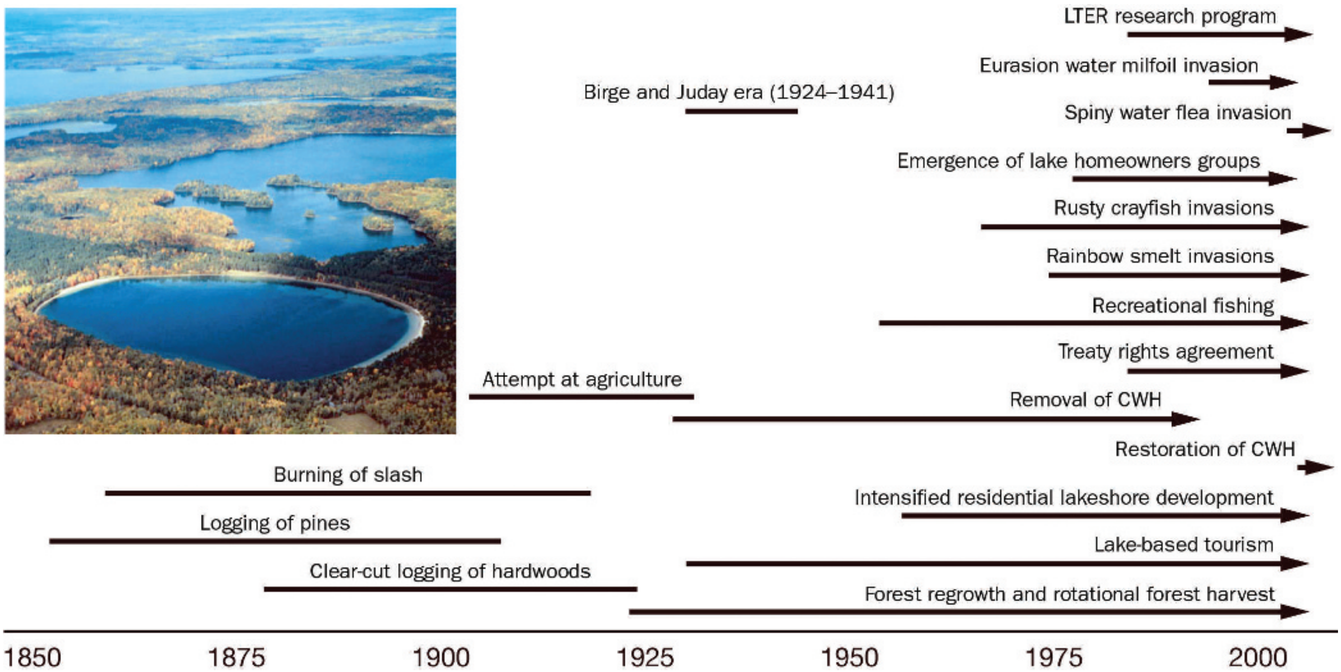

Figure 4. Timeline of major changes in lakes of the Northern Highland Lake District, 1850 to present. Abbreviations: CWH, coarse woody habitat; LTER, Long Term Ecological Research. Photograph: Carl Bowser.

to eutrophication by nutrient enrichment (Beisner et al. 2003).

Residential and recreational development of lakeshores is a central driver of three types of biotic change: (1) loss of coarse wood that provides habitat for aquatic organisms, (2) introduction of exotic species, and (3) greater fishing pressure. Our long-term perspective on lake ecosystems, in combination with whole-lake manipulations, provides a basis for understanding biotic change associated with residential and recreational development of lakes.

Removal of coarse wood. Dead trees and woody material that fall into lakes provide critical habitat for many game fish species and their prey (Schindler et al. 2000). This coarse wood offers fish spawning habitat, refuge from predators, and substrate for benthic macroinvertebrates that are important components of fish diets (Sass et al. 2006). Residential development leads to the removal of coarse wood from littoral zones (Christensen et al. 1996, Marburg et al. 2006). Housing density correlates inversely with littoral coarse wood density and bluegill growth rates (figure 5b).

We have experimentally investigated the ecological significance of coarse wood through whole-ecosystem manipulation of two lakes. Little Rock Lake is divided into two basins (treatment and reference) with a curtain. Removal of more than 75% of the coarse wood from the treatment basin eliminated the habitat refuge of yellow perch, leading to population collapse within two years (Sass et al. 2006). Largemouth bass, which prey on perch, exhibited decreased growth rates and shifted diets to riparian prey such as mice, shrews, and frogs. On the other side of the lake, where coarse wood levels were left unmanipulated, perch numbers increased by 77% over this period, and bass growth rates remained high (Sass et al. 2006). Correspondingly, in nearby Camp Lake, the experimental addition of coarse wood resulted in increased bass growth rate and spawning success (Sass et al. 2006). These results highlight the impact of residential development on lake food webs as mediated through alterations of coarse wood in the littoral zone.

Invasive species. Lakes in the NHLD have been invaded by species such as rainbow smelt (*Osmerus mordax*) and rusty crayfish (*Orconectes rusticus*). Bait buckets and recreational boat traffic are the major vectors for these species' spread (Hrabik and Magnuson 1999), highlighting the link between residential and recreational uses of lakes and the probability of invasion. Rusty crayfish and rainbow smelt create conditions that favor their own success. Smelt prey on larval walleye and consequently reduce the recruitment of a species that, in its adult stage, is the most important predator of smelt (Krueger and Hrabik 2005). Rusty crayfish invasion is followed by dramatic declines in macrophytes, zoobenthos, and sunfishes (*Lepomis*), the latter being an important predator of juvenile crayfish (figure 5c; Wilson et al. 2004, Roth et al. 2007). Experimental removal of invasive rainbow smelt and rusty crayfish in Sparkling Lake, Wisconsin, has been successful in reducing their abundance (figure 5d) and ecological impacts, and offers a step toward development of improved strategies for invasive species management (Krueger and Hrabik 2005, Hein et al. 2006). Macpherson and colleagues (2006) show that

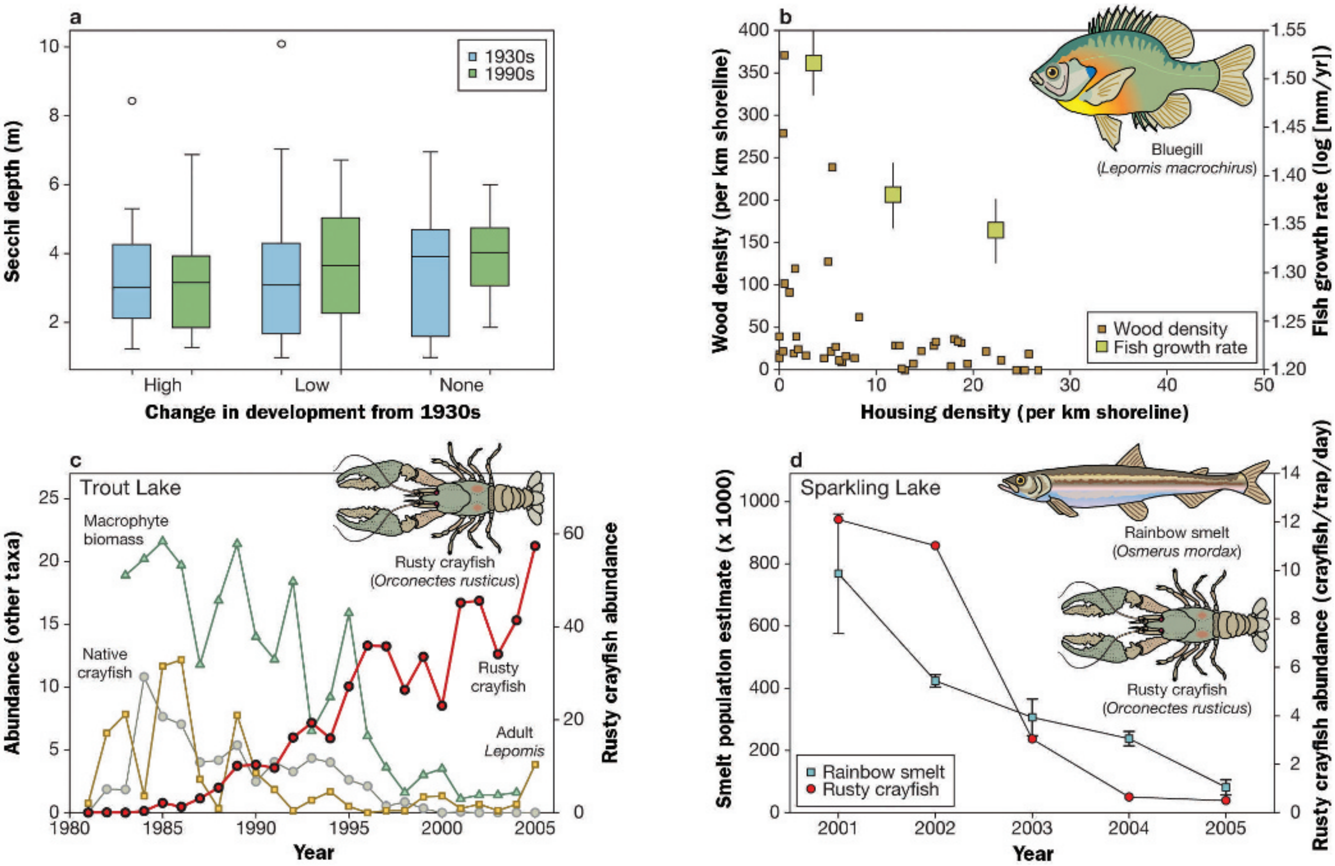

*Figure 5. Selected changes in the Northern Highland Lake District. (a) Comparison of Secchi disk transparency in the 1930s and 1990s for lakes that underwent different degrees of development during the intervening period. (b) Relationships between lakeshore housing density, density of coarse woody habitat (logs > 10 centimeters in diameter per kilometer of shoreline), and growth rates of bluegill (*Lepomis macrochirus*). (c) Declines in sunfish (*Lepomis *spp.*), macrophytes, and native crayfish in Trout Lake over time, following the invasion of rusty crayfish. (d) Declines in rainbow smelt and rusty crayfish abundance during the removal of these invasive species in Sparkling Lake. Source: Christensen et al. 1996, Schindler et al. 2000, Wilson et al. 2004, Marburg 2006, Marburg et al. 2006, Sass et al. 2006. Abbreviations: km, kilometer; m, meter; mm, millemeter; yr, year.*

for human-mediated aquatic species invasions, decisions about invasive species management must be made at the regional rather than the lake level. Management decisions made for any particular lake have implications for the probability of an invasion into neighboring lakes, because they affect how boaters distribute themselves across a lake system. Lake-level management that does not account for such spillovers may ultimately abet the invasion across the lake system.

Increased fishing effort. Because residential and recreational development increases lake use and fishing effort (Reed-Andersen et al. 2000), the overfishing of inland waters is of growing concern (Post et al. 2002, Allan et al. 2005). In northern Wisconsin, where the primary use of small boats is fishing, the number of registered boats increased by 60% between 1968 and 1989 (Penaloza 1991). Reed-Andersen and colleagues (2000) found that lake access and boating facilities were important predictors of the amount of boating activity. Because of the predilection of anglers to target larger game fishes, overfishing may trigger trophic cascades that increase the vulnerability of lakes to nutrient-driven eutrophication (Carpenter et al. 2001, Beisner et al. 2003). Coupled social–ecological models of fishing on a lake-rich landscape show that fishery changes on any given lake have spillover effects on neighboring lakes (Carpenter and Brock 2004). Fishery regulations that do not consider neighbor effects risk large-scale overharvest of fish stocks (Carpenter and Brock 2004).

Integrating biotic and social–economic processes. Residential development, and the associated increase in recreational activity, is the central driver of biotic change in the NHLD. The three forms of biotic change highlighted here (removal of coarse wood, species invasions, and overfishing) can interact in ways that accentuate their impacts. For example, overfishing of top predators may make lakes more vulnerable to invasions (Krueger and Hrabik 2005, Roth et al. 2007). The introduction of exotics, in turn, can result in the decline of sport fish (Wilson et al. 2004, Roth et al. 2007). At the same time, the removal of coarse wood may destabilize predator–prey interactions, making fisheries more vulnerable to overfishing (Sass et al. 2006, Roth et al. 2007).

If current development trends continue, all nonpublic lands in the NHLD will most likely be developed within 20 years (Peterson et al. 2003). However, the rate of development is likely to be nonlinear because of social–ecological feedbacks driven by changes in the natural environment brought about by development, and because of broader demographic and economic trends. For example, the substantial net immigration of wealthy retirees over the past several decades (Reeder 1998) is likely to have important consequences for socioecological dynamics. This demographic group has gained influence in local government and has supported local restrictions on lakeshore development. Restrictions on development have increased local lakeshore property values (Spalatro and Provencher 2001), because they protect ecosystem services that flow to lakeshore residents. These services include those affecting recreational activities such as fishing and swimming; property values fall as the ecosystem services providing quality recreation degrade. Of course, for lakes with public access, the recreational value of water quality is only partly captured by local property values, because it is possible to enjoy the lake without actually living on it, and for this reason the reduction in property values captures only part of the lost recreational value of the lake.

Recent analysis predicts that local environmental zoning will lead to sorting of residents among lakes, according to the value they place on controlling lakeshore development. This self-organizing redistribution of people may lead to differential trajectories of biotic change among lakes, even among lakes that begin in the same initial state. For instance, as lake ecosystem services degrade on lakes where shoreline regulations are weak, households re-sort, with some households leaving the lake to be replaced by new households. These new households are less concerned with the quality of ecosystem services, and participate in recreational activities for which these services are less integral to the quality of the experience. This evolution in recreation activities feeds back to the ecological dynamics of the lake system.

Agriculture and urbanization in the Yahara River Lake District

Human use of the Yahara watershed has expanded substantially since European settlement of the area in the early 1800s (figure 6). By about 1870, most of the arable land was converted for agriculture (Lathrop 1992). Madison's poorly treated sewage was being discharged to the lakes downstream of Lake Mendota by the early 1900s. Smaller amounts of effluent began entering Lake Mendota via upstream tributaries a few decades later. Algal blooms were occurring by the time formal research in limnology began in the 1880s (Carpenter et al. 2006). Biotic changes such as carp introductions, the spread of the exotic Eurasian water milfoil, losses of native macrophytes, changes in the fish community, and the collapse of deep-water invertebrate populations occurred through the 20th century (Carpenter and Lathrop 1999, Carpenter et al. 2006). By the 1950s, the severe deterioration of water quality led to management programs aimed at cleaning up the lakes (Carpenter et al. 2006). Sewage was diverted from the lakes by 1971. However, recovery was slowed by massive nonpoint-source inputs of phosphorus, as well as recycling of phosphorus from lake sediments (Lathrop et al. 1996, 1998, Carpenter et al. 2006). In the late 1980s, a major enhancement of piscivorous fishes (biomanipulation) increased grazing by zooplankton and improved water clarity (Kitchell 1992, Lathrop et al. 2002). An ambitious program to reduce nonpoint-source pollution began in the late 1990s (Betz et al. 2005); its benefits are not yet known.

At present, the immediate drivers of ecological change in the Yahara watershed appear to be hydrologic trends,

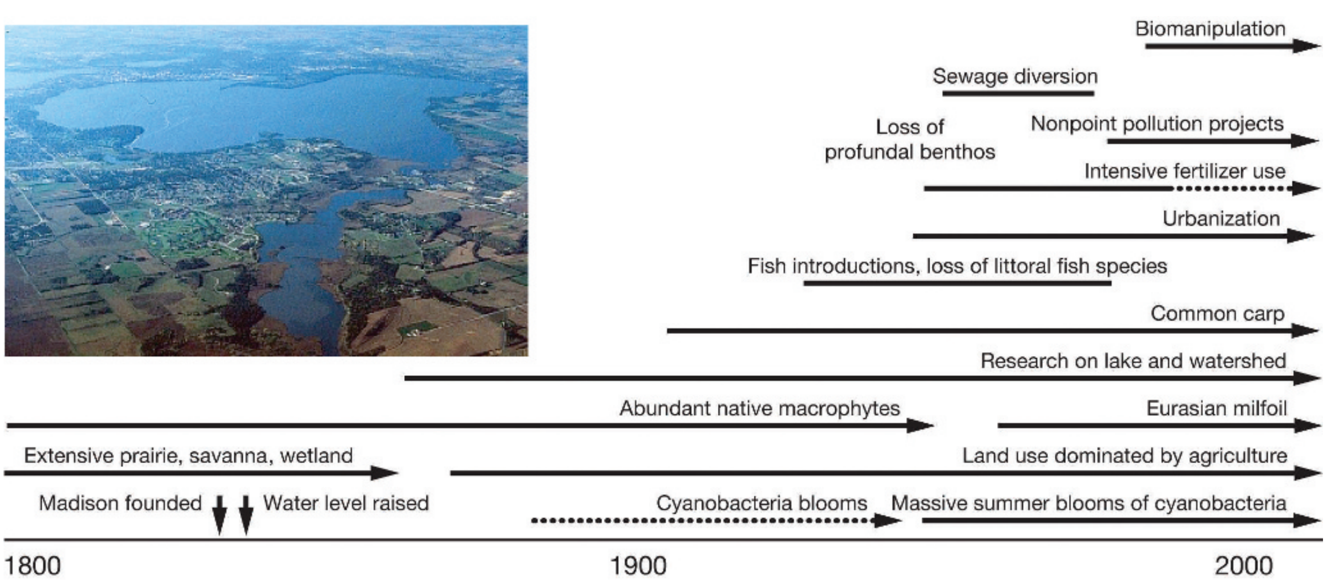

Figure 6. Timeline of major changes in lakes of the Yahara River Lake District, 1800 to present. Photograph: Dick Lathrop.

eutrophication, and biotic change. These are embedded in a larger context of institutional and socioeconomic change. Below, we emphasize changes in the watershed of Lake Mendota, the largest subwatershed for the largest lake. Lake Mendota is also the principal source of water and nutrients for the downstream lakes.

Hydrologic trends. Annual discharge from the Yahara River has trended upward since 1930 (figure 7a). In part this represents increases in precipitation of about 1.1 centimeters per decade since 1930. The increase in river discharge of more than 50 million cubic meters (m^3) per year occurred despite a decrease of groundwater flows to the lakes of 34 million m^3 per year from presettlement times due to increased municipal well pumping from the underlying deep aquifer (Lathrop et al. 2005). The shift from groundwater to surface flows of runoff is associated with the draining of wetlands and the expansion of impervious urban surface area in the watershed. These changes in watershed land use are also associated with increased variability in lake level (Wegener 2001). The change in lake level per unit of precipitation increased 19% from the 1930s to the 1990s. These hydrologic changes led directly to changes in nutrient loading and to eutrophication.

Eutrophication. Annual average concentrations of phosphorus in Lake Mendota increased as a result of an upsurge in sewage discharge in the late 1940s (figure 7b). After sewage diversion was complete in 1971, phosphorus concentrations remained high and variable because of nonpoint-source runoff and internal recycling (Lathrop et al. 1996, 1998). Lower phosphorus concentrations were associated with the drought of 1987–1988, and relatively high concentrations followed the floods of 1993 and 1995. These patterns indicate that phosphorus levels in the lakes are responsive to changing inputs, despite substantial internal recycling. This responsiveness suggests that eutrophication can be mitigated if there are sustained reductions of nonpoint-source phosphorus inputs. Economic studies show net social benefits of more than 50 million dollars (in 1999) from mitigating eutrophication (Stumborg et al. 2001), and institutional changes are moving toward this goal.

Nonpoint-source phosphorus inputs to the Yahara lakes result from high levels of phosphorus in the soils of the watershed, a legacy of intensive fertilizer and manure application (Bennett et al. 1999). A shift toward farming practices that diminish soil phosphorus concentrations, runoff, and impacts on water quality began in earnest in the Lake Mendota watershed during the mid-1990s (Betz et al. 2005). These practices include soil erosion control, nutrient management plans for farms, barnyard modifications to reduce runoff and contain manure, wetland restoration, stream bank modifications to reduce erosion, erosion controls at construction sites, storm-water management, street sweeping, detention basins, rain gardens, and mitigation of soil compaction (Betz et al. 2005). While some progress has been made in reducing nonpoint-source phosphorus inputs to the lakes, dealing with the legacy of intensive nutrient use is a challenge. Future water quality is constrained by nutrient overuse a generation ago.

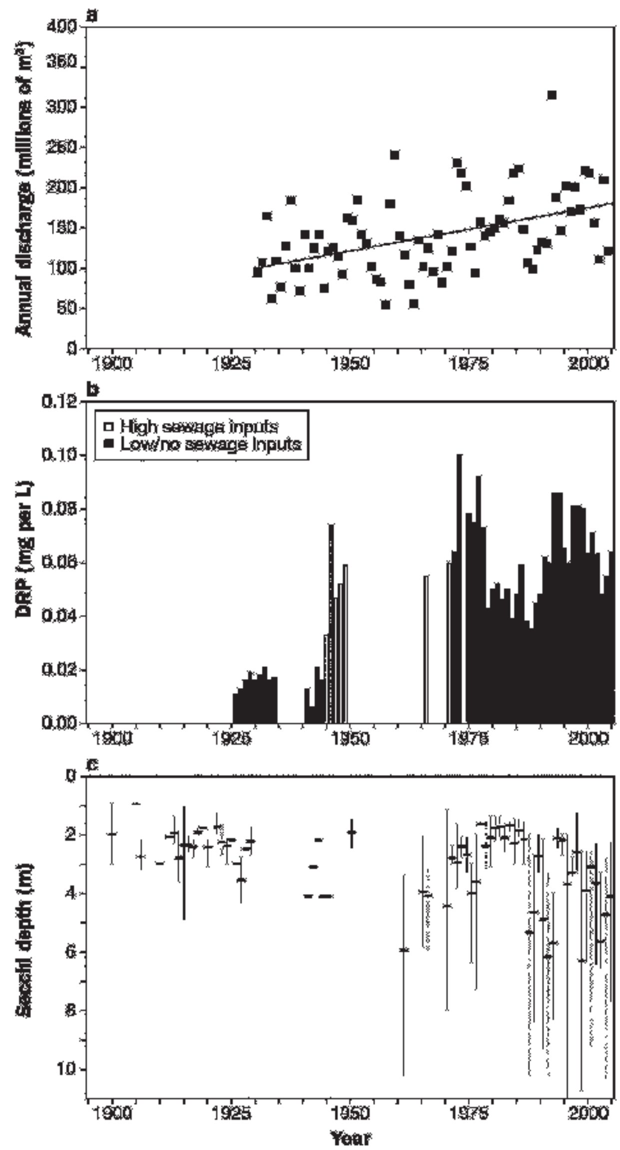

Figure 7. Selected changes in the Yahara River Lake District, 1900–2005. (a) Flow for the Yahara River. Measurements were made below the third lake in the chain, Lake Waubesa, and corrected for discharge from the Madison Metropolitan Sewage District from 1931 through 1958. (b) Annual average dissolved reactive phosphorus (DRP) concentrations in surface waters of Lake Mendota (Lathrop et al. 1996). (c) Secchi disk transparency during spring turnover in Lake Mendota (mean and range), illustrating the role of Daphnia *in water clarity and variability (Lathrop et al. 1996). Abbreviations: L, liter; m, meter; mg, milligram.*

Biotic change. As in northern Wisconsin, species invasions and losses have ongoing impacts on the Yahara lakes. Eurasian water milfoil (*Myriophyllum spicatum*) transformed the macrophyte communities of the lakes in the 1960s (Nichols and Lathrop 1994). Milfoil has declined somewhat from its peak abundance in the 1970s but remains a significant element of littoral communities. The fish community also has changed extensively. For example, in Lake Mendota, about a third of the original species have been lost and replaced by introduced species (Magnuson and Lathrop 1992). Carp (*Cyprinus carpio*), which was introduced as a food source in the 1880s, is abundant and has significant effects on benthic fauna and macrophyte communities. The Yahara lakes are vulnerable to many of the species that have successfully invaded the Great Lakes, including the zebra mussel (*Dreissena polymorpha*).

Biomanipulation of Lake Mendota showed that trophic cascades known from smaller experimental lakes (Carpenter et al. 2001) could improve the water quality of a large eutrophic lake in an urbanizing agricultural watershed (Kitchell 1992, Lathrop et al. 2002). Before the biomanipulation in 1987, small-bodied *Daphnia galeata mendotae* dominated the zooplankton, and water clarity was low (Lathrop et al. 1996). After the biomanipulation, large-bodied *Daphnia pulicaria* dominated (Lathrop et al. 2002), and water clarity became both higher and more variable (figure 7c). *D. pulicaria* have prevailed since the biomanipulation, but this situation could reverse if effective planktivores such as cisco (*Coregonus artedi*) increase in biomass.

Integrating ecological and socioeconomic changes. Change in the Yahara lakes has reflected social and economic trends (Carpenter et al. 2006). The early onset of eutrophication was most likely a consequence of erosion and sewage discharge. Eutrophication became more intense in the late 1940s as human populations and sewage discharges increased, as the use of manufactured fertilizers increased, and as growing dairy herds produced greater amounts of manure. By about 1990, it was clear that changes in the food web and hydrology interacted with the nutrient drivers of eutrophication.

Institutions for managing eutrophication have developed since the 1950s. The priorities and missions of these organizations have tracked changes in public concerns and scientific understanding. At present, much of the management effort for the lakes derives from a state institution (Wisconsin Department of Natural Resources) and a county government (Dane County Lakes and Watersheds Commission). The Yahara Lakes Association, a private group of lakeshore property owners, advocates for shoreline regulations and the control of nuisance macrophytes. A small grassroots organization, Friends of Lake Wingra, arose in the late 1990s to address watershed-scale issues pertinent to the smallest of the Yahara lakes (Lorman and Liebl 2005). This group has helped focus public attention on goals for management of the entire watershed of Lake Wingra. Other local conservation groups have also become active throughout the Yahara lakes watershed in recent years (Jones 2005).

Over the next 20 years, a substantial area of farmland will be converted to suburban and urban uses in the Yahara watershed. These developments are likely to increase runoff, variability of lake water levels, and erosion of nutrient-rich soil from construction sites. These changes could exacerbate the lakes' hydrologic and eutrophication problems. On the other hand, suburban and urban residents of the watershed tend to be supportive of environmental goals such as mitigation of eutrophication. Thus demographic trends could furnish political motivation to manage the lakes even as pressures on the lakes increase.

Patterns of regional change

There are both similarities and differences in the major changes and issues of concern within our two focal regions (figure 8). In the NHLD, biotic change is the most prominent ecosystem change, and public concern focuses on the management of shorelands, fisheries, and invasive species. Biotic change has also been extensive in the YRLD, where the public is concerned about fisheries and invasive species. However, the massive changes in hydrology and biogeochemistry associated with land use in the YRLD have increasingly focused public attention on issues associated with persistent eutrophication.

The future of both regions is expected to be influenced by changing climate, more intensive use of ecosystems by growing human populations, and biotic invasions (figure 8). Current trends suggest that shoreland management and fishing will continue to affect the northern lakes, and hydrologic and biogeochemical factors will affect the southern lakes. However, the future is hard to forecast because of the many nonlinear feedbacks in social–ecological systems (Gunderson and Holling 2002, MA 2005, Carpenter and Folke 2006). For the NHLD, we have used a set of qualitative scenarios to assess a diverse range of plausible futures (Peterson et al. 2003, *http://lakefutures.wisc.edu*). Current research involves the development of tools for quantitative analysis of scenarios for regional change.

Despite pronounced differences in the landscapes and key drivers in each region, complex interactions of social and ecological processes across a wide range of spatial and temporal scales are common to both regions (table 1). At the broadest spatial scales, climate change affects both regions. In addition, the YRLD is influenced by national—and even global—trends in food demand, meat production, and soil management, while the NHLD reflects national trends in demographics, retirement, and job availability. At finer scales, lake-specific biotic properties interact with local institutions to introduce heterogeneity among lakes in each region.

In the YRLD, differences in food webs and rates of in-lake recycling of phosphorus create unique biophysical conditions. Policies for lake management are guided by the Dane County Lakes and Watershed Commission, an institution for the entire watershed and all the lakes. In the NHLD, differences in lake biota, landscape position, and organic carbon loading create heterogeneity among lakes, but lake associations

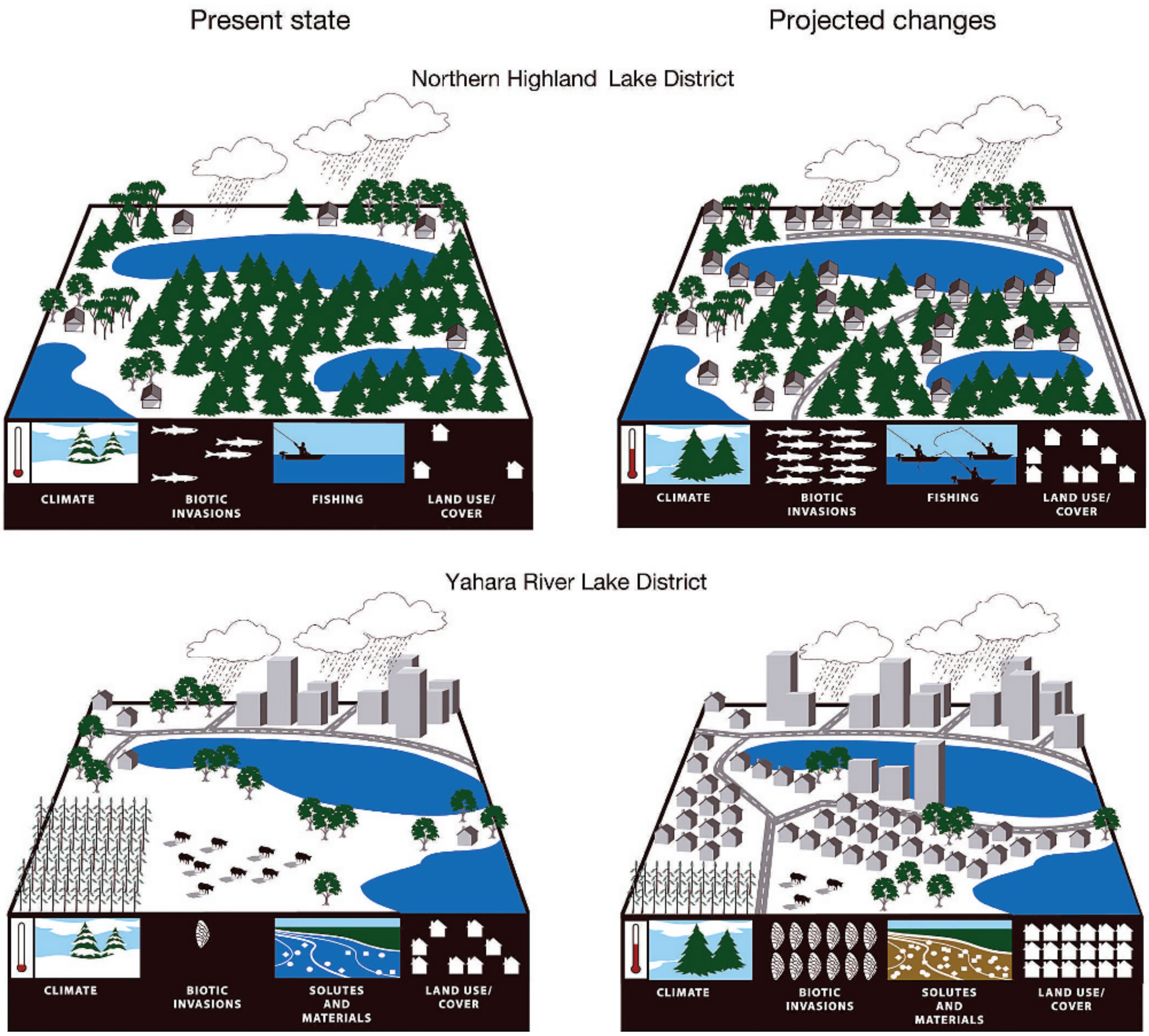

Figure 8. Present state and plausible conditions of the Northern Highland and Yahara River lake districts if present trends continue.

formed for individual lakes influence lake management policies. Across temporal scales, the long-term legacies of human activities and land use are perhaps the most striking examples of complex interactions. Both regions have persistent legacies of species removals and introductions. In the YRLD, the legacies of enriched soils throughout the watershed and the expansion of impervious surfaces will affect the lakes for decades and centuries to come. In the NHLD, the legacy of forest harvesting is still detectable today, and the removal or augmentation of coarse wood on lakeshores will similarly affect the lakes decades in the future (Marburg 2006).

Our work thus far has generated new insights into the regional patterns of change in these lakes, but it has also identified a number of key unknowns. In particular, in both regions it is difficult to anticipate how, when, and why people will respond to changes in lakes. Are there qualitative changes that produce individual or institutional responses? If so, what variables elicit the greatest response, and where are the thresholds? Can scientific knowledge prompt intervention before some catastrophic change occurs? How do local and regional management institutions differ in their responses, and where is each most effective? The differences in institutional scale (regional commission versus local lake associations) offer an interesting point of comparison for future research on the dynamics of these regions.

Understanding regional change

Although the two regions differ in many particulars, their general similarities suggest they can be understood within a common framework that links fundamental topics of ecosystem science with social dynamics at regional scales (figure 9). This framework considers exogenous drivers (e.g., climate and

Table 1. Key factors across a range of spatial and temporal scales that are associated with patterns of regional change in two north-temperate lake districts.

	Key factors	
Scale	**Biotic change in the Northern Highland Lake District**	**Persistent eutrophication in the Yahara River Lake District**
Spatial extent		
National or international	Social, political, and economic drivers of human migration, species introductions, and fishing Climate change	Social, political and economic drivers of food demand, animal production, soil management practices, and land-use change Climate change
Lake district	Attitudes and behaviors of people toward exotics Resource management agencies Regional patterns of exotic species spread and impact	Patterns of land-use change Resource management agencies Soil management practices Spatial dynamics of phosphorus
Lake	Lake associations Species introductions Food web change	Phosphorus cycle of the lake Species introductions Food web change
Time horizon		
Century	Shift from resource extraction to recreation Legacy of logging	Rise of agriculture Rise of urbanization Legacy of agriculture for soil phosphorus
Decades	Dispersal of exotics Turnover time of logs in lakes	Emergence of new issues (point-source pollution, nonpoint-source pollution, hydrologic change, food web change)
Years	Life span of key organisms Organization of a lake association	Life span of key organisms Hydraulic residence times Interannual variation of inputs

the economic, political, and social context of the nation and world), regional forces (e.g., economic or demographic forces and the demand for ecosystem services), ecosystem properties of lakes and their surroundings (e.g., water quality and biotic communities), and human uses of ecosystem services (e.g., agriculture, industry, municipal water supplies, fishing, and recreation). The feedbacks among ecosystem dynamics, human uses, social dynamics, and policy and practice are fundamental to regional change.

The importance of studying regional change is increasingly recognized in ecology, but conceptual frameworks and methods for conducting integrated analyses at broad scales are still evolving. Several studies have integrated spatial models of land-use change with projections of ecological, institutional, or economic consequences (Wear and Bolstad 1998, Costanza et al. 2002, Black et al. 2003, Turner et al. 2003). Integrating quantitative spatial analysis with policy and management is common to most studies, and some researchers have developed narratives of regional change to relate human population and resource dynamics to adaptive management (Hessburg and Agee 2003). Integrating biophysical and socioeconomic constraints in the context of sustainability planning has also emerged as a theme (Riebsame et al. 1994, MA 2005). We combine the insights gained from narratives of regional change with quantitative spatial analyses, ecological process studies, socioecological responses, and integrated models in two distinct lake districts to elucidate the drivers and feedbacks that underlie the change in our study landscapes.

Our approach to regional research maintains an overarching framework while allowing individual initiative to guide the creativity of small groups of interdisciplinary collaborators. There is general agreement on the spatial and temporal scales

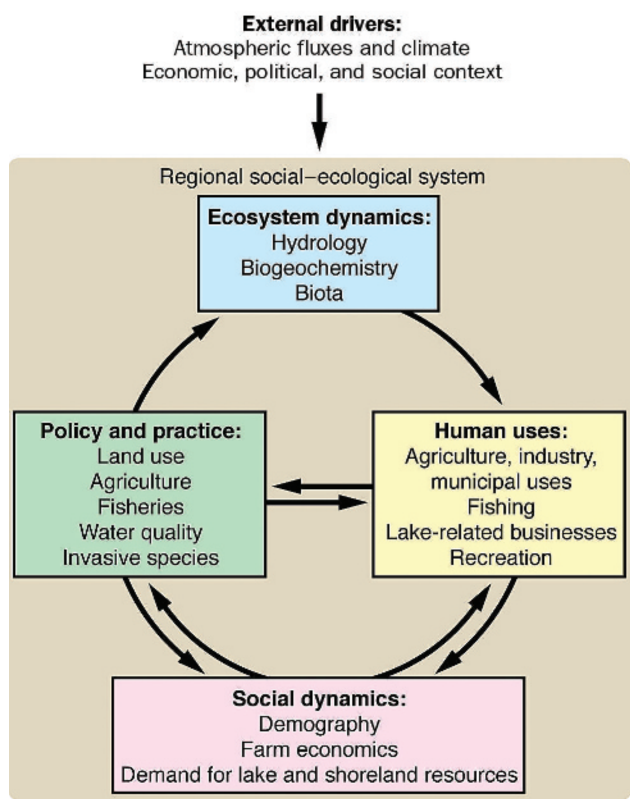

Figure 9. Integration of socioecological dynamics, human uses, and policies and practices for regional lake districts.

of interest, the need for interdisciplinary work, and the focus on lakes as sentinel ecosystems for regional change. Within this broad arena, however, specific research topics are defined by small groups of collaborators. The particular topics change over time as the science advances and investigators move in and out of the program. As a result, the coverage of topics is not uniform but instead focuses on selected priority areas that researchers have judged to be the most exciting and promising. The approach focuses limited resources on key priorities while maintaining a coherent framework.

We believe that this comparative approach to understanding regional change can be extended to a wide range of regions, and that more extensive comparisons will be a powerful means of understanding regional change. The most important—and also the most challenging—aspect is the imperative of understanding the linkages between the biophysical and social components of the system. Interactions between components are reciprocal, and no isolated part is sufficient to understand the behavior of the regional system. Furthermore, feedbacks (either positive or negative) may generate changes that are counterintuitive and hard to anticipate. Thus, our framework demands interdisciplinary study, as do other frameworks that have been used for regional assessment and research (Gunderson and Holling 2002, Baker et al. 2004, MA 2005, Radeloff et al. 2005). Yet at present the nucleation of interdisciplinary research seems to depend too much on serendipity. If we are to build the necessary science, serendipity is insufficient. Instead, agencies and foundations should provide the sustained funding that is needed to build and nurture interdisciplinary teams for regional understanding.

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