The impacts of climate change on ecosystem structure and function

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Recent climate-change research largely confirms the impacts on US ecosystems identified in the 2009 National Climate Assessment and provides greater mechanistic understanding and geographic specificity for those impacts. Pervasive climate-change impacts on ecosystems are those that affect productivity of ecosystems or their ability to process chemical elements. Loss of sea ice, rapid warming, and higher organic inputs affect marine and lake productivity, while combined impacts of wildfire and insect outbreaks decrease forest productivity, mostly in the arid and semi-arid West. Forests in wetter regions are more productive owing to warming. Shifts in species ranges are so extensive that by 2100 they may alter biome composition across 5–20% of US land area. Accelerated losses of nutrients from terrestrial ecosystems to receiving waters are caused by both winter warming and intensification of the hydrologic cycle. Ecosystem feedbacks, especially those associated with release of carbon dioxide and methane release from wetlands and thawing permafrost soils, magnify the rate of climate change.

Climate fundamentally controls the distribution of ecosystems, species ranges, and process rates on Earth. As a component of the US National Climate Assessment, to be released in 2014, a group of over 60 ecological experts from academic, governmental, and nongovernmental organizations assessed the state of knowledge about how climate change has affected and will affect species, biodiversity, and ecosystem structure, function, and services in the US. Here, we summarize key findings on the impacts of climate change on ecosystems, focusing on the fluxes of matter and energy and the biotic and abiotic parts of ecosystems that contribute most to those fluxes.

Ecosystem patterns and processes, such as rates of primary productivity or input–output balance of chemical elements, respond in complex ways to climate change because of multiple controlling factors. For example, whether a forest is a carbon (C) source or sink depends on the balance of primary production and ecosystem respiration, processes that respond to different drivers. Physical changes in ecosystems – for instance, changes in thermal stratification patterns in lakes and oceans, flood and drying regimes in streams and rivers, or intensification of the hydrologic cycle across large basins – lead to changes in ecosystem structure and function that have economic and human consequences. Often the extremes or changes in timing have greater impact than changes in average conditions and incur greater societal impacts and costs. Recognizing these issues, climate-change action plans and management strategies have begun to account for forecasted changes in extremes or seasonality.

■ Seven key impacts

Although climate change is affecting US ecosystems in numerous ways, seven findings emerged from our assessment as representing the most critical climate-change impacts on ecosystem structure and function in the US, supported by compelling evidence from the past 4 years (Figure 1). Only a few of the important references can be cited in this article due to space limitations, and we refer

In a nutshell:

- Recent research confirms that climate change is altering the structure and function of aquatic and terrestrial ecosystems in the US and identifies mechanisms for those impacts
- Rising temperature, changes in seasonality, increased frequency and magnitude of extreme events, and acceleration of the hydrologic cycle will shift ecosystem types, process rates, and connections to other ecosystems, often irreversibly
- Changes in ecosystem productivity, food-chain relationships, disease spread, pollutant transport, and climate feedbacks have important societal consequences
- The human and financial costs of climate change in the US are so high – equivalent to hundreds to thousands of human lives and tens to hundreds of billions of dollars – that many businesses and government agencies now incorporate climate-change-related considerations into their plans and actions

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Figure 1. Major historical changes at the ecosystem level detected in the US and attributed to climate change, including thermal stratification, bark beetle infestations, biome shifts, increased forest growth, forest mortality, stream intermittency, increased streamflow and accelerated nutrient flushing, and wildfire. Land cover: North American Land Cover 2005. Natural Resources Canada, US Geological Survey, Insituto Nacional de Estadística y Geografía, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, and Comisión Nacional Forestal. Icons: Integration and Application Network, University of Maryland. For more detailed descriptions of each of these changes, see WebTable 1; for associated citations, see WebReferences.

readers to the WebReferences for additional supporting references.

Climate effects on sea ice, lakes, and coastal ecosystems

The late summer extent of Arctic sea ice continues to decline, with a record low set in 2012 (www.climate-watch.noaa.gov/article/2012/arctic-sea-ice-breaks-2007-record-low). This low extent exceeds the previous record set in 2007 (Figure 2a). The Arctic Ocean is projected to be ice-free in late summer before the middle of the 21st century, radically changing patterns of marine productivity associated with ice edges (Arrigo *et al.* 2012). In the Southern Hemisphere, the population size of krill – a key component of whale and other marine vertebrate diets – is positively correlated with the extent of sea ice (Atkinson *et al.* 2004). As the oceans warm and land-based ice melts, sea level is rising steadily (Figure 2b) and threatening habitat-forming species such as corals and mangroves in coastal ecosystems, as well as infrastructure and liveli-hoods of people living on coasts (Doney *et al.* 2012).
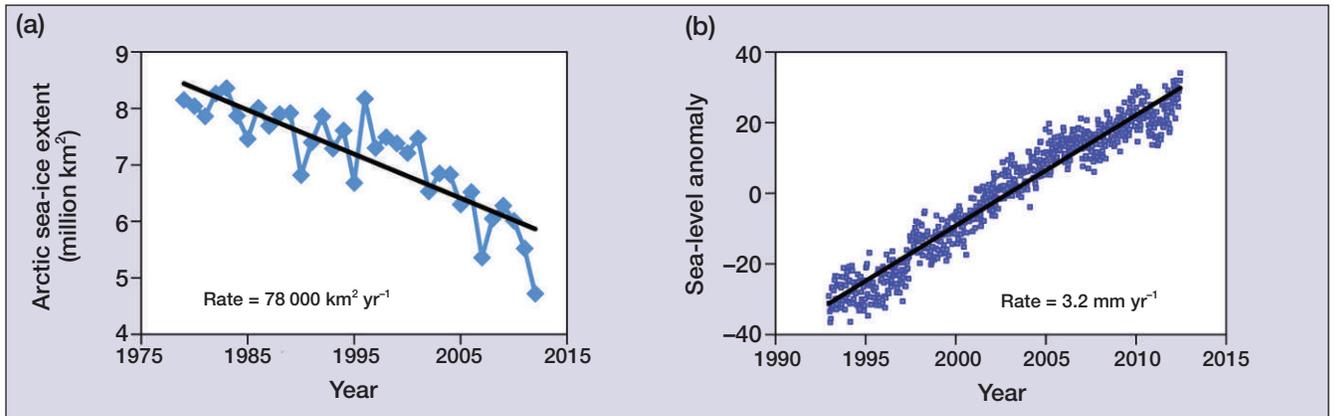
Figure 2. *Ocean ecosystems cover most of the Earth and are changing in fundamental ways in response to climate warming (Doney et al. 2012). Two of the clearest sentinels of change are (a) loss of Arctic sea ice and (b) sea-level rise. The anticipated disappearance of sea ice in the Arctic before the mid-21st century will further increase heat absorption by the oceans, accelerating warming. Increases in sea level are due to both expansion of the oceans as they warm and melting of land-based ice. In addition to the serious economic costs to coastal human populations associated with repairing extensive damage and adapting to a higher sea level, key habitat-forming species in coastal ecosystems, such as corals and mangroves, are in decline. Higher ocean temperatures and CO_2 concentrations are causing severe bleaching of coral reefs, acidification that inhibits skeletal formation in many invertebrates, coastal algal blooms, and decreases in open ocean productivity. Sea-ice data from http://nsidc.org/data/docs/noaa/g02135_seaice_index/index.html; sea-level data from http://sealevel.colorado.edu/.*

Large lakes are warming twice as fast as the surrounding air (Schneider and Hook 2010), decreasing ice-cover periods by an average of 12 days per century (Livingstone *et al.* 2010) and increasing the frequency of harmful algal blooms (Paerl and Huisman 2008). Greater amounts of precipitation reduce water transparency to ultraviolet radiation and thereby reduce the ability of sunlight to disinfect surface waters, potentially increasing epidemics of parasites in species – ranging from zooplankton (Overholt *et al.* 2012) to amphibians (Ortiz-Santaliestra *et al.* 2011) and humans (Connelly *et al.* 2007) – that play key roles in ecosystems. Insect outbreaks, wildfires, and other climate-related disturbances in terrestrial vegetation (Figure 1) are also altering dissolved organic matter, which contributes to the production of carcinogenic disinfection byproducts during chlorination of surface waters used for human drinking (Beggs and Summers 2011). Thermal stratification of large lakes and oceans has also increased (Figure 1), reducing mixing of surface waters with deeper, nutrient-rich waters. This mechanism appears to be largely responsible for recently observed decreases in primary productivity of up to 1% per year in 8 out of 10 of the major ocean basins of the world (Boyce *et al.* 2010).

Biome shifts

Climate-change-induced shifts in plant species distributions are changing the characteristics of biomes (ecosystems with the same dominant plant life-forms), altering structure and ecosystem functioning. For example, increased tree growth is occurring in forests at or near latitudinal and altitudinal tree lines, and trees are moving into adjacent tundra (Figure 3a). Species shifts occur in areas of high climate-change velocity – the rate at which an area of constant temperature moves across the Earth (Loarie *et al.* 2009) – in both the US and globally (Figure 3a; Gonzalez *et al.* 2010). Velocities of up to 20 km per year were observed in the US from 1960 to 2009 (Figure 3a; Burrows *et al.* 2011), as compared with velocities of 0.002 km per year from the last glacial maximum 21 000 years ago to today (Sandel *et al.* 2011). Field observations and biogeochemical models suggest that biome shifts have contributed to increased net primary productivity (NPP) at zones of forest expansion, as a result of warming, whereas reduced NPP has been observed at the boreal–temperate transition due to drought stress.

Projected climate-change velocities under an Intergovernmental Panel on Climate Change scenario of aggressive human management of carbon dioxide (CO_2) release to the atmosphere (scenario A1B) exceed 1 km per year for much of the US (Loarie *et al.* 2009). Consequently, vegetation models project climate-change-driven biome shifts across 5–20% of US land area by 2100 CE (Figure 3, b and c; Gonzalez *et al.* 2010). Spatial analysis of historical climate changes and projected vegetation indicates that one-seventh to one-third of North American ecosystems may be highly vulnerable to biome shifts (Figure 3d; Gonzalez *et al.* 2010). Biome shifts that expand tree cover may tend to increase standing biomass, C, NPP, radiation-use efficiency, canopy closure, and leaf area while decreasing grass-to-tree and root-to-shoot ratios (Euskirchen *et al.* 2009). In contrast, regional tree dieback in the Southwest (Breshears *et al.* 2005) could potentially convert temperate woodlands into temperate grasslands, leading to opposite trends in functional properties. Climate change influences wildfire and its interaction with biome distributions, yielding projections of extensive changes in wildfire occurrence
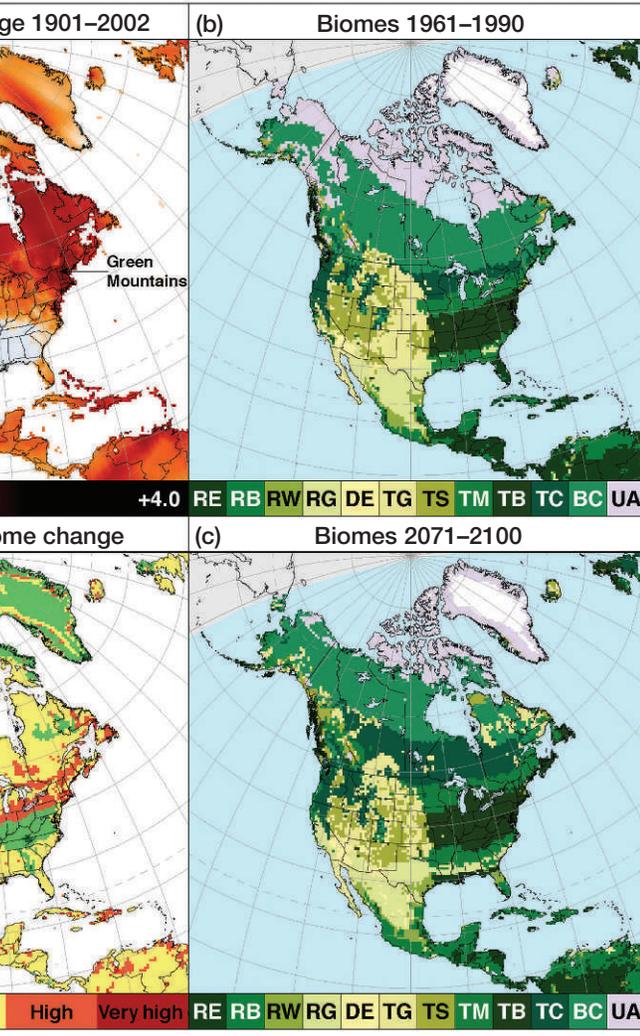
and extent (Figure 1; Gonzalez *et al.* 2010).

Ecosystem state change

Many of the aforementioned biome shifts are stabilized by feedbacks that maintain these ecosystems in their new state, making it difficult to reverse the changes. For instance, the Sahel changed from a tropical forest to grassland and then to desert within a few thousand years (Kröpelin *et al.* 2008). Rapid or abrupt transitions, such as desertification or collapse of coral reefs, may occur when a threshold is crossed (Scheffer *et al.* 2001). Movement of trees into tundra or grassland tends to shade out short-statured plants and to alter rates of C and nutrient cycling in ways that support the persistence of forest. Similarly, chronic drought in deserts reduces grass cover, which exacerbates erosion and facilitates the spread of shrubs like creosote bush (*Larrea tridentata*), a ubiquitous desert shrub. Shrubs exert a positive feedback to warming by altering surface energy balance and promoting higher nighttime temperatures (D'Odorico *et al.* 2010).

Among the many global-change factors contributing to the nonlinear responses of ecosystems and abrupt transitions, climate change is particularly likely to push ecosystems across thresholds. Experiments have shown that climate change can induce ecosystem changes. Warming-induced shifts in species composition have been

Figure 3. *Biome shifts detected in the US and attributed to climate change. (a) Observed linear temperature trend 1901–2002 (°C per century), showing field sites of detected shifts (see WebTable 1 for details). (b) Potential vegetation under observed 1961–1990 climate. Biomes: tropical evergreen broadleaf forest (RE), tropical deciduous broadleaf forest (RB), tropical woodland (RW), tropical grassland (RG), desert (DE), temperate grassland (TG), temperate shrubland (TS), temperate mixed forest (TM), temperate broadleaf forest (TB), temperate conifer forest (TC), boreal conifer forest (BC), and tundra and alpine (UA). (c) Potential vegetation under projected 2071–2100 climate (nine general circulation model–emissions scenario combinations). (d) Vulnerability of ecosystems to biome shifts based on historical climate and projected vegetation. Vulnerability classes: very low (confidence less than 0.05), low (0.05 ≤ confidence less than 0.2), medium (0.2 ≤ confidence less than 0.8), high (0.8 ≤ confidence less than 0.95), and very high (confidence ≥ 0.95). Data from Gonzalez* et al. *(2010).*

broadly observed in grasslands (Yang *et al.* 2011) and tundra ecosystems (Walker *et al.* 2006). Woody invasion of high-latitude, herb-dominated ecosystems has been reported to result from warming (Sturm *et al.* 2001). The increase in shrubs and grass-like plants could reduce the competitive performance of other plant types and therefore alter the competitive hierarchy within a community (Niu and Wan 2008).

Changes in precipitation regimes are likely to have a particularly strong influence on arid and semi-arid ecosys-

tems and may reverse historical regime shifts, such as the desertification of grasslands (ie transition to dominance by woody shrubs; Peters *et al.* 2011). The complex interactions of grazing, interannual precipitation variability, precipitation seasonality, fire, and pests can result in rapid ecosystem transitions (eg between stable states with high and low vegetation biomass; Holmgren and Scheffer 2001). Results from a decade of climate-change experiments manipulating these variables suggest that precipitation seasonality, timing, variability, and magnitude are

all involved (Jentsch *et al.* 2007), and that these may be altered in future climates.

Ecosystem state transitions can dramatically affect ecosystem functions, including changes in NPP, water and nutrient cycling, regulation of regional climate, and trophic interactions (Zavaleta 2006), with important consequences for the services provided to society. Marked changes in ecosystem state can have substantial impacts on the Earth system, and are beginning to be captured by Earth-system and climate models (Euskirchen *et al.* 2009).

Paleoecological analyses of vegetation changes usually reveal broad-scale patterns of ecosystem state changes over time, but these rarely offer insight into fundamental mechanisms. Model predictions are normally calibrated against contemporary vegetation distributions but have not been carefully tested against experimental evidence, largely because most global-change experiments are short term. The Hierarchical Response Framework proposed by Smith *et al.* (2009) postulates that a long-term global-change experiment could trigger a hierarchy of mechanisms that occur sequentially: physiological changes, followed by species reorganization within communities, and finally species loss and immigration. Long-term experiments are needed to reveal the detailed mechanisms underlying ecosystem state transitions, which may offer new insights into thresholds and tipping points in ecosystem responses to climate changes. Understanding such nonlinear responses is essential for model development and benchmark analysis.

Forest growth, mortality, pests, and wildfire

Climate change has increased the extent of insect outbreaks through a combination of elevated plant drought stress, greater insect overwinter survival, and shortened insect development and reproduction cycles (Raffa *et al.* 2008). Over the course of the past decade, these factors have led to the most extensive insect outbreaks in western forests seen in the past 125 years. Warmer and drier conditions have also led to more extensive and severe wildfires. Climate has been the dominant factor controlling burned area in the 20th century, even during periods of human fire suppression (Littell *et al.* 2009). Collectively, these disturbances have caused widespread reductions in forest productivity, greater tree mortality, and increased opportunities for colonization by plants that initiate changes in ecosystem state (Figure 1). If trends continue, baseline tree mortality rates in western forests are projected to double every 17–29 years (van Mantgem *et al.* 2009).

Changes in forest productivity are not uniformly distributed in North America, nor are they always in the same direction (Figure 1). Sustained negative trends in remotely sensed vegetation indices have been detected from 1982 to 2008 on millions of hectares of boreal forests in Alaska and Canada (Beck and Goetz 2011), whereas positive trends have also been identified for some

regions in the US where ecosystem productivity is less constrained by water availability (Nemani *et al.* 2009). For example, in the more humid eastern forests, where fire and pest outbreaks are less frequent, warming has caused a net increase in productivity (McMahon *et al.* 2010). Overall, climate change is a leading cause of forest change, especially in the western part of the country, although fire suppression, land-use change, and species invasions are also important factors contributing to changes in forest productivity in some regions.

Impact of winter warming

Climate warming in the US has been most pronounced in winter, causing a cascade of unanticipated consequences. The most direct effects have been a shortening of the snow season and a reduction in snow pack, which exposes soils to more frequent freezing events and alters the seasonality of water runoff to streams and reservoirs. At high latitudes, declining areal extent and duration of the snow- and ice-covered season increases energy absorption by ecosystems and strengthens the winter-warming trend (Euskirchen *et al.* 2007).

Snow is an important insulator of soil; a lack of snow can produce the somewhat unexpected phenomenon of colder/frozen soils in a warmer world. Manipulation experiments to simulate reductions in snow cover caused soil freezing in the eastern US and Canada and in Colorado led to increases in root mortality; leaching losses of nitrogen (N), phosphorus (P), and base cations; and increases in nitrous oxide (N_2O) fluxes (Brooks *et al.* 2011). These results suggest that winter climate change will increase the delivery of nutrients to receiving waters, with negative effects on water quality.

Changes in winter conditions also influence patterns of runoff and provision of drinking water in water-supply watersheds. Alpine ecosystems are particularly vulnerable to climate change because warming is proceeding at a disproportionately rapid rate at high elevations. In the Colorado River basin, water shortages are expected as a consequence of changes in snowmelt timing and may be most acute later in the summer, when water is most needed in this region (Barnett and Pierce 2009). Recent modeling and observational studies in the Catskill Mountains in New York (which supply water to New York City) show that the combined effect of elevated winter air temperatures, increased winter rain, and earlier snowmelt may result in more runoff during winter. Consequently, water-storage levels in reservoirs, as well as the number of reservoir water releases and spill events, will likely increase during the winter, and reservoirs would also refill earlier in the spring (Matonse *et al.* 2011).

Recent research in agricultural ecosystems suggests that winter climate changes may result in reduced soil C levels and ecosystem C sequestration (Senthilkumar *et al.* 2009). At the Kellogg Biological Station Long Term Ecological Research site in southwest Michigan, decreases in total soil

C were observed in a wide range of agricultural management treatments established between 1986 and 1988 and resampled in 2006 and 2007, as well as in never-tilled grasslands sampled at the same times. Modeling analyses attributed the losses to higher rates of soil respiration during the dormant season, driven by increased winter temperatures.

Intensification of the hydrologic cycle

Stream discharge has increased in many regions of the US, particularly in New England, the mid-Atlantic, the Midwest, and South–Central states (Lins and Slack 1999). In contrast, stream discharge has decreased in many streams in the Pacific Northwest and the Southeast and is projected to decrease in the arid Southwest (Miller *et al.* 2011). The most important driver of these trends is changing precipitation amounts (Kunkel *et al.* 2010); however, land-use change also plays a role. Streams that exhibit increased discharge are transporting more nutrients (Raymond *et al.* 2012) and base cations (Godsey *et al.* 2009), which cause eutrophication and affect the pH of receiving waters: streams, lakes, and coastal zones (Figure 4).

Observed increases in heavy rainfall (Kunkel *et al.* 2010) are translated directly to more "flashy" hydrographs (ie very rapid rise and fall of stream discharge) that produce stream flooding and can cause drying if the same amount of rain falls in brief episodes rather than as sustained inputs. Increased flooding can overcome the natural retention capabilities of ecosystems and therefore increase the delivery of sediments, dissolved organic matter, contaminants, and disease organisms, often in a nonlinear fashion. Flashy export of these materials associated with large events can have critical impacts on ecosystems, organisms, and drinking-water facilities (Semenza *et al.* 2012) and can modulate the strength of connections between terrestrial and aquatic ecosystems. Alteration of the drying sequence of streams and rivers can lead to altered food-web structures (Sabo *et al.* 2010) and affect the ecological integrity of water courses (Carlisle *et al.* 2011). Finally, heavy storms, although often short in duration, can have major impacts on the metabolic and greenhouse-gas budgets of inland waters (Klug *et al.* 2012).

Extreme hydrologic events are also essential to understanding how streams and riparian zones will respond to climate change. While the responses of some riparian forests will be similar to their upland counterparts (Perry *et al.* 2012), such forests are more strongly influenced by hydrologic variability (both flood and drought). Their future composition, extent, and functioning will depend upon changes in hydrologic regimes, which are likely to vary regionally (Poff and Zimmerman 2010). For the Southwest, if dry conditions prevail, as predicted, a decline in minimum flows and increased intermittency is likely to lead to conversion of native cottonwood–willow forests to exotic tamarisk or other non-native species that are more drought tolerant (Stromberg *et al.* 2010). These ecosystem transitions would fundamentally change the character of southwestern riparian ecosystems.

Feedbacks from ecosystem function to climate

Terrestrial ecosystems account for more than half of the CO_2 naturally exchanged between the biosphere and

Figure 4. Extreme events can accelerate the transport of dissolved and particulate materials to the coastal ocean and other receiving systems. This satellite image shows the visible export of sediment from the Connecticut River in August 2011, following a rainfall event associated with Hurricane Irene that exceeded 15–20 cm (>25 cm in some locations) in the Connecticut River's 28 500 km^2 watershed. River discharge rose to a peak nearly 64× baseflow, and the event flooded farmland and washed away numerous homes. NASA Earth Observatory image taken 2 Sep 2011 by R Simmon, using Landsat 5 data from the US Geological Survey Global Visualization Viewer.

atmosphere (120 of >200 petagrams [Pg] of C per year; IPCC 2007), store as much as 3000 Pg organic C (more than four times the atmospheric CO_2 pool), and constitute the largest sources of methane (CH_4) and N_2O to the atmosphere. Thus, changes in ecosystem function as a result of climate change have strong potential to alter the climate, acting as either positive or negative feedbacks. For example, the permafrost soils of the world contain about 1600 Pg C, which is roughly 50% of the total organic C reservoir and equivalent to twice the amount of CO_2 in the atmosphere (Tarnocai *et al.* 2009). As permafrost thaws, C becomes exposed to microbial attack and decomposition, with the potential to be released as either CO_2 or CH_4. The release of these gases is sensitive to hydrologic changes, which are currently uncertain in the permafrost zone. Forests in the continental US have been a net sink for CO_2 for most of the past century (Zhang *et al.* 2012). This sink is attributed to regrowth after disturbance as well as fertilization by elevated CO_2 and N deposition, although several processes, including wildfire and forest dieback as a result of insect outbreaks, weaken the terrestrial C sink. Dry areas show evidence of becoming C sources at regional and continental scales (Zhao and Running 2010).

Terrestrial ecosystems can function as either sources or sinks for CH_4 and N_2O. However, modeling studies incorporating climate-change drivers, land-use data, and ecosystem processes demonstrate that the conterminous US is a source of atmospheric CH_4. Wetland CH_4 emissions increase with temperature and precipitation and CH_4 uptake by forests decreases with N deposition; both processes contribute more CH_4 to the atmosphere (Xu *et al.* 2010). The US is also a net source of N_2O, with forest and cropland ecosystems accounting for most emissions. Climate-change factors (precipitation events, increased temperature) together with land conversion to agriculture, fertilization, and N deposition are likely increasing emissions at the continental scale (Xu *et al.* 2012). The equivalent of about 20–25% of the land-based sink for CH_4 and CO_2 is released back to the atmosphere by inland waters. Because of regional variability in CO_2 and CH_4 emissions, it is uncertain to what degree warming-induced changes in these emissions for US ecosystems as a whole have altered the rate of climate change.

■ Societal implications: social costs and adaptation planning

As our understanding of climate change evolves, so does our understanding of the resources at risk and the financial consequences of inaction. For instance, extreme weather events comprise more than 90% of natural disasters in the US (Changnon and Easterling 2000). The 14 climate- and weather-related disasters that occurred in 2011 (breaking the 2008 record of nine) resulted in the deaths of 800 people, cost an estimated US$53 billion, and took a toll on society in terms of additional injuries and the devastation of thousands of homes.

In response, federal and state natural resource management agencies have begun to integrate climate-change science into resource management plans and adaptation actions (Bierbaum *et al.* 2013). For example, the US National Park Service is analyzing historical and projected climate-change trends in all 401 national parks and adjusting park management plans to address specific ecosystem-level impacts and vulnerabilities. Federal and state agencies and Indian tribes will play a leading role in such adaption (Stein *et al.* 2013). Indeed, a new level of coordination and partnership is emerging among federal, state, and tribal governments in the form of the 2013 National Fish, Wildlife, and Plants Climate Adaptation Strategy, the first joint effort of these three levels of government to identify actions to conserve natural resources under climate change, reduce costly future damage, and take advantage of possible beneficial opportunities. Historical impacts and future vulnerabilities at the ecosystem level challenge resource agencies to manage for potential future conditions, rather than to manage for past conditions that may no longer exist under climate change.

■ Acknowledgements

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