



Biodiversity Sector Midwest Technical Input Report National Climate Assessment

Climate Change in the Midwest: Impacts on Biodiversity and Ecosystems

WHITE PAPER PREPARED FOR THE U.S. GLOBAL CHANGE RESEARCH PROGRAM
NATIONAL CLIMATE ASSESSMENT
MIDWEST TECHNICAL INPUT REPORT

Kimberly Hall
The Nature Conservancy, Great Lakes Project

Recommended Citation:

Hall, K., 2012: Climate Change in the Midwest: Impacts on Biodiversity and Ecosystems. In: *U.S. National Climate Assessment Midwest Technical Input Report*. J. Winkler, J. Andresen, J. Hatfield, D. Bidwell, and D. Brown, coordinators. Available from the Great Lakes Integrated Sciences and Assessments (GLISA) Center, http://glisa.msu.edu/docs/NCA/MTIT_Biodiversity.pdf.

At the request of the U.S. Global Change Research Program, the Great Lakes Integrated Sciences and Assessments Center (GLISA) and the National Laboratory for Agriculture and the Environment formed a Midwest regional team to provide technical input to the National Climate Assessment (NCA). In March 2012, the team submitted their report to the NCA Development and Advisory Committee. This white paper is one chapter from the report, focusing on potential impacts, vulnerabilities, and adaptation options to climate variability and change for the biodiversity sector.



Contents

Five key points:	3
Introduction.....	4
Linking climate impacts to species and system sensitivities	4
Observed responses to temperature	5
Changes in species ranges and relative abundances	6
Changes in phenology.....	9
Changes in genetics and morphology	10
Changes in key disturbance factors and processes	11
Linking observations to future changes.....	11
Assessing vulnerabilities.....	12
Helping species and systems adapt in the Midwest.....	13
References	17

Five key points:

- 1) Rapid climate change over the next century will stress a majority of species in our region, and is likely to accelerate the rate of species declines & extinctions (very likely). In the Midwest, key drivers of these stresses and extinctions are likely to be interactions between climate change and current stressors, and adaptive responses will often be constrained by factors like habitat loss and lack of connectivity, invasive species, and hydrologic modifications. Direct effects of temperature increases are likely to be most critical for aquatic species that require cold to cool stream habitats.
- 2) Due to geographic factors (relatively flat topography and moderate to high latitudes), species in the Midwest that respond to increasing temperatures by shifting ranges will need to move particularly fast relative to species in many other parts of the continental U.S. to track projected changes (likely). Further, movements will often be limited by a lack of natural land cover, or a lack of appropriate aquatic habitats, and the presence of both natural and anthropogenic barriers on land and in aquatic systems (very likely).
- 3) One pro-active approach for helping a wide range of species adapt is to start by identifying large-scale patterns in projected exposure to climate change, and patterns in current factors that influence local-scale climate exposure (i.e., land that remains cooler than other areas due to proximity to a Great Lake; streams fed by cold groundwater). When these climatic patterns are combined with maps that describe variation in key factors that correlate with differences in habitat conditions (soil type, slope and aspect, hydrologic factors), we can strive to protect a variety of conditions, or “stages” for species to inhabit. The goal of protecting a diversity of conditions on the landscape and in aquatic systems can be pursued with more certainty in terms of defining the actions to take than one focused on protecting a particular list of species (or “actors” on the stages), as each species may respond to changes in surprising ways. In effect, this is a way to hedge our bets in favor of biodiversity: If we can protect and connect a network of lands and waters that encompass the widest possible range of abiotic factors, this range of available habitats should continue to promote a high diversity of species, and provide a complement and safety-net to traditional species- and habitat-focused approaches.
- 4) For freshwater and coastal species in the Midwest, it is particularly important to recognize the interaction between climate change, changes in land cover, and changes in hydrology. Land cover plays a very important role in determining the water and energy balance of a natural system. When vegetation is removed, or experiences a major change in composition or structure, these balances tend to shift in ways that increase run-off, and promote flooding, both of which contribute to stressors that put sensitive species and habitats at risk (very likely).
- 5) When the natural systems that act to slow or store stormwater are protected and restored, both people and nature benefit. Pro-active partnerships can help reduce additional losses of these key systems and ecological services, thus preventing actions that further disrupt our region’s hydrologic balance.

Introduction

At a global scale, rapid changes in climate are expected to lead to increases in extinction risk across all types of life forms, and to reductions in the ability of natural systems to provide key services upon which human societies depend (Thomas et al. 2004, Field et al. 2007, Brook et al. 2008, Maclean and Wilson 2011, Bellard et al. 2012). The rate at which changes in temperature and other climate factors are occurring in the Midwest suggests that many, if not most, wild species and natural systems will experience climate change as a major stressor. Like other regions at moderate to high latitudes, both observed rates of temperature change, and climate change projections for the Midwest region are higher than projections for the global average (e.g., as illustrated in Girvetz et al. 2009). This region is also quite flat, so shifting up in altitude is typically not an option as a response to increasing temperatures. As a result, moving to a place with lower temperatures typically means shifting across long distances, suggesting that if species are not highly mobile, they are unlikely to be able to disperse fast enough to “track” preferred climatic conditions. For many species, including some that are able to show flexible responses within a limited range of temperature increases, genetic changes are likely to occur too slowly for natural selection to keep pace with the rapid warming in the environment. As species “fall behind” in terms of adapting to changing conditions, we are highly likely to see more examples of reductions in fitness, population declines, and eventual extinctions (Parmesan 2006, Foden et al. 2008). In addition, species that are able to adapt quickly to new conditions may put additional pressures (e.g., as competitors, predators, or parasites) on those that are not able to move or adapt, further accelerating the process of species loss (Parmesan 2006, Brook et al. 2008).

The high degree to which terrestrial and aquatic systems in the Midwest region have been altered by human actions makes it clear that as we frame our understanding of what species and ecosystem services are at risk, we need to think beyond high profile examples of the observed responses of species and natural systems. Given the current low proportion of natural land cover in the southern part of the Midwest region, the dominance of non-native invasive species in our aquatic systems, and impacts from pollution and barriers to movement, species lost from natural areas may only rarely be replaced with “native” species moving north. Thus, though the species and systems of the Midwest region may not stand out as being highly vulnerable to climate change when compared to those threatened by loss of polar ice cover or sea level rise, the long-term viability of our species and systems may be at high relative risk due to climate-driven enhancement of existing stressors – the same stressors that have been the focus of decades of conservation and management efforts.

Linking climate impacts to species and system sensitivities

Observed changes, along with ecological theory, allow us to develop “rules of thumb” for how species are likely to respond to the most direct aspects of climate change (e.g., changes in air or water temperature). In addition, experimental studies and predictive models may provide clues as to how several climate factors (temperature, precipitation patterns) may interact, and we can weave these tools together with observations from both current and past climate changes to improve our understanding of vulnerability (Dawson et al. 2011). While these data and tools are useful, it is important to recognize that because many climate factors, species, and ecological processes are likely to be changing simultaneously, species and systems may show very complex responses. This complexity is likely to lead to surprises, and makes it hard to categorize relative risk, and to define meaningful management approaches to reduce risk. Assessing the relative vulnerability of species becomes even more uncertain when we try to put climate change-related risks in the context of all of the other stressors that wild species and ecosystems currently face, such as habitat loss, invasion by non-native species, changes in hydrology, and pollution. To be comprehensive in our risk assessment, we also need to try to anticipate the changes species and systems will face in the future, including actions that societies take in response to changes in climate. Many researchers describe climate change as exacerbating current threats (e.g., Brook et al. 2008), a role that is likely to increase in importance and complexity as the rate of change continues to accelerate.

Understanding how climate change will impact species, systems, and ecological services is further complicated by the fact that several aspects of climate change involve feedback loops, or can impact species through multiple pathways. For example, surface waters of the upper Great Lakes (Lakes Michigan, Huron, and Superior) are showing summer temperature increases that exceed regional temperature increases on land, in part due to positive feedbacks on the warming rate due to reductions in ice cover. Overall, the Great Lakes have shown a 71% reduction in average ice cover from 1973-2010 (Wang et al. 2011). Specifically, ice reflects energy from the sun, and insulates the water from the warming air, but melts more quickly when the air is warmer; this loss of ice cover accelerates the rate of surface water warming (Austin and Colman 2007, 2008; Dobiesz and Lester 2009). Warmer waters can stress species because the increase in temperature reduces the oxygen holding capacity of water, and because at higher temperatures, the respiration rate of organisms, which determines how much oxygen is needed, is higher. These increases in temperature are triggering a whole range of system-wide impacts, including increases in wind and current speeds, and increases in the duration of

the stratified period (Austin and Colman 2007 & 2008; Desai et al. 2009; Dobiesz and Lester 2009). Predicting ecological responses to rapid changes would be challenging under any circumstances, but the fact that food webs and the flow of energy in Great Lakes systems are continually shifting as a result of human-facilitated invasions by exotic species (Vander Zanden et al. 2010), makes understanding changes in these critical systems a particular challenge.

As with changes in temperature, there is little doubt that changes in precipitation have great potential to impact species, systems, and ecosystem services. However, at this time, it is much harder to make the case that changes in the amount and timing of precipitation that have occurred in the recent past, or may be observed, are consistent with what is expected due to climate change. This is because long-term patterns of precipitation across space have tended to be more variable than temperature, and are associated with many short and long term cycles. In other words, while we know that too much or too little rain can lead to mortality or reduced fitness, it is often hard to detect a climate change signal within the “noise” of historic variation, and thus attribute observed changes in species that may result from precipitation changes to climate change as a key driver. Similarly, projections for precipitation amount and seasonal patterns tend to vary strongly across the suite of General Circulation Models used to evaluate possible future conditions (Winkler et al. 2012). With respect to extreme precipitation events rather than mean values, however, there is general agreement that the frequency of extreme rain events (intense storms) is likely to increase, though some projections suggest this trend will vary from little change to substantial increases across the Midwest Region (Winkler et al. 2012). Agreement increases with storms defined by higher and higher thresholds; for example, recent change projections for the Midwest suggest increases in the frequency of days with storm events with greater than 1 inch of precipitation, with highest increases suggested for the frequency of the highest volume storms (Kunkel 2011). In general, these trends agree with observed patterns of increases in peak storm events over the second half of the last century for the upper Midwest (CCSP 2009, based on updates to Groisman et al. 2004, Groisman et al. 2012). Further, even while future precipitation patterns are uncertain, we can be confident that rain falling in a warmer climate will evaporate or be transpired by plants more quickly, leading to higher potential for drought stress even if a given suite of future projections does not suggest an overall decrease in the amount of rain.

When considering how to rank vulnerabilities and prioritize our efforts to protect and restore key systems in the Midwest and Great Lakes region, it is particularly important to understand the interaction between climate change and changes in land cover. Land cover plays a very important role in determining the water and energy balance of a system, in that vegetation cover slows water down,

removes water from the system through evapotranspiration, and influences local temperature due to variations in albedo (reflectance) and by shading the ground surface. When vegetation is removed or shows a major change in composition or structure, such as when forest is converted to agriculture, all of these relationships have the potential to change in ways that increase run-off and promote flooding (Mao and Cherkauer 2009, Mishra et al. 2010). The impacts of changes in landcover on aquatic systems can be quite strong. This is especially true in landscapes with high proportions of agriculture or urban land uses, which act as sources of pollutants and fertilizers when large volumes of water flow across them into rivers and coastal areas. In formerly forested watersheds, reductions in the tree cover around streams have likely been leading to increases in stream temperatures as well. Further, the region has lost capacity to store water as a result of dramatic, large-scale draining and filling of wetland ecosystems. In the northern half of the region (Michigan, Minnesota, and Wisconsin), estimates of conversion rates from circa 1780 surveys in comparison to 1980s Wetland Inventory Maps range from 42-50 percent, while in the southern Midwest region states (Illinois, Indiana, Iowa, and Ohio) losses are estimated at between 85-90 percent (Mitsch and Gosselink 2007, Appendix A). These diverse systems often occurred on areas with fertile soils that were drained for agriculture, although major cities like Chicago were also built upon drained wetlands. Thus, for the Midwest, changes to the timing, form (snow or rain), and amount of precipitation are acting on a system that is already highly altered in ways that tend to promote lower evapotranspiration and higher rates of surface run-off that leads to flooding. Although these systems can sometimes be restored, protection is crucial. Even when we invest in restoring these critical systems, it is typical for important services and structural components to lag behind conservation goals based on conditions in less disturbed wetlands, even after a decade or two of restoration efforts (Moreno-Mateos et al. 2012).

Observed responses to temperature

A majority of wild species show predictable changes in responses to increasing temperatures, and the role of temperature in shaping species life histories is strong. In other words, temperature regime is a key element to which species have adapted over long (evolutionary) time periods. The potential effects of temperature changes are most apparent for ectothermic (“cold-blooded”) animals such as insects, reptiles, and fish, for which body temperature, the key determinant of metabolic rate, strongly tracks the environmental temperature. For most ectotherms, these changes in internal temperature are associated with exponential increases in the rate of metabolic reactions that underlie body maintenance and growth (Deutsch et al. 2008, Zuo et al. 2011). Rates of key processes increase to an

optimal threshold, after which they rapidly decline as organisms get closer to maximum temperature thresholds (Deutsch et al. 2008, Kearney et al. 2009).

At lower environmental temperatures, disruption in the availability of energy influences a wide array of physiological and behavioral traits, such as activity patterns and rates of growth and reproduction. In a warming Midwest region, research suggests that ectotherms like insects and reptiles will have longer active periods (prior to becoming dormant for the winter) and overall may experience higher fitness (Deutsch et al. 2008). However, metabolic costs will increase, especially for species that cannot avoid higher temperatures through behavioral changes or movements, for example by moving to cooler microhabitats, or avoiding activity in the hottest parts of the day (Kearney et al. 2009). An increase in metabolic rate leads to a cascade of changes, including higher food requirements. In “whole lake” warming experiments, Biro et al. (2007) found an increase in the time spent searching for food was one mechanism leading to increased mortality of young rainbow trout (*Oncorhynchus mykiss*); in warmer conditions they found higher rates of mortality that they attributed to predation. Homeothermic (“warm-blooded”) animals—birds and mammals—maintain a relatively constant body temperature but still can experience heat-related stress as temperatures continue to increase, especially when they inhabit areas where they are already close to thermal tolerance limits. For example, moose (*Alces alces*), which are at their southern range limit in the northern edge of the Midwest region, are highly sensitive to increases in temperature, and have shown declines in survival that are correlated with recent warming trends (Lenarz et al. 2009, 2010). As with ectotherms, there is some evidence that species that can moderate their exposure to climatic extremes through “sleep or hide” types of responses (hibernation or torpor during cold period, use of burrows or other shelters during the hottest part of the day) may be at reduced risk relative to other species with otherwise similar characteristics (Liow et al. 2009).

Plants also have temperature tolerances, though sensitivity to high temperatures is also strongly linked to water availability (i.e., drought stress). The seeds of some plants also require a period of cold temperatures so that they can germinate, suggesting that if that period is shortened as a result of warming minimum temperatures, fitness of some plants may be reduced. Similarly, some plants require a chilling period prior to budburst, and changes in climate may alter the pattern of bud and leaf development (Morin et al. 2009).

Although an increasingly wide array of responses of species and systems to temperature-related stresses have been classified (e.g., Root et al. 2003, Parmesan 2006, Geyer et al. 2011, Maclean and Wilson 2011) for the purposes of this review, responses are grouped into five basic types: 1)

spatial shifts in ranges boundaries (e.g., moving north in the Midwest region); 2) spatial shifts in the density of individual animals or plants within various subsections of a species’ range; 3), changes in phenology (the timing of events), such as when leaves emerge in spring, or when birds lay their eggs; 4) mismatches in the phenology of interacting species; and (5) changes in morphology and genetics. These categories are not mutually exclusive, as, for example, a change in the timing of bird migration can represent both a phenological shift and a shift in gene frequencies (genetics).

Changes in species ranges and relative abundances

Shifts in where species occur can result from several different mechanisms. For many species, changes in climate conditions will enhance a given species’ survival rate, growth rate, and/or reproductive rate in some parts of the species’ range, and reduce one or more of these rates in other locations. Thus, even without dispersal (movement away from previously occupied habitats), these changes can lead to shifts in the subset of areas within a range where species are common, rare, or absent, and eventual changes in range. Changes in vital rates like survival can be linked back to the physiological constraints of balancing energy reserves under specific climatic conditions, as individuals in highly suitable climatic conditions will often have higher reproduction, survival, or both, than individuals in habitats that are more “costly” (e.g., higher cost of foraging due to heat or cold stress, higher metabolic rate due to higher water temperature for aquatic species).

Movements in mobile species can be direct responses to temperature, such as fish seeking out deeper, colder water, or can be the result of natural selection acting on more random movements by populations of individuals, as those that become established in areas with more suitable climates are more likely to survive and reproduce. Similarly, for species like plants, which are rooted in one location, shifts in range occur as a result of a life stage like seeds being dispersed (e.g., by wind or birds) and becoming established in new areas that are now presumably more suitable than they had been in the past.

For species to “track” changes in temperature by shifting ranges, they need to be mobile in some stage of their life history, and to have a suitable path to follow (“permeable” landcover, a freshwater system that is free of barriers and contains suitable habitat). As a general rule, range shifts in response to warming temperatures result in species moving to higher latitudes or altitudes, although factors like topography, distance to water bodies, and factors like shading by tall vegetation influence regional and local temperatures, and can contribute to variations in the spatial pattern of how species respond (Ashcroft et al. 2009,

Dobrowski 2011, Klausmeyer et al. 2011). Areas that are consistently cooler than other locations due to persistent factors (altitude, aspect, proximity to water) can act as climatic “refugia,” in that they can support species that otherwise would be lost from an area. In the Midwest region, the most notable influence on regional climate is the “lake effect” in areas around the Great Lakes, which acts to modify both high and low temperatures in coastal areas and on Great Lakes islands (Scott and Huff 1996). Similarly, in the Midwest it is possible to have streams within the same watershed that vary enough in temperature to support different fish assemblages (e.g., cold water, cool water, or warm water fish) due to local variation in geography and variation in the extent to which the stream is supplied by cold groundwater (Ficke et al. 2007, Chu et al. 2008, Lyons et al. 2010).

Landscapes in the Midwest are typically fairly flat, so shifting up in altitude is typically not an option as a response to increasing temperatures. For terrestrial species, in the absence of some form of climatic refugia, moving to a place with lower temperatures typically means shifting across long distances. The combination of higher latitudes and relatively flat topography suggests that species “tracking” changes in temperature by shifting their ranges will require more rapid movement in this region than in other geographies where rates of temperature increase are lower, and/or where they could shift up in altitude to reach cooler habitats (Guralnick 2007, Jump et al. 2009, Loarie et al. 2009, Chen et al. 2011). In effect, the lack of topographic diversity in most parts of the Midwest can be thought of as increasing a species’ exposure to climate change, or as a factor that reduces extrinsic adaptive capacity (i.e., the component of a species’ potential to adapt to changing conditions that is linked to its current environment, rather than intrinsic factors like traits or genetic diversity). For example, to reach terrestrial areas that are 1 degree C cooler, a species in mountainous terrain could shift approximately 167 m in altitude, while achieving the same shift in flat terrain would mean a shift of roughly 145 km to the north (Jump et al. 2009).

A recent global study suggests that in most of the Midwest, tracking changes in temperature in the second half of the century (2050-2100, A1B emissions scenario) will require that terrestrial species move over 1 km/year; in comparison, the global average estimate of the “velocity” of dispersal needed to track changes in terrestrial systems was less than half that rate, at 0.42/km year (Loarie et al. 2009). Similar estimates were attained in modeling work that focuses on estimating the “temperature maintaining distance” for small mammals in northern Indiana: Francl et al. (2010) suggest that to track changes in average January temperature that occurred during the mid 20th century, species would have needed to move north at between 0.4 and 2.1 km/year, with that estimate increasing in projections for this century. Rates of 1 km/year and higher

are currently being achieved in some locations by some taxa (Chen et al. 2011), but such rates are likely to be unattainable for many species, especially in highly modified landscapes, or in aquatic systems with limited connectivity. If emissions exceed the A1B scenario projections and are closer to A2, tracking change in the Midwest will require even faster movements (e.g., several km/year or more, Loarie et al. 2009 supplemental figure S17).

Recent work by Schloss et al. (2012) evaluating mammal vulnerability incorporates both temperature and precipitation changes, which reduces the extent to which the Midwest stands out among other locations in North America/the western Hemisphere in terms of the velocity of change (see Figure 2), but highlights that even this mobile group has some highly vulnerable members. Specifically, their work incorporating dispersal ability into range change projections for the western hemisphere suggests that on average about 9% of mammals at a given location are likely to be unable to keep pace with climate change, with many locations in the Midwest modeled to have higher vulnerabilities, up to about 39% (Schloss et al. 2012, Figure 1). Their work provides estimates of dispersal velocities for several hundred mammals, and shows the variety of rates possible within one taxonomic group. In the Midwest, values range from fast dispersers like the gray wolf (*Canis lupus*), which they estimate can move about 40 km/year, to much smaller animals for which dispersal events are short and rare, like northern short-tailed shrews (*Blarina brevicauda*) with an estimated movement rate of 0.40 km/year (Schloss et al. 2012 Supplement, dataset S1).

From a vulnerability standpoint, species that can move rapidly (e.g., birds, large mammals) are typically seen as more likely to be able to keep up with climate change than other species with lower dispersal capacities (e.g., amphibians, most plants, sessile aquatic invertebrates, insects that are poor dispersers). However, it is important to remember that suitable climatic conditions are necessary but not sufficient; persistence in new habitats also depends on how well new areas meet an organism’s needs for food and shelter, and habitat for movement needs to be available between current and future ranges. Schloss et al.’s (2012) assessment of mammal vulnerability integrates land use as well as the projected velocity of change in both temperature and precipitation, which for the Midwest highlights the importance of land conversion as a barrier to species movements (Schloss et al. 2012 - Figure 5). Further, even mobile species that depend on food sources or habitat components that shift at slower rates will be vulnerable if the species that they depend on decline. In addition to moving north within river systems or large lakes, as noted above, some aquatic species also may be able to move into deeper, cooler waters within the same water body, although these deeper habitats may not have all of the other resources that a given species’ requires. A tie to stream habitats may suggest high vulnerability for many species, as

even in aquatic systems that appear to have high connectivity (few barriers to movement due to structures or pollution) many taxa (like stream insects) can be limited in their movements by unsuitable habitats or hydrologic conditions (Strayer 2006), or be connected to other areas that do not contain cooler habitats (i.e., east-west connectivity rather than north-south).

Examples of species showing range and abundance changes in and near the Midwest region are beginning to accumulate, with the best documented examples coming from researchers conducting long-term research on topics such as community composition and population dynamics. The forest-focused review by Handler et al. (2012) includes summaries of work examining both observed and projected change in tree species ranges; most trees are expected to shift more slowly than optimal given the changes in climate. For birds, which are clearly very mobile, several recent papers document range shifts, with changes dominated by northern shifts over a range of distances, and also some evidence for shifts in other directions (Zuckerberg et al. 2009 in New York state; Hitch and Leberg 2007 breeding ranges in North America, LaSorte and Thompson 2007 winter ranges in North America). Work by Myers and colleagues (2009) on mammals in Michigan documents rapid changes in ranges for several common species, including northern range edge shifts of over 225 kilometers since 1980 for white-footed mice (*Peromyscus leucopus*). Similar rates of movement appear to have been occurring with southern flying squirrels (*Glaucomys volans*), although the authors suggest that small, hard to detect populations may also have been rapidly expanding and contributing to the shift in range (Myers et al. 2009). The movement of white-footed mice is of concern from a public health perspective, as these mice are key hosts for the ticks that carry Lyme disease (Ostfeld 1997). Bowman et al. (2005) also documented rapid northern shifts of southern flying squirrels in Ontario over a series of years with relatively warm winters and higher food availability (tree mast) – they document a 200 km northward shift over 9 years (1994-2003), but the range contracted to its historical limit following a very cold winter in 2004 that was associated with mast failure. The same research team documented a relative reduction in genetic diversity within squirrels trapped at the northern edge of this range expansion, providing evidence that even for species that can shift quickly, there may be fitness consequences associated with these rapid responses (Garroway et al. 2011).

Species are also showing changes in abundance within current ranges. Studies on moose (*Alces alces andersoni*) provide an indication of the complexity of the sensitive relationship between a species' population numbers and environmental temperature. Two separate research teams focused on understanding factors such as birth rates, parasite loads, and survival of moose in northwestern Minnesota (Murray et al. 2006) and on Isle Royale in Lake

Superior (Vucetich and Peterson 2004; Wilmers et al. 2006) suggest that warming temperatures are contributing to local population declines through increases in heat stress-related effects. Modeling by the northwestern Minnesota teams suggests that, given the observed relationships between vital rates (birth rates, survival) and temperature, that population of moose will not persist over the next 50 years (Murray et al. 2006). Population monitoring and modeling also suggest that a third population of moose in northeastern Minnesota is declining, though at a slower rate (Lenarz et al. 2009, Lenarz et al. 2010).

As in the examples above, documenting changes in species viability and ranges represents a major challenge, especially for wide ranging or hard to detect species. As a result, many researchers have used predictive modeling tools to try to understand current and future impacts on species distributions. Due to their strong dependence on relatively narrow temperature regimes, freshwater fish have been the subject of many research studies examining the impacts of temperature change on distributions. Early work suggested major impacts, such as a 50% reduction in North America's cold and cool water fish with a temperature increase of 4°C (Eaton and Scheller 1996), and highlighted the Midwest as a region with particularly high impacts. Recent work in the Midwest region has added complexity and additional factors (presence of invasive species, changes in land use) to the modeling approaches used in the past, but continues to suggest high potential for major reductions in fish diversity due to temperature increases. In a model-based study of potential changes in the distribution of 50 common stream fish species in Wisconsin, Lyons et al. (2010) estimated that with warming, all of the cold and cool water species (23 of the 50) and four of the warm water species would be expected to show declines, while 27 of the warm water specialists would be expected to stay the same or increase in population. Under the highest warming scenario they tested (a 5°C increase in air temperature, 4°C increase in stream temperature), three of the cold water species were predicted to go extinct in the state (Lyons et al. 2010). In work focused on cisco (*Coregonus artedii*) in Wisconsin, a species of conservation concern that is found primarily in larger, deeper, cooler lakes, Sharma et al (2011) looked at 78 different climate change projections (B2, A1, and A2 scenarios) and estimated that 25-70% of populations in the state will be extirpated by 2100. As the complexity of the models used to project changes in fish distributions has increased to include habitat and land use variables, we have gained insight into how we might slow the rate of species losses (e.g., Jones et al. 2006, Steen et al. 2010). For example, in work focused on nine game fish in the Muskegon River watershed of Michigan that included both changes in land cover and temperature increases, cold water fish were projected to show declines, but results suggest some of these changes could be slowed through increasing forest cover near stream habitats (Steen et al. 2010).

When species are mobile and suitable habitat is present in the right location, range shifts may represent a viable response to changing conditions. However, range and abundance changes are of concern for several reasons. First, species that are not able to disperse will have the stress of climatic conditions that are becoming less and less favorable, and the added impacts of species moving in from warmer areas that are less challenged by the same climatic conditions. The species moving in may directly compete for key resources and also may contribute to the decline of resident species by spreading diseases and parasites. Second, range shifts by species that act as forest or crop pests, or that are detrimental to public health (i.e., carry diseases, create toxic algal blooms) are key concerns in the Midwest, and are important subjects of observational and model-based research studies (e.g., Hong et al. 2006, Jactel et al. 2011). In particular, many invasive, non-native pests are likely to be more successful at surviving in our region as minimum winter temperatures continue to rise (Bierwagen et al. 2008, Vander Zanden et al. 2010). Third, we are concerned about range and abundance shifts because species movements will often be independent of shifts of other species. We expect species to shift independently, as the set of constraints that describe the habitat and ecological niche for each species (factors like temperature, food availability, soil types, and stream flow characteristics) is unique (Parmesan 2006). In effect, we expect to see the “tearing apart” of sets of species that typically interact, and many of these interactions may be critical to the survival one or more of the interacting species (Root and Schneider 2006).

Changes in phenology

In many species and systems, seasonal changes in temperature act as cues that trigger transitions in the seasonal cycles, such as metamorphosis (e.g., transition from egg to larvae), the development of new leaves, or the initiation of phytoplankton blooms that transfer energy through aquatic food webs. In addition to triggering changes in timing, known as changes in “phenology”, warming trends can impact species indirectly by influencing other key seasonal events that trigger changes in their seasonal cycles, such as shifting the timing of snowmelt or flooding, or lake stratification. Further, timing issues become important in the context of ephemeral (temporary) habitats, like small streams or wetlands that dry out in the summer. When increasing temperatures promote faster drying, this can put species like amphibians and aquatic invertebrates at risk if habitats dry before they have completed aquatic life stages (Brooks 2009).

Several early phenology studies that were highly influential in raising awareness that species were responding to changes in climate focused on, or included, study sites in or

near the Midwest/Great Lakes region. These included evidence of 10 to 13 day advances in frog calling dates (an indicator of timing of breeding) in western New York in response to a 1 to 2.3°C increases in temperature in key months (Gibbs and Breish 2001), advances in the timing of many spring events (bird arrivals, plant blooming) on a Wisconsin farm in the 1980s and 1990s relative to observations taken by Aldo Leopold in the 1930s and 1940s (Bradley et al. 1999), and a nine day advance in the laying date of tree swallows (*Tachycineta bicolor*) across the continental U.S. over 32 years (1959-1991; Dunn and Winkler 1999). Phenology changes can also be linked to indirect climate change impacts, such as timing of seasonal disappearance of ice (ice-out) in spawning streams. Recent work by Schneider et al. (2011) suggests that both ice-out and walleye (*Sander vitreus*) spawning are occurring earlier in Minnesota.

In most cases, the implications of change in phenology on fitness are unclear, but as we build longer term datasets in the Midwest, it is likely that patterns will continue to emerge. For example, a recent paper documenting long-term (approximately 100 years) changes in phenology and abundance of 429 plant species in Concord, Massachusetts (many of which are also found in this region) showed that although there has been an overall shift of 7 days in flowering phenology associated with a 2.4°C temperature increase in the study area, some plant families are showing less of a response to temperature than others (Willis et al. 2008). In many cases this failure to shift flowering time in response to changes in seasonal temperature was associated with strong declines in abundance (Willis et al. 2008).

Work by two teams of researchers that have documented climate-related changes in nesting patterns in freshwater turtles in Illinois over the past two decades (painted turtles *Chrysemys picta* - Schwanz and Janzen 2008; and red-eared sliders, *Chrysemys picta elegans* – Tucker et al. 2008) shows how complex predicting responses to climate can be. Like many reptiles, these turtles exhibit temperature-dependent sex determination, which means that the temperature at which the eggs are incubated determines the sex ratio of the eggs within the clutch. However, the relationship between air temperature and sex ratio is not simple, because vegetation cover can influence the nest temperature, and nests that are created early in the season may be in soils that are still cooler than ambient air (Tucker et al. 2008, Schwanz and Janzen 2008, Schwanz et al. 2010). In the study by Schwanz and Janzen (2008), initiation of nests has become earlier over time, with advances linked most strongly to years with warm winters; second and third clutches of eggs in the same season have also become more common. In Tucker et al.’s (2008) work, the site has experienced a more consistent warming trend, and responses appear stronger; these include significantly earlier first nesting dates (2.23 days earlier per year), and a

lengthening of the nesting season by 1.2 days per year between 1995-2006. As a result of these changes, especially the additional clutches per year, the total number of offspring in the Tucker et al. (2008) study has increased, with one surprising twist: Warmer temperatures produce more females in this species, but in recent years, the trend has been towards more males. The authors suggest that shifts towards earlier first clutches, plus a higher frequency of later season clutches, has meant more eggs developing under cooler soil conditions.

The term phenology mismatches describes situations where species that interact in some important way respond differently to a temperature change. The potential importance of mismatches may be easiest to imagine in systems where attainment of a threshold temperature cues the emergence of leaves of a dominant tree or grass, or algal growth. In such a system, a shift in the timing of spring warming that alters when these plants grow or bloom could represent a key change in the foundation of the food web that determines energy flows throughout that entire ecological system. If other species in the same system do not shift in the same direction and at a similar rate, they may be at a strong disadvantage in terms of their ability to survive and reproduce relative to other species.

As described above for fitness impacts, although a wide variety of species are likely vulnerable to phenological mismatches, it is rare to have direct evidence that species are experiencing declining fitness through this mechanism. However, it is not very hard to pull together information to make the case that these types of changes should be of concern. For example, the northern Great Lakes region and the Mississippi River corridor stand out within North America as regions that support vast numbers of birds during spring and fall migration. One group, songbirds, depends upon a ready source of insect prey, both along their migration routes, and in their breeding habitats. Studies in Europe have documented advances in insect emergence relative to bird arrivals at breeding habitats, and suggest that these timing mismatches are leading to reduced breeding (Visser et al. 2006; Both et al. 2009). In the U.S., Marra et al. (2005) compared the median capture dates of 15 long distance migrants from bird monitoring stations in coastal Louisiana and two stations in the Great Lakes region, Long Point Bird Observatory (on the north shore of Lake Erie) and Powdermill (western Pennsylvania). They also compared the duration of time between the median arrivals for the same species at the southern and northern sites. They found that median capture dates were earlier in years with warmer spring temperatures (mean April/May temperature) for almost all of their focal species, at a rate of roughly 1 day earlier per each 1°C increase in temperature. However, they note that in indicator plants (lilac, *Syringa vulgaris*), budburst occurred 3 days earlier for the same temperature increment, a similar rate to the average reported for plants

in the Willis et al. (2008) study described above. Similarly, Strode (2003) suggests that North American wood warblers are not advancing in phenology as fast as key prey are likely to be responding to increased temperatures (e.g., the eastern spruce budworm, *Choristoneura fumiferana*). Earlier arrivals were at least in part achieved through faster migration (as opposed to earlier departure dates) as the duration of migration between the southern and northern locations decreased by 0.8 days with every 1°C increase (average of 22 days; Marra et al. 2005).

One message from this body of work is that patterns in phenology will vary both in time and space, and that our ability to predict changes in timing, and potential mismatches, is very uncertain. For example, recent work from Minnesota and South Dakota shows that many species migrating through the prairies are arriving significantly earlier, especially those that are typically earliest and tend to feed on aquatic insects (Swanson and Palmer 2009). While patterns emerged in terms of which species are arriving earlier, the strength of trends for the same species varied across the two states. Interestingly, strong changes were detected even though temperatures in spring for the region have not shown much change, although winter temperatures have significantly increased (Swanson and Palmer 2009).

Changes in genetics and morphology

Most studies documenting responses to climate change focus on readily-observable characteristics such as phenological shifts; however, increasing numbers of studies are showing that changes in other characteristics, such as morphology (body shape or size), behavior, and underlying gene frequencies, can be linked to rapidly warming temperatures. As with other areas of response to climate, well-documented patterns that are not necessarily directly climate-related lead us to expect genetic impacts, such as well-documented patterns of reduced genetic diversity in populations at the “leading edge” of directional range expansions (Excoffier et al. 2009, Sexton et al. 2009; see also the Garroway et al. 2011 northern flying squirrel example cited above). Demonstrating changes in gene frequencies in response to climate change is a major challenge, as it requires these frequencies to have been measured in many generations. As a result, most examples are studies of short-lived insects like fruit flies (*Drosophila* species) and use comparative approaches. Work on fruit flies around the world has demonstrated shifts in how chromosomes are arranged that correlate with geographic patterns, i.e., populations in the north shift toward showing patterns like those to the south as climate warms (Levitan 2003; Balanyá et al. 2006; Etges and Levitan 2008). These changes tend to be discussed in terms of “heat tolerance,” yet the actual benefit of these changes in terms of enhanced

viability have not yet been established (Gienapp et al. 2008).

Strong evidence of similar genetic changes in vertebrates in response to climate change is very rare (Gienapp et al. 2008), but one notable exception comes from long-term research focused on red squirrels (*Tamiasciurus hudsonicus*) in western Canada. Work by Réale et al. (2003) demonstrated that shifts toward earlier breeding phenology in response to climate-induced changes in food supply are the result of both phenotypic plasticity (87 percent of the change) and an evolutionary response (13 percent). Recent work by Pergams and Lacy (2008) documented rapid genetic and morphological changes in Chicago-area mice (*Peromyscus leucopus*), though the mechanism for this change likely includes a complex set of environmental factors, in addition to recent climate changes.

Although results suggest that some species may be able to respond quickly to changes, many others may lack the genetic variation that might allow selection, and thus adaptation, to occur. In other cases, as has been demonstrated for a Minnesota population of a native prairie plant (*Chamaecrista fasciculata*), adaptive responses can be slowed even when variation is present, due to linkages between traits that are “antagonistic”, such that one confers benefits in a new climate, and another does not (Etterson and Shaw 2001).

Changes in key disturbance factors and processes

In addition to the many direct and indirect influences of climatic factors on species and ecological systems described above, climate change can also alter key processes that influence the viability of species and characteristics of systems. For terrestrial systems in the Midwest region, processes with a strong link to climate include fire frequency and intensity, flooding frequency and volume, drought, and with possibly less certainty, wind and ice storms. These disturbances and some interactions (i.e., in trees, drought stress tends to correlate with increased damage when trees are attacked by insect pests or disease outbreaks) are described for forest systems in Handler et al. (2012). Some systems are likely to benefit from changes in disturbance regime, and may be easier to restore or maintain on the landscape as a result of these changes. For example, prairie ecosystems (which have been drastically reduced in extent in the central U.S.), along with several species of oak and pine are favored by frequent fires.

Changes in temperature, both direct and through the ice and wind-related mechanisms described above in the impacts section, have the potential to profoundly change how large lakes in our region function (see also the review by Mackey 2012). Specifically, these climate change factors

may drive changes in the timing or duration of stratification. The differences in temperature, light availability, and other factors that occur as a result of stratification provide a diversity of habitats within stratified lakes, which allows species with a wide variety of temperature and other habitat requirements to persist. The timing of stratification, as well as the timing of the fall “turnover”, when the oxygen-rich surface waters cool and increase in density and finally sink down and mix with the others, can be a critical factor influencing the viability of lake species, especially cold-water fish (Magnuson et al. 1997). Given that changes in temperatures for the upper Great Lakes are projected to continue to match or exceed the air temperature increases, we should expect to see longer stratified periods and increased risk of oxygen deficits below the thermocline in late summer (Magnuson et al. 1997; Jones et al. 2006; Dobiesz and Lester 2009). Increases in the duration of the stratified period of over two weeks have already been observed for Lake Superior (Austin and Colman 2008), and projections for the end of this century suggest that we could see lakes stratify for an additional one and a half months (Lake Erie for a lower emissions scenario and thus less climate change) to three months (Lake Superior under the assumption of higher future emissions; Trumpickas et al. 2009). As the depth and latitude of a lake, lake basin, or bay decreases, it is less likely to show stratification, but some shallow water bodies will exhibit oxygen-poor “dead zones” because shallow water warms more rapidly, and warmer water holds less oxygen and leads to increases in respiration rates for aquatic species. As warming continues, we should expect more and more areas to develop “dead zones”, and for others to transition from stratifying in summer to not stratifying at all, with resultant loss of species that depend on habitats characterized by colder water.

Linking observations to future changes

Thus far, the weight of evidence suggests that the most appropriate expectation for how species may respond to climate change is to anticipate more of the types of changes we have already seen -- i.e., changes in ranges (evading the change), and changes in phenology and behavior that allow species to persist in the same range. Not all changes in observed characteristics (phenotypes) that allow a species to persist in the same place require a change at the genetic level. Many species are able to show flexible responses to temperature as conditions vary among years. Thus, when conditions change in a given location, we can expect to see both “flexible” changes in some species (phenotypic plasticity), and, if diversity is present and individuals that best tolerate the new conditions produce more offspring, heritable changes (i.e., evolution - a change in how common given genes are within the population). In general, phenotypic plasticity can be thought of as a “short-term” solution, as the limits to these responses will eventually be

exceeded as a population experiences a long-term increase or decrease in an environmental factor (Gienapp et al. 2008). Thinking about both mechanisms for change highlights a caution for our ability to manage over the long term: Many species that appear to be tracking changes in climate, or thriving even as factors change, may show sudden declines in viability once the temperature shift exceeds some critical threshold beyond which their “flexible” response is not enough. The potential for evolution in response to climate change is constrained by the degree to which genetic variation for particular traits is present in a given population. For example, traits that contribute to increased heat or drought tolerance must be present in a population for natural selection to favor the individuals that have those traits, and eventually lead to an overall change in the proportion of individuals that have that “adaptive” trait in later generations. For many of the Midwest’s species of greatest conservation concern, we already suspect that population declines, habitat fragmentation, and other stressors have reduced the level of genetic variation such that there is little variation left upon which natural selection can act. It is, however, exceedingly rare to actually have data on genetics over time that can be used to confirm or refute this suspicion. Similarly, evidence for genetic responses to climate change is extremely rare, as it requires genetic data to have been sampled over time (Balanyá et al. 2006). As of yet, while there are many examples of changes in species in response to climate change, there are no documented examples of genetic shifts in thermal tolerances that appear to allow species to remain viable in the same location following a change that would have otherwise led to reduced survival or reproduction (Parmesan 2006; Bradshaw and Holzapfel 2008; Gienapp et al. 2008).

Assessing vulnerabilities

The vulnerability of a species, system, or ecological service can be described as a function of three factors: (1) exposure to some form of change in climate (e.g., temperature increase, change in timing of flooding); (2) sensitivity to the change, and (3) adaptive capacity, or the potential for that species, system, or process to respond, move, or even transform in a way that allows persistence or maintenance of key functions as conditions rapidly change (Schneider et al. 2007, Foden et al. 2008, Williams et al. 2008, Klausmeyer et al. 2011). While these categories are helpful from framing discussion, the concepts of sensitivity and adaptive capacity can be hard to disentangle in environments with a strong human influence. For example, a species or system may be much more sensitive to changes in hydrology (timing and amount of water availability) if invasive species, or drainage infrastructure, have already changed the way water moves through the system. For this reason, it is often helpful to think of both sensitivity and adaptive capacity in terms of intrinsic and extrinsic characteristics.

Intrinsic aspects of sensitivity include physiological tolerances for temperature or drought, while related intrinsic components of adaptive capacity include genetic diversity of a population (potential that some individuals have traits that lead to higher tolerances), and traits that allow movement or flexible timing for key life events. Following the temperature tolerance example, an animal may be more sensitive to increases in temperature if they are already stressed by some other factor, such as exposure to pollution or water with low levels of dissolved oxygen. Extrinsic elements of adaptive capacity include the geographic context in which the exposure to climate change takes place – for example, fish in deeper rivers or lakes are more likely to be able to persist as temperatures warm, because they can move into deeper water. Similarly, species that are likely to respond to changes in climate by shifting their range have higher intrinsic capacity to do so if they can swim, fly, or run, and higher extrinsic adaptive capacity to do so if they are currently found in a landscape or aquatic system that is connected to more northern habitats. From a management and conservation standpoint, we are typically trying to move “levers” that reduce the impact of extrinsic factors – can we reduce other stressors (like pollution or habitat loss) that increase sensitivity, or reduce adaptive capacity? Can we remove barriers to movement? Can we work with partners in other sectors to reduce changes in hydrology? However, in many if not most parts of the Midwest, there will be at least some species or system types for which there is little we can do to reduce the impacts of climate change, and little intrinsic potential for the species or system to adapt. For these cases, reducing the rate of change through reduction of greenhouse gas emissions is the only meaningful strategy.

Characteristics often identified as indicators of species that are at greatest risk of population decline or possibly even extinction due to climate change impacts include (Parmesan 2006, Brook et al. 2008, Foden et al. 2008; see also the list for trees in Handler et al. 2012):

- Occur at high altitude or latitude (can’t shift range further up or to the north in the Northern hemisphere).
- Occur in isolated habitats surrounded by developed land, or adjacent to natural barriers that inhibit dispersal.
- Near limits of physiological tolerance.
- Limited dispersal ability.
- Very specific habitat requirements, including ties to a particular timing of water availability.
- Highly dependent on interactions with one or a few other species (susceptible to phenology mismatches, and mismatches in rate or location of range shifts).
- Long generation time (slow potential pace of microevolution).

- Low genetic variability and/or low phenotypic plasticity. Low genetic variability may arise due to population reductions, or to a long history of occupying a relatively narrow set of climatic and habitat conditions.

In general, for the Midwest, vulnerability assessments often highlight aquatic species that depend on cold water as being among the most vulnerable, as these species often have narrow tolerance limits, and aquatic systems are often degraded and not well connected. While the high vulnerability of cold water fish (described in an earlier section) are of concern for many due to ecological, recreational, and commercial values, there are many other species that are likely at risk in aquatic systems as water temperatures rise and smaller streams dry up more quickly during longer, hotter summers. Connecting patterns of geologic history, current species diversity, and potential climate impacts suggests other particularly vulnerable taxa. While the Great Lakes are a “young” freshwater system (i.e., species there moved in after the last glacier retreated, some 14,000-16,000 years ago), the southern part of the Midwest region sustains species with much longer ecological histories in the area, which leads to higher specialization and species diversity. Work by DeWalt and colleagues indicates that unglaciated areas of southern Illinois, southern and central Indiana, and southern Ohio could lose many rare aquatic insect species if changes in precipitation patterns and increasing evapotranspiration rates promote more rapid drying of small, isolated ephemeral streams (DeWalt et al. 2005, DeWalt and Grubbs 2011, DeWalt et al. 2012). Similarly, the combination of several risk factors suggests that freshwater mussel species, already highly imperiled in the Midwest, have strong potential to be highly vulnerable. Freshwater mussels are temperature sensitive, have low mobility and high habitat specificity, and have a strong dependence on the presence of one or a few host species (often fish) during their larval stage when they are obligate parasites, and these hosts are also likely to be vulnerable (Strayer et al. 2006, Pandolfo et al. 2010).

Because the suite of potential impacts is so large, and impacts are often inter-related, our “best guesses” on impacts and species vulnerability may vary considerably depending on how many risk factors are considered. For example, Jones et al. (2006) found that projections of the potential impact of climate change on Lake Erie walleye (*Sander vitreum*) based simply on water temperature change were very different from results incorporating changes in climate-sensitive factors such as water levels and light penetration. Adding more factors played out differently for different subsets of the population: For river spawning fish, adding habitat factors suggested a more optimistic outcome (fewer model runs were associated with reduced fish recruitment), while for lake spawning fish, adding information on possible lake level declines to the thermal tolerance information suggested a higher potential

for reduced recruitment. This work relied upon decades of research on this fish’s habitat needs and biology, and illustrates that for well-known species like walleye, the challenge to managers and conservation practitioners may focus on characterizing a complex set of direct and indirect climate-related changes that may interact and influence species survival. For most other species, a lack of baseline information from which to even begin the process of understanding potential impacts is often the most daunting challenge.

Considering the range of climate change drivers, and diversity of impacts described for both terrestrial and aquatic systems, it seems likely that one of our most challenging systems to protect will be Great Lakes coastal ecosystems (reviewed by Mackey 2012). The region’s Great Lakes coastal ecosystems have experienced dramatic changes due to accidental and intentional introductions of non-native species, and are already under stress from a wide range of factors (pollution, coastal development, reduced connectivity to streams and rivers). Due to their location at the interface between terrestrial and aquatic systems, coasts are susceptible to an unusually high number of climate-driven factors as well. In particular, interactions between invasive species, increasing run-off from terrestrial systems during storms combined with temperature increases in shallow waters and surface waters, and potential changes in wind and current directions, make understanding and responding to changes in these systems a major challenge. Yet, both the wild species and people of our region depend on productive, clean coastal systems as the base of food chains and local economies.

Helping species and systems adapt in the Midwest

Increase connectivity and “soften” management. Within the region, the ability of species to shift locations in space is likely to vary widely, both as a result of differences in movement ability and as a function of the condition of the landscape or freshwater system (Parmesan 2006). In much of the Midwest, there are many barriers to movement, including both natural features like the Great Lakes, and vast expanses of land that may be inhospitable due to current land use (e.g., conversion to agriculture or other forms of development; Mitsch and Gosselink 2007, also see Handler et al. 2012). A key goal for helping species and systems adapt in our region is improving connectivity by restoring natural habitats in areas where key connections have been lost, and by working to “soften” management in lands managed for multiple purposes, such that the ability of wild species to inhabit and move through those areas is increased.

By increasing connectivity in both terrestrial and aquatic systems, we have the potential to increase the capacity of biodiversity to adapt to climate change through at least three mechanisms. First, restoring connectivity at local scales (i.e., connecting neighboring forest patches or stream reaches) increases the chances that genetic diversity in an area will be maintained by allowing increased mixing of populations. Higher rates of mixing, or “gene flow,” should promote future populations with a wider range of variation in key traits (e.g., heat tolerance, growth rate under drought), increasing the odds that some individuals will be able to persist and thrive under new climatic conditions. Second, restoring connectivity can improve adaptive capacity by allowing mobile species access to cooler or moister microclimates (north facing hillsides, streams with high forest cover) within the same local area so that individuals can shift into these habitats when conditions are severe. Third, again for mobile species, increasing the connectivity of habitats provides a pathway for long-term shifts in range, as species shift north in our region to “track” their most favorable temperature regime. In addition to these three species-focused mechanisms, increasing the connectivity of ecological systems promotes resilience by allowing large scale ecological processes like flooding to occur, which provides essential mixing of energy and materials between aquatic and terrestrial systems. By restoring the connectivity and extent of natural systems like floodplains and allowing this natural process to occur in natural areas, we can also help prevent people and property from being harmed as flood frequencies increase.

For terrestrial animals, ways to increase connectivity include taking actions that enhance the likelihood that animals can move through our landscapes, such as restoring key habitats that have been lost, and working with landowners to enhance habitat values (“soften” management) on highly managed or modified lands. These types of actions should also benefit plants, which may be moved either by animals, or by wind. To help fish and other aquatic species respond to increasing temperatures by shifting ranges, we need to identify barriers in streams and rivers, and, balancing the risk of allowing access by invasive species (e.g., sea lamprey), take action to remove key barriers to movement. Understanding and developing responses to potential shifts in freshwater species are a particular challenge, because there is typically less information available on the distribution of aquatic species, and conservation areas are often more strongly tied to terrestrial, rather than aquatic, species diversity (Strayer 2006, Hieno et al 2009, Herbert et al. 2010). Further, for aquatic invertebrates with limited dispersal abilities, different natural habitats within streams can act as barriers, potentially preventing shifts in range in response to climate change (Strayer 2006).

Continue to pro-actively address the threat of invasives. In the upper Midwest/Great Lakes region, we have many

native species, especially plants, which are best suited to survive and compete for resources when winter conditions are harsh and growing seasons are relatively short. As winter warms and the growing season extends, plants that can grow faster and take advantage of these changes are likely to dominate, and this increased competition is likely to increase the rate of loss of the region’s native species. These more competitive species may be native, may be species from south of the region’s boundary, or may be non-native invasive species that have not been able to persist here before, but will be able to survive here in the future. While some changes in species are to be expected and even promoted as conditions change, to maintain overall plant diversity, we need to be even more vigilant about keeping potential invasive species from outside of North America from gaining a foothold. Strategies to address these challenges include increasing support for partnerships like Weed Management Cooperatives that focus on early detection and eradication, and increasing investment in education-focused partnerships with stakeholders that are sources of non-native plants, such as the landscaping/gardening industry. Further, we need to be careful as we select seed and plant sources for restoration activities, as using seed sources from farther south in a species’ range may make sense in some situations if we want to be pro-active, but may contribute to declines in rare local populations if planted in proximity to locally produced plants (Holmstrom et al. 2010). Invasive species issues are a pervasive problem in the Midwest’s aquatic systems, most notably in the Great Lakes, and they are also addressed in a climate change context in Mackey et al. 2012.

Shifting some of our conservation attention from species to “stages.” Historically, efforts to identify key places to conserve in order to protect biodiversity have focused on mapping patterns of where species are found, and choosing to purchase or protect areas based on “diversity hot spots” suggested by these distributions. Given that many species are likely to shift distributions in response to changing conditions, and that individual species’ responses to climate change will be complex and individualistic (Root and Schneider 2006, Chen et al. 2011), these maps in essence represent a snapshot, not a long term picture. As a result, it makes sense to think about protecting factors that correlate with or “drive” patterns of diversity at the scale of a region or landscape. This perspective of moving from a focus on species toward a focus on landscapes or watersheds is not new, but it takes on a higher importance and includes some additional elements (saving the “stage” and protecting climatic refugia) as we update conservation and management to incorporate climate change (Groves et al. 2012).

Specifically, a key strategy for “climate smart” biodiversity conservation involves broadening our perspective from species to think about the diversity of conditions on landscapes and watersheds (Strayer 2006). As we prioritize

areas for protection, consistent patterns of variation in climate factors should be recognized and integrated with consistent patterns in drivers of biodiversity (e.g., variation in geomorphology, hydrology – Anderson and Feree 2010, Beier and Brost 2010). These consistent landscape-scale units of variation have been referred to as “stages” (in the sense of a location where actors, or species, might appear – Anderson and Feree 2010) or “land facets” (Beier and Brost 2010). If we can map these stages, we can focus land protection or conservation efforts on capturing the widest possible variety of these land or aquatic units. When these gradients are protected, we maximize the potential for heat-stressed individuals of a wide range of species to encounter cooler micro-sites without having to move long distances. Further, adapting our conservation work to include the goal of capturing the range of factors that underlie variation in species should help protect a wider range of species within taxa that are typically not represented as conservation areas are designated, such as mollusks and other aquatic invertebrates (Lydeard et al. 2004, Strayer 2006).

In the Midwest, one element of capturing the breadth of land facets or stages to conserve will involve increasing our understanding of how exposure to climate change varies across landscapes, stream networks, and within large lakes and rivers. Individuals of a species respond to the climate they experience, not average conditions (Walther et al. 2002), and what they experience varies with factors like latitude, landform, distance from a Great Lake, and water source (groundwater or surface water; Chu et al. 2008, Andersen and Feree 2010, Beier and Brost 2010, Klausmeyer et al. 2011, Magness et al. 2011). Thus, a key step toward updating our approach to conservation involves answering questions like: “What factors influence the spatial distribution of warming?” Once we have a better understanding of current variation, we can develop conservation strategies that take advantage of naturally cooler areas, or climate “refugia”, such as the cooling influence of the Great Lakes on nearby terrestrials systems, and do a better job of protecting the thermal regime of streams (e.g., by restoring riparian vegetation, protecting groundwater inputs, and minimizing exposure to urban runoff; Chu et al. 2008, Steen et al. 2010, Groves et al. 2012).

Increasing “green infrastructure” to handle stormwater. As climate change continues, we will need to be much more pro-active in how we address issues related to storms and flooding. Natural systems are at risk from these changes, but can also be a key part of the solution – by increasing the proportion of forests near rivers, wetlands and other natural systems in areas prone to flooding, water can be slowed down and held, reducing the risk to both aquatic systems, and to people (Kousky et al. 2010, 2011). To reduce the problem of flooding and pro-actively prepare for increases in storm intensities, restoring systems like forests and wetlands in flood prone areas are essential components of adaptation strategies to benefit people and

nature. This approach is supported by research showing how hydrology in the Upper Great Lakes region has changed as a result of large-scale conversion of forests into agriculture and other forms of land use with lower rates of evapotranspiration and infiltration (Mao and Cherkauer 2009, Mishra et al. 2010, Groisman et al. 2012). Most opportunities and potential benefits to biodiversity from engaging with actions taken in other sectors are not new, but they may now rise in importance, as we expect adaptive actions to take place in these sectors.

A good example of a persistent stressor that fits this description are overflows of combined sewer and stormwater handling systems in which rainwater, sewage, and industrial wastewater are transported in the same pipe and to sewage treatment plants, where water is treated and discharged to a water body. At this time approximately 746 cities in the US (U.S. EPA 2004 and 2008; references include a map) have combined sewer systems, and many of these are in the upper Midwest. Heavy rain or rapid snowmelt, both of which are predicted to be enhanced in the Great Lakes region can lead to overflow, which means direct discharge of wastewater into water bodies. Overflows are a threat to both water quality and public health, as output can include microbial pathogens, suspended solids, biochemical oxygen demand (BOD), toxic materials, nutrients, and debris (US EPA 2004). In many locations, infrastructure for handling wastewater is in need of updating, and sectoral climate change vulnerability assessments emphasize the need to plan for increases in stormwater volume (U.S. EPA 2008). When updates to these systems are planned, the conservation community can play important roles in promoting the implementation of “green infrastructure” (e.g., wetland restoration, riparian buffers, rain gardens) and in ensuring risks to biodiversity are accounted for as new standards and policies for these systems are put into place.

Protect people and nature by restoring functional ecosystems in watersheds dominated by agriculture. Direct and indirect impacts of climate change have great potential to reduce the effectiveness of conservation strategies focused on protecting rivers and streams in watersheds dominated by agriculture. First, these aquatic systems will be affected by temperature changes and are highly sensitive to changes in the timing of and amount of precipitation. Further, an increase in the intensity of peak storm events (Kunkel 2011, Groisman et al. 2012, Winkler 2012) suggests an increase in some of the most important current threats. For example, big storms, especially storms that occur when soils are saturated, lead to overland movement of sediments and pollution from agricultural fields into streams, which can drastically reduce the suitability of these systems for the region’s native fish and aquatic invertebrates (Strayer 2006, Sowa et al. 2007, Herbert et al. 2010).

Responses by farmers to changes in the climate also have the potential to put sensitive species and aquatic systems at greater risk. For example, increases in temperature influence what farmers can grow, may lead farmers to have crops in the field for longer periods and add additional fertilizer or pesticide treatments. Temperature increases are also expected to lead to increased evaporation, which promotes drought stress and reduced stream flows (Mishra et al. 2010) even without a decrease in precipitation. In some places, increased drought stress may promote increased investments in irrigation, and increased withdrawal pressure on ground and surface water supplies. Interactions with water are also important in the spring: In many watersheds, farms have very effective systems for quickly shunting spring precipitation off of fields to allow earlier planting of crops. As the intensity of storms continues to increase, we expect to see more farmers adding to their drainage infrastructure. However, drainage, and the simple conversion of land to forms that have low capacity to absorb water or to slow the overland flow of water, promotes flooding of all sorts of land types, including farms, residential areas, and cities. As this example suggests, thinking through possible interactions between the agricultural sector and natural resource management highlights the fact that successful adaptation will require collaborative solutions. One key strategy for reducing the risk of flooding is to work in partnership to reconnect and re-vegetate natural floodplains along streams and rivers. Natural floodplains provide the essential services of holding and absorbing flood waters, which protects people and property, while also promoting connectivity for a wide variety of species that use them as corridors through what is often an inhospitable landscape (Opperman et al. 2009, Kousky et al. 2010).

Moving toward smarter conservation. As we work to update our conservation plans and make them “climate smart”, it is vitally important that we also update or approaches to management such that they become more agile and able to shift strategies quickly in the face of new information and surprises. With respect to anticipating surprises, we expect that surprises for resource managers will take at least three forms: 1) Exceedance of thresholds (e.g., thermal tolerance thresholds, leading to strong declines in fitness); 2) new interactions among species, and/or new or synergistic impacts related to interactions with climate and other stressors (e.g., invasive species); and (3) higher frequency of extreme weather events with catastrophic impacts on focal systems (floods, ice storms, “typical” cold periods in spring that now occur after a prolonged spring warming).

Acting in a climate smart way will also require that we improve our ability to share and synthesize the information we do have, and improve our tools for acting in the face of uncertainty. We will also need to do a better job of separating scientific data from values, and work more closely with a broader range of stakeholders to craft cross-

sector solutions (Hobbs et al. 2010, Groves et al. 2012). Evidence that addressing climate change helps promote larger-scale approaches to conservation can be seen in the recent emergence of many regional scale collaborations, including a recent agreement between the states of Michigan and Wisconsin to share information and work together on adaptation, and a suite of federal initiatives, including USFWS’s Landscape Conservation Cooperatives, NOAA’s Regional Integrated Sciences and Assessments teams, USGS’s Regional Climate Hubs, and the USFS’s Shared Landscape Initiative. Given all of these new opportunities, we need to be ready to pursue actions that improve conservation more broadly by improving communication, collaboration, and connectedness of efforts. Although encouraging in many respects, this growing list of entities that seek to lead on climate change through creating regional partnerships suggests that while key agencies agree on an appropriate scale for consideration of the challenge, we face a major coordination challenge if we intend to use our limited resources efficiently.

References

- Anderson, M. G. and C. E. Ferree. 2010. Conserving the stage: climate change and the geophysical underpinnings of species diversity. *PLoS ONE* **5**:e11554.
- Ashcroft, M. B., L. A. Chisholm, and K. O. French. 2009. Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. *Global Change Biology* **15**:656-667.
- Austin, J. A. and S. M. Colman. 2007. Lake Superior summer water temperatures are increasing more rapidly than regional air temperatures: A positive ice-albedo feedback. *Geophysical Research Letters* **34**:L06604, doi:06610.01029/02006GL029021.
- Austin, J. A. and S. M. Colman. 2008. A century of warming in Lake Superior. *Limnology and Oceanography* **53**:2724-2730.
- Balanyá, J., J. M. Oller, R. B. Huey, G. W. Gilchrist, and L. Serra. 2006. Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science* **313**:1773-1775.
- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters*. <http://dx.doi.org/10.1111/j.1461-0248.2011.01736.x>
- Beier, P. and B. Brost. 2010. Use of land facets to plan for climate change: Conserving the arenas, not the actors. *Conservation Biology* **24**:701-710.
- Bierwagen, B. G., R. Thomas, and A. Kane. 2008. Capacity of management plans for aquatic invasive species to integrate climate change. *Conservation Biology* **22**:568-574.
- Biro, P. A., J. R. Post, and D. J. Booth. 2007. Mechanisms for climate-induced mortality of fish populations in whole-lake experiments. *Proceedings of the National Academy of Sciences of the United States of America* **104**:9715-9719.
- Both, C., M. van Asch, R. G. Bijlsma, A. B. van den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* **78**:73-83.
- Bowman, J., G.L. Holloway, J.R. Malcolm, K.R. Middel, and P.J. Wilson. 2005. Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck. *Canadian Journal of Zoology* **83**:1486-1494.
- Bradley, N. L., A. C. Leopold, J. Ross, and W. Huffaker. 1999. Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America* **96**:9701-9704.
- Bradshaw, W. E. and C. M. Holzapfel. 2008. Genetic response to rapid climate change: it's seasonal timing that matters. *Molecular Ecology* **17**:157-166.
- Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**:453-460.
- Brooks, R. 2009. Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. *Climatic Change* **95**:469-483.
- CCSP. 2009. Global Climate Change Impacts in the United States. U.S. Climate Change Science Program, Unified Synthesis Product. U.S. Climate Science Program <http://www.globalchange.gov/publications/reports/scientific-assessments/us-impacts>, Washington, D.C.
- Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**:1024-1026.
- Chu, C., Jones, N.E., Mandrak, N.E., Piggott, A.R. and Minns, C.K. 2008. The influence of air temperature, groundwater discharge and climate change on the thermal diversity of stream fishes in southern Ontario watersheds. *Canadian Journal of Fisheries and Aquatic Sciences* **65**: 297-308.
- Dawson, T. P., S. T. Jackson, J. L. House, I. Colin Prentice, and G. M. Mace. 2011. Beyond predictions: Biodiversity conservation in a changing climate. *Science* **332**:53-58.
- Desai, A. R., J. A. Austin, V. Bennington, and G. A. McKinley. 2009. Stronger winds over a large lake in response to weakening air-to-lake temperature gradient. *Nature Geosciences*:<http://dx.doi.org/10.1038/ngeo1693>.
- Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* **105**:6668-6672.
- DeWalt, R. E., C. Favret, and D. W. Webb. 2005. Just how imperiled are aquatic insects? A case study of stoneflies (Plecoptera) in Illinois. *Annals of the Entomological Society of America* **98**:941-950.
- DeWalt R. E., and S.A. Grubbs. 2011. Updates to the stonefly fauna of Illinois and Indiana. *Illiesia* **7**: 31-50.
- DeWalt, R., Y. Cao, T. Tweddale, S. Grubbs, L. Hinz, M. Pessino, and J. Robinson. 2012. Ohio USA stoneflies (Insecta, Plecoptera): species richness estimation, distribution of functional niche traits, drainage affiliations, and relationships to other states. *ZooKeys* **178**:1-26.
- Dobiesz, N. E. and N. P. Lester. 2009. Changes in mid-summer water temperature and clarity across the Great Lakes between 1968 and 2002. *Journal of Great Lakes Research* **35**:371-384.
- Dobrowski, S. Z. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* **17**:1022-1035.
- Dunn, P. O. and D. W. Winkler. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London Series B-Biological Sciences* **266**:2487-2490.
- Eaton, J. G. and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography* **41**:1109-1115.

- Etges, W. J. and M. Levitan. 2008. Variable evolutionary response to regional climate change in a polymorphic species. *Biological Journal of the Linnean Society* **95**:702-718.
- Etterson, J. R. and R. G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. *Science* **294**:151-154.
- Excoffier, L., M. Foll, and R. Petit. 2009. Genetic consequences of range expansions. *Annual Review of Ecology Evolution and Systematics* **40**:481-501.
- Francl, K. E., K. Hayhoe, M. Saunders, and E. P. Maurer. 2010. Ecosystem adaptation to climate change: Small mammal migration pathways in the Great Lakes states. *Journal of Great Lakes Research* **36**:86-93.
- Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. *Reviews in Fish Biology and Fisheries* **17**:581-613.
- Field, C. B., L. D. Mortsch, M. Brklacich, D. L. Forbes, P. Kovacs, J. A. Patz, S. W. Running, and M. J. Scott. 2007. North America. Pages 617-652 in M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson, editors. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Foden, W., G. Mace, J.-C. Vié, A. Angulo, S. Butchart, L. DeVantier, H. Dublin, A. Gutsche, S. Stuart, and E. Turak. 2008. Species susceptibility to climate change impacts. In J.-C. Vié, C. Hilton-Taylor, and S. N. Stuart, editors. *The 2008 Review of The IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland.
- Garroway, C. J., J. Bowman, G. L. Holloway, J. R. Malcolm, and P. J. Wilson. 2011. The genetic signature of rapid range expansion by flying squirrels in response to contemporary climate warming. *Global Change Biology* **17**:1760-1769.
- Geyer, J., I. Kiefer, S. Kreft, V. Chavez, N. Salafsky, F. Jeltsch, and P. L. Ibisch. 2011. Classification of climate-change-induced stresses on biological diversity. *Conservation Biology* **25**:708-715.
- Gibbs, J. P. and A. R. Breisch. 2001. Climate warming and calling phenology of frogs near Ithaca, New York, 1900-1999. *Conservation Biology* **15**:1175-1178.
- Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merilä. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology* **17**:167-178.
- Girvetz, E. H., C. Zganjar, G. T. Raber, E. P. Maurer, P. Kareiva, and J. J. Lawler. 2009. Applied climate-change analysis: The Climate Wizard tool. *PLoS ONE* **4**:e8320. doi:8310.1371/journal.pone.0008320.
- Groisman, P. Y., R.W. Knight, T. R. Karl, D. R. Easterling, B. Sun, and J. H. Lawrimore. 2004. Contemporary changes of the hydrological cycle over the contiguous United States, trends derived from *in situ* observations. *Journal of Hydrometeorology* **5**:64-85.
- Groisman, P.Y., R.W. Knight, and T.R. Karl. 2012. Changes in intense precipitation over the central United States. *Journal of Hydrometeorology* **13**:47-66.
- Grosbois, V., O. Gimenez, J. M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A. P. Moller, and H. Weimerskirch. 2008. Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews* **83**:357-399.
- Groves, C. R., E. T. Game, M. G. Anderson, M. Cross, C. Enquist, Z. Ferdana, E. H. Girvetz, A. Gondor, K. R. Hall, J. Higgins, R. Marshall, K. Popper, S. Schill, and S. L. Shafer. 2012. Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation* **21**:1651-1671.
- Guralnick, R. 2007. Differential effects of past climate warming on mountain and flatland species distributions: a multispecies North American mammal assessment. *Global Ecology and Biogeography* **16**:14-23.
- Handler, S.D., C.W. Swanston, P.R. Butler, L.A. Brandt, M.K. Janowiak, M.D. Powers, and P.D. Dutton. Climate change vulnerabilities within the forestry sector for the Midwestern United States. Whitepaper prepared for the Midwest Technical Input Report, U.S. National Climate Assessment.
- Heino, J., R. Virkkala, and H. Toivonen. 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews* **84**:39-54.
- Herbert, M. E., P. B. McIntyre, P. J. Doran, J. D. Allan, and R. Abell. 2010. Terrestrial reserve networks do not adequately represent aquatic ecosystems. *Conservation Biology* **24**:1002-1011.
- Hitch, A. T. and P. L. Leberg. 2007. Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology* **21**:534-539.
- Hobbs, R. J., D. N. Cole, L. Yung, E. S. Zavaleta, G. H. Aplet, F. S. Chapin, P. B. Landres, D. J. Parsons, N. L. Stephenson, P. S. White, D. M. Graber, E. S. Higgs, C. I. Millar, J. M. Randall, K. A. Tonnessen, and S. Woodley. 2010. Guiding concepts for park and wilderness stewardship in an era of global environmental change. *Frontiers in Ecology and the Environment* **8**:483-490.
- Holmstrom, R. M., J. R. Etterson, and D. J. Schimpf. 2010. Dune restoration introduces genetically distinct American beachgrass, *Ammophila breviligulata*, into a threatened local population. *Restoration Ecology* **18**:426-437. <http://dx.doi.org/410.1111/j.1526-1100X.2009.00593.x>.
- Hong, Y., A. Steinman, B. Biddanda, R. Rediske, and G. Fahnenstiel. 2006. Occurrence of the toxin-producing Cyanobacterium *Cylindrospermopsis raciborskii* in Mona and Muskegon Lakes, Michigan. *Journal of Great Lakes Research* **32**:645-652.
- Jactel, H., J. Petit, M.-L. Desprez-Loustau, S. Delzon, D. Piou, A. Battisti, and J. Koricheva. 2011. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology*:n/a-n/a.

- Jones, M. L., B. J. Shuter, Y. Zhao, and J. D. Stockwell. 2006. Forecasting effects of climate change on Great Lakes fisheries: models that link habitat supply to population dynamics can help. *Canadian Journal of Fisheries and Aquatic Sciences* **63**:457-468.
- Jump, A. S. and J. Penuelas. 2006. Genetic effects of chronic habitat fragmentation in a wind-pollinated tree. *Proceedings of the National Academy of Sciences of the United States of America* **103**:8096-8100.
- Jump, A. S., C. Matyas, and J. Penuelas. 2009. The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology & Evolution* **24**:694-701.
- Kaushal, S. S., G. E. Likens, N. A. Jaworski, M. L. Pace, A. M. Sides, D. Seekell, K. T. Belt, D. H. Secor, and R. L. Wingate. 2010. Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment* **8**:461-466.
- Kearney, M., R. Shine, and W. P. Porter. 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proceedings of the National Academy of Sciences* **106**:3835-3840.
- Klausmeyer, K. R., M. R. Shaw, J. B. MacKenzie, and D. R. Cameron. 2011. Landscape-scale indicators of biodiversity's vulnerability to climate change. *Ecosphere* **2**:art88. <http://dx.doi.org/10.1890/es11-00044.1>
- Kousky, C. 2010. Using natural capital to reduce disaster risk. *Journal of Natural Resources Policy Research* **2**:343-356. <http://dx.doi.org/310.1080/19390459.19392010.19511451>.
- Kousky, C., S. Olmstead, M. Walls, A. Stern, and M. Macauley. 2011. The Role of Land Use in Adaptation to Increased Precipitation and Flooding: A Case Study in Wisconsin's Lower Fox River Basin (RFF Report). *Resources For The Future*, Washington, D.C. <http://www.rff.org/Publications/Pages/PublicationDetails.aspx?PublicationID=21688>.
- Kunkel, K. E. 2011. Midwest Regional Climate Outlooks. Draft document prepared for the National Climate Assessment, dated October 5, 2011.
- La Sorte, F. A. and F. R. Thompson. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* **88**:1803-1812.
- Lenarz, M. S., M. E. Nelson, M. W. Schrage, and A. J. Edwards. 2009. Temperature mediated moose survival in Northeastern Minnesota. *Journal of Wildlife Management* **73**:503-510.
- Lenarz, M. S., J. Fieberg, M. W. Schrage, and A. J. Edwards. 2010. Living on the edge: Viability of moose in Northeastern Minnesota. *Journal of Wildlife Management* **74**:1013-1023.
- Levitani, M. 2003. Climatic factors and increased frequencies of 'southern' chromosome forms in natural populations of *Drosophila robusta*. *Evolutionary Ecology Research* **5**:597-604.
- Liow, L. H., M. Fortelius, K. Lintulaakso, H. Mannila, and N. C. Stenseth. 2009. Lower extinction risk in sleep-or-hide mammals. *American Naturalist* **173**:264-272.
- Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. *Nature* **462**:1052-1055.
- Lydeard, C., R. H. Cowie, W. F. Ponder, A. E. Bogan, P. Bouchet, S. A. Clark, K. S. Cummings, T. J. Frest, O. Gargominy, D. G. Herbert, R. Hershler, K. E. Perez, B. Roth, M. Seddon, E. E. Strong, and F. G. Thompson. 2004. The global decline of nonmarine mollusks. *Bioscience* **54**:321-330.
- Lyons, J., J. S. Stewart, and M. Mitro. 2010. Predicted effects of climate warming on the distribution of 50 stream fishes in Wisconsin, U.S.A. *Journal of Fish Biology* **77**:1867-1898.
- Maclean, I. M. D. and R. J. Wilson. 2011. Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences* **108**:12337-12342.
- Mackey, S.D. Great Lakes nearshore and coastal systems. 2012. Whitepaper prepared for the Midwest Technical Input Report, U.S. National Climate Assessment.
- Magness, D. R., J. M. Morton, F. Huettmann, F. S. Chapin III, and A. D. McGuire. 2011. A climate-change adaptation framework to reduce continental-scale vulnerability across conservation reserves. *Ecosphere* **2**: Article 112. doi: 110.1890/ES1811-00200.00201.
- Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evans, E. J. Fee, R. I. Hall, L. R. Mortsch, D. W. Schindler, and F. H. Quinn. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. *Hydrological Processes* **11**:825-871.
- Mao, D. Z. and K. A. Cherkauer. 2009. Impacts of land-use change on hydrologic responses in the Great Lakes region. *Journal of Hydrology* **374**:71-82.
- Marra, P.P., C.M. Francis, R.S. Mulvihill, and F.R. Moore. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia* **142**: 307-315.
- Mishra, V., K. A. Cherkauer, D. Niyogi, M. Lei, B. C. Pijanowski, D. K. Ray, L. C. Bowling, and G. X. Yang. 2010. A regional scale assessment of land use/land cover and climatic changes on water and energy cycle in the upper Midwest United States. *International Journal of Climatology* **30**:2025-2044.
- Mishra, V., K. A. Cherkauer, and S. Shukla. 2010. Assessment of drought due to historic climate variability and projected future climate change in the Midwestern United States. *Journal of Hydrometeorology* **11**:46-68.
- Mitsch, W.J. and J.G. Gosselink. 2007. *Wetlands*, 4th ed., John Wiley & Sons, Inc., New York.
- Morin, X., M. J. Lechowicz, C. Augspurger, J. O'Keefe, D. Viner, and I. Chuine. 2009. Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology* **15**:961-975.

- Moreno-Mateos, D., M. E. Power, F. A. Comín, and R. Yockteng. 2012. Structural and functional loss in restored wetland ecosystems. *Plos Biology* **10**(1) e1001247.
- Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. *Wildlife Monographs* **166**:1-30.
- Myers, P., B. L. Lundrigan, S. M. G. Hoffman, A. P. Haraminac, and S. H. Seto. 2009. Climate-induced changes in the small mammal communities of the Northern Great Lakes Region. *Global Change Biology* **15**:1434-1454.
- Opperman, J. J., G. E. Galloway, J. Fargione, J. F. Mount, B. D. Richter, and S. Secchi. 2009. Sustainable floodplains through large-scale reconnection to rivers. *Science* **326**:1487-1488.
- Ostfeld, R. S. 2009. Climate change and the distribution and intensity of infectious diseases. *Ecology* **90**:903-905.
- Pandolfo, T. J., W. G. Cope, C. Arellano, R. B. Bringolf, M. C. Barnhart, and E. Edward Hammer. 2010. Upper thermal tolerances of early life stages of freshwater mussels. *Journal of the North American Benthological Society* **29**:959-969.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Systematics* **37**:637-669.
- Pergams, O. R. W. and R. C. Lacy. 2008. Rapid morphological and genetic change in Chicago-area *Peromyscus*. *Molecular Ecology* **17**:450-463.
- Reale, D., A. G. McAdam, S. Boutin, and D. Berteaux. 2003. Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society of London Series B-Biological Sciences* **270**:591-596.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**:57-60.
- Root, T. L. and S. H. Schneider. 2006. Conservation and climate change: The challenges ahead. *Conservation Biology* **20**:706-708.
- Schloss, C. A., T. A. Nuñez, and J. J. Lawler. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences* (online early) DOI: 10.1073/pnas.1116791109.
- Schneider, K. N., R. M. Newman, V. Card, S. Weisberg, and D. L. Pereira. 2010. Timing of walleye spawning as an indicator of climate change. *Transactions of the American Fisheries Society* **139**:1198-1210.
- Schneider, S. H., S. Semenov, A. Patwardhan, I. Burton, C. H. D. Magadza, M. Oppenheimer, A. B. Pittock, A. Rahman, J. B. Smith, A. Suarez, and F. Yamin. 2007. Assessing key vulnerabilities and the risk from climate change. Pages 779-810 in M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson, editors. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Schwanz, L. E. and F. J. Janzen. 2008. Climate change and temperature-dependent sex determination: Can individual plasticity in nesting phenology prevent extreme sex ratios? *Physiological and Biochemical Zoology* **81**:826-834.
- Schwanz, L. E., R.-J. Spencer, R. M. Bowden, and F. J. Janzen. 2010. Climate and predation dominate juvenile and adult recruitment in a turtle with temperature-dependent sex determination. *Ecology* **91**:3016-3026.
- Scott, R. W. and F. A. Huff. 1996. Impacts of the Great Lakes on regional climate conditions. *Journal of Great Lakes Research* **22**:845-863.
- Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* **40**:415-436.
- Sharma, S., M. J. Vander Zanden, J. J. Magnuson, and J. Lyons. 2011. Comparing climate change and species invasions as drivers of coldwater fish population extirpations. *PLoS ONE* **6**(8)e22906. doi:10.1371/journal.pone.0022906.
- Sowa, S.P., G. Annis, M.E. Morey and D.D. Diamond. 2007. A gap analysis and comprehensive conservation strategy for riverine ecosystems of Missouri. *Ecological Monographs* **77**:301-334.
- Steen, P. J., M. J. Wiley, and J. S. Schaeffer. 2010. Predicting future changes in Muskegon River Watershed game fish distributions under future land cover alteration and climate change scenarios. *Transactions of the American Fisheries Society* **139**:396-412.
- Strayer, D. L. 2006. Challenges for freshwater invertebrate conservation. *Journal of the North American Benthological Society* **25**:271-287.
- Strode, P. K. 2003. Implications of climate change for North American wood warblers (Parulidae). *Global Change Biology* **9**:1137-1144.
- Swanson, D. L. and J. S. Palmer. 2009. Spring migration phenology of birds in the Northern Prairie region is correlated with local climate change. *Journal of Field Ornithology* **80**:351-363.
- Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* **427**:145-148.
- Trumpickas, J., B. J. Shuter, and C. K. Minns. 2009. Forecasting impacts of climate change on Great Lakes surface water temperatures. *Journal of Great Lakes Research* **35**:454-463.
- Tucker, J. K., C. R. Dolan, J. T. Lamer, and E. A. Dustman. 2008. Climatic warming, sex ratios, and red-eared sliders

- (*Trachemys scripta elegans*) in Illinois. Chelonian Conservation and Biology **7**:60-69.
- U.S. Environmental Protection Agency (EPA). 2004. Report to Congress: impacts and controls of CSOs and SSOs. Office of Wastewater Management, Washington, D.C.; EPA/833/R-04/001. Available online at http://cfpub.epa.gov/npdes/cso/cpolicy_report2004.cfm.
- U.S. Environmental Protection Agency. 2008. A screening assessment of the potential impacts of climate change on combined sewer overflow (CSO) mitigation in the Great Lakes and New England regions. Global Change Research Program, National Center for Environmental Assessment, Washington, DC; EPA/600/R-07/033F. Available from the National Technical Information Service, Springfield, VA, and online at <http://www.epa.gov/ncea>.
- Vander Zanden, M. J., G. J. A. Hansen, S. N. Higgins, and M. S. Kornis. 2010. A pound of prevention, plus a pound of cure: Early detection and eradication of invasive species in the Laurentian Great Lakes. *Journal of Great Lakes Research* **36**:199-205.
- Visser, M. E., L. J. M. Holleman, and P. Gienapp. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147**:164-172.
- Vucetich, J. A. and R. O. Peterson. 2004. The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**:183-189.
- Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* **416**:389-395.
- Wang, J., X. Bai, H. Hu, A. Clites, M. Colton, and B. Lofgren. 2011. Temporal and spatial variability of Great Lakes Ice Cover, 1973–2010. *Journal of Climate* **25**:1318-1329.
- Williams, S. E., L. P. Shoo, J. L. Isaac, A. A. Hoffmann, and G. Langham. 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *Plos Biology* **6**:2621-2626.
- Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, and C. C. Davis. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America* **105**:17029-17033.
- Wilmers, C. C., E. Post, R. O. Peterson, and J. A. Vucetich. 2006. Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecology Letters* **9**:383-389.
- Winkler, J.A., R. Arritt, and S. Pryor, 2012: Climate projections for the Midwest: Availability, interpretation and synthesis. In: U.S. National Climate Assessment Midwest Technical Input Report. J. Winkler, J. Andresen, J. Hatfield, D. Bidwell, and D. Brown, coordinators. Available from the Great Lakes Integrated Sciences and Assessment (GLISA) Center, http://glisa.umich.edu/NCA/MTIT_FutureClimate.pdf.
- Zuckerberg, B., A. M. Woods, and W. F. Porter. 2009. Poleward shifts in breeding bird distributions in New York State. *Global Change Biology* **15**:1866-1883.
- Zuo, W., M. E. Moses, G. B. West, C. Hou, and J. H. Brown. 2011. A general model for effects of temperature on ectotherm ontogenetic growth and development. *Proceedings of the Royal Society B* (published online 30 November 2011) doi: 10.1098/rspb.2011.2000.