Ecology in a connected world: a vision for a "network of networks"

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We live in a connected world. Global economists and health professionals who track infectious diseases have long known this. But what does it mean in terms of how we operate as ecologists? How do we adjust our thinking about ecological systems and modify our sampling strategies to account for the fluxes and flows of materials among locations? What are the consequences of connectivity, not only at the global scale, but also at relevant continental, regional, and local scales? How do we identify connections among non-adjacent and seemingly disconnected locations, to both minimize the element of surprise and mitigate or avert potential impacts? These are the kinds of questions addressed in the papers in this Special Issue of *Frontiers*.

As ecologists, we need to recognize the extent to which system dynamics are driven by connectivity and to assess the consequences of changes (decreases or increases) in connectivity. Fortunately, we have resources available to attack these problems. The connectivity framework described in Peters *et al.* (p 229) provides the perspective, sampling strategy, and predictive capability needed to better understand these dynamics. Although the framework was developed for continental-scale research, the principles are applicable at a broad range of spatial scales.

In an ecological context, connectivity is defined as the transfer of materials by wind, water, humans, and animals between locations. Studying this phenomenon at local to continental scales will require new approaches that build on and augment existing scientific resources in novel ways. Most research groups and sites are part of networks that recognize the value and importance of measuring similar responses and drivers in different ecosystem types. However, simply collecting similar types of data is insufficient in a connected world. For example, the hundreds of research sites within the US will need to be integrated to capture the biotic, climatic, and environmental heterogeneity that characterizes this country. Existing sites have the expertise, instrumentation, and infrastructure to serve as the foundation for an interconnected network of sites. But it is only through collaborative, multi-agency research efforts that we can hope to create the "network of networks" required to address connectivity issues.

In some cases, such as at US Department of Agriculture (USDA) sites, data collection has been ongoing for nearly a century; sites within the National Science Foundation's (NSF) Long Term Ecological Research (LTER) program have been sampling intensively for nearly 30 years. This wealth of long-term data is the most reliable way to document historical patterns and to disentangle future directional trends from short-term variability and cyclic behavior. Existing efforts are an important step in gaining access to thousands of long-term datasets from many sites (eg www.ecotrends.info), but inclusion of more datasets and involvement of more sites are needed to build the required knowledge and research infrastructure.

Advances in remote sensing, combined with spatial and temporal analytical tools, including simulation models, will be invaluable in obtaining information across scales. The seamless integration of these multi-scale measurements and models will be needed before we can predict the impacts of propagating events, such as Hurricane Katrina. Admittedly, we need to go beyond the continental scale, by interacting effectively with other countries and continents.

Efforts are underway to begin to develop a "networks of networks". Existing networks recognize the importance of including more sites in their study designs (eg LTER Decadal Plan, www.lternet.edu/decadalplan); these networks are poised to address connectivity questions. Other efforts use the internet to link many sites (> 600 to date; www.p2erls.net). Designs of emerging networks, such as the National Ecological Observatory Network (www.neoninc.org), include common measurements at the continental scale. But to be successful, proposed networks must take advantage of the comprehensive coverage in time and space provided by the hundreds of existing sites. At present, it remains to be seen if these proposed initiatives will collect the multi-scale measurements required for connectivity studies.

The papers in this Special Issue provide examples of research questions and approaches that we believe are necessary for conducting effective research at the continental scale. New insights are discussed for five topics (spread of invasive species and infectious diseases, p 238; climate change and aquatic systems, p 247; climate change and coastal systems, p 255; climatic and societal gradients across landscapes, p 264; climate change and terrestrial systems, p 273) that are critical elements of our connected world, now and in the future. The authors and I are grateful to NSF, USDA–ARS, the LTER network, and the Consortium for Regional Ecological Observatories (COREO) for funding this Special Issue.

Emergence of ecological networks

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Ecosystems have changed more in the past 50 years than at any time in human history, according to the Millennium Ecosystem Assessment (www.MAweb.org). Many of the most important changes are non-linear and hard to reverse. Thus, the emergence of big ecological changes from seemingly local events, known as "greenlash", underlies many of the ecological surprises that we face today. Such disparate phenomena as rising flood frequency, persistent drought, emergence or re-emergence of pandemic disease, harmful invasions of exotic organisms, and pollutant magnification in ecosystems are examples. Greenlash involves contagious spread from local to continental scales, with the most extreme impacts in zones of convergence, where multiple drivers come together. Understanding greenlash requires a new kind of social–ecological science that builds on insights from biogeochemistry, demography, geography, hydrology, landscape ecology, and other disciplines to synthesize new perspectives.

New phenomena can emerge in science as well as in ecosystems. Research challenges posed by non-linear or cross-scale phenomena are being identified and understood by new networks of environmental scientists. The process is driven by those who recognize the need for novel approaches to study the connections among local, regional, and continental change. Some networks are bootlegged from existing funding, and others are funded by agencies or foundations that perceive the need to understand multi-scale ecological change and monitor the factors that cause it. The power of the networks derives from strong intellectual support by a variety of scientists from many disciplines, who are motivated by the excitement and importance of the research questions. Now, new networks are being developed and the older networks are re-organizing into "networks of networks" to address fresh challenges as they are identified.

In this Special Issue of *Frontiers*, diverse groups of environmental scientists discuss the current frontiers of research on continental change, focusing on North America. The framework for continental-scale science articulated by Peters *et al.* (p 229) brings together existing capacities, such as the National Science Foundation's Long Term Ecological Research network (http://lternet.edu), networks maintained by mission agencies of many countries, including Mexico's Commission for Knowledge and Use of Biodiversity (www.conabio.gob.mx), the Sub-global Assessments of the Millennium Ecosystem Assessment, international research networks such as the Global Lake Ecological Observatory Network (GLEON; http://gleon.org), and new networks currently under development, such as the National Ecological Observatory Network (NEON; www.neoninc.org). Other papers in this issue describe insights and opportunities for network research. Freshwater ecosystems serve as sentinels for their airsheds and watersheds, providing a natural matrix for continental sensor networks (Williamson *et al.*, p 247). Contrasting ecosystem responses across gradients of urban impact and climate change reveal the effects of major human drivers (Grimm *et al.*, p 264). Invasive species and emergent diseases can be strong drivers of greenlash, due to their capacity for contagious spread across landscapes (Crowl *et al.*, p 238). Coastal ecosystems face some unique stressors, such as rising sea level and intensification of windstorms, suggesting important hypotheses to be tested across networked coastal sites (Hopkinson *et al.*, p 255). In this century, climate change is the over-arching environmental shift, establishing the context in which other drivers will act (Marshall *et al.*, p 273). Networks of long-term observation sites are crucial for understanding how multiple drivers, acting across gradients of climate, land use, and ecosystem type, are changing the ecosystem services that support human well-being.

Interdisciplinary assessments to synthesize data in policy-relevant form place increasing demands on the environmental sciences. Yet a recent evaluation of global ecosystems performed by the Millennium Ecosystem Assessment found that data were variable in quality. It was even more troubling that current data were sometimes inferior to historical information, so that recognition and understanding of ecosystem transformation was deteriorating even as change accelerated. In a world of greenlash, successful adaptation requires synoptic, continental-scale data on ecosystem change. The growing capacity of ecological networks is a remarkable step, addressing novel environmental challenges through self-organization of science. The site-specific depth and evolving connections of these networks do more than enable the frontier of environmental science – they are the frontier of environmental science. This Special Issue gives readers of *Frontiers* a bird's eye view of this rapidly developing area of inquiry.

Living in an increasingly connected world: a framework for continental-scale environmental science

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The global environment is changing rapidly, as the result of factors that act at multiple spatial and temporal scales. It is now clear that local processes can affect broad-scale ecological dynamics, and that broad-scale drivers can overwhelm local patterns and processes. Understanding these cross-scale interactions requires a conceptual framework based on connectivity in material and information flow across scales. In this introductory paper to *Frontiers'* Special Issue on *Continental-scale ecology in an increasingly connected world*, we (1) discuss a multi-scale framework, including the key drivers and consequences of connectivity acting across spatial and temporal scales, (2) provide a series of testable hypotheses, predictions, and an approach, and (3) propose the development of a "network of networks", which would take advantage of existing research facilities and cyberinfrastructure. This unique framework and associated technology will enable us to better forecast global environmental change at multiple spatial scales, from local sites to regions and continents.

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The interplay between fine-scale patterns and processes and broad-scale dynamics is increasingly being recognized as key to understanding ecosystem dynamics, particularly as the number and magnitude of global change drivers increases over time (Huston 1999; Rodó *et al.* 2002; King *et al.* 2004). Cross-scale interactions (CSI) are processes at one spatial or temporal scale that interact with processes at another scale, often resulting in non-linear dynamics with abrupt threshold responses (Holling 1992; Carpenter and Turner 2000; Peters *et al.* 2004a, 2007). These interactions may generate behavior that emerges at broader scales and cannot be predicted based on observations at single or even multiple independent scales (Michener *et al.* 2001). Redistribution of material, energy, and information flow within and among spatial units (ie connectivity) is one potentially powerful explanation for these cross-scale interactions. The degree of connectivity is determined both by the spatial structure of the environment and by the way in which this structure influences the change in redistribution rate – a definition similar to one used by landscape ecologists (With *et al.* 1997).

All ecosystems around the world are connected through a globally mixed atmosphere and, historically, regional connections existed through a variety of both biotic and abiotic processes. This connectivity has been altered through human transport of propagules, toxins, and diseases, as well as anthropogenic disturbances and changes in land use (Reiners and Driese 2003; MA 2005; Herrick and Sarukhán 2007). Thus, changes in one location can have dramatic influences on both adjacent and distant areas, either at fine or broad scales. For example, the extreme drought of the 1930s in the central Great Plains of the US interacted with cultivation of marginal croplands to generate high rates of soil erosion from individual fields, which subsequently resulted in the Dust Bowl (Figure 1). This site- to regional-scale set of events spread across the continent, to affect broad-scale patterns in soil and air quality, migration patterns, human health, and the economy (Peters *et al.* 2004a).

In a nutshell:

- The world is becoming increasingly connected through the flow of materials, organisms, and information, both within and among regions that may or may not be adjacent or even close to each other
- Connectivity pathways allow fine-scale processes to propagate and impact large areas; in some cases, broad-scale drivers can overwhelm fine-scale processes to alter ecosystem dynamics
- Changes in connectivity have the potential to produce rapid and dramatic changes in ecosystem dynamics unlike any observed in recorded history
- Understanding global connectivity and its consequences requires the creation of an international ecological "network of networks" for observation and experimentation, and the accompanying cyberinfrastructure for analysis and synthesis

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Beyond the Frontier: Listen to Debra Peters discussing this Special Issue on *Frontiers'* monthly podcast, at www.frontiersinecology.org.

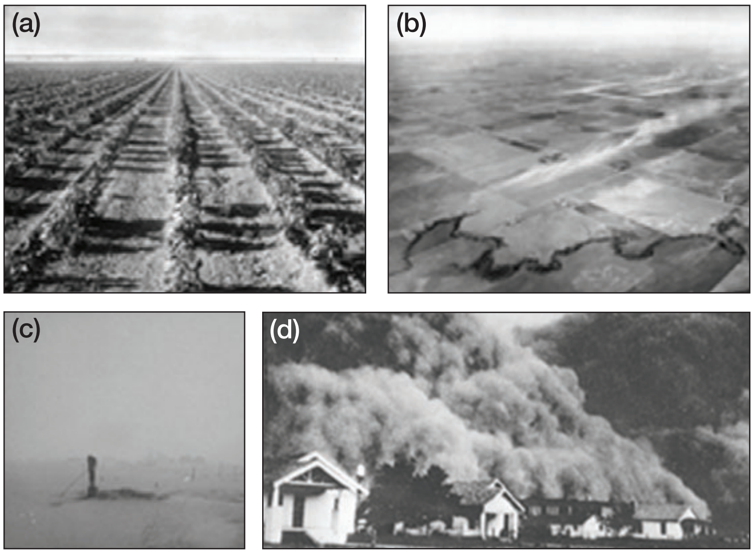

Figure 1. *Development of the US Dust Bowl, an event that propagated from the cultivation of many individual fields on marginal land in the 1920s to widespread abandonment in the 1930s during a severe drought, which led to continental-scale impacts of massive dust storms (www.weru.ksu.edu). (a) Many individual fields cultivated in the Great Plains in the 1920s (b) became highly connected following drought and strong winds in the 1930s, through wind erosion. (c) Extensive areas of soil were eroded, creating (d) massive dust storms, with effects on human health, the economy, and migration across the continent.*

Connectivity across scales can also link continents: hurricanes along the east coast of North America often originate as fine-scale thunderstorms in eastern Africa (Price *et al.* 2007). In 2003, it took only 8 months for severe acute respiratory syndrome (SARS) to spread from a single province in China to 29 countries, resulting in over 8400 confirmed cases around the globe (WHO 2003). Ozone, carbon monoxide, mercury, and other particles from degraded land in China cross the Pacific Ocean to affect air quality in North America (Jaffe *et al.* 2003). The ecological consequences of these broad-scale connections for phenomena at finer scales, from sites to regions and continents, are often unknown. Furthermore, the influence of fine-scale ecological patterns and processes at local sites on broader-scale patterns at regional to continental and global scales is poorly understood.

Here, we provide a conceptual framework to understand and predict broad-scale ecosystem dynamics based on connectivity in material and information flow, linking multiple scales of observation, from local sites to regions and continents. Although we focus on dynamics in the US, as a major part of North America, our framework applies to all continents and to inter-continental dynamics as well. We also suggest an approach to test hypotheses about interactions across scales, and to predict future dynamics. Finally, we describe how our cross-scale framework can be used to leverage existing and emerging research networks to integrate datasets and ecological knowledge.

Connectivity framework: a hierarchy of interacting scales

A theory of connectivity across scales is emerging, and it builds on concepts from diverse disciplines, including landscape ecology, Earth-system science, population ecology, macroecology, hydrology, and biogeochemistry. This theory provides one key to forecasting large-scale, multi-process phenomena, and is the basis for our conceptual framework. Our basic premise is that the climate system and human activities operate across multiple, and often disparate, spatial and temporal scales to influence, and be influenced by, ecological systems (Figure 2). Three major scales of climate drivers may lead to synchronicity in ecosystem responses as a result of connectivity via air masses. We use the term "driver" to refer to broad-scale processes and human activities that directly or indirectly influence ecological and socioeconomic systems. This definition allows for interactions among drivers as well as feedback mechanisms between drivers and responses. One example is seen in climatically induced shifts in vegetation that produce changes in surface-energy balance, which then feed back to alter weather patterns that affect both ecosystems and human society (eg Pielke *et al.* 2007). Observed precipitation and temperature patterns at site to regional and continental scales (Figure 3) result from a combination of three climate drivers:

(1) global circulation patterns and other broad-scale drivers, such as solar insolation, which influence long-term climatic averages, with resulting effects on ecosystem structure and function across large regions;
(2) sub-continental to continental-scale phenomena driven by patterns such as the Northern Annular Mode (NAM), the Pacific–North American pattern (PNA), and the El Niño–Southern Oscillation (ENSO); and
(3) mesoscale patterns from a few to several hundred kilometers , as weather interacts with local to regional topography and land surface properties.

However, along with these multi-scale patterns in climate, other gradients are often needed to explain regional- and continental-scale variability in ecosystem dynamics. For example, connectivity along major river systems leads to variable patterns in land use, human settlement, invasive species, and nutrient distribution in soil or sediment that overlay climate-based variations in connectivity (WebFigure 1). Human activities at local scales increasingly drive and connect ecosystem dynamics and land change at broader, regional scales (Luck *et al.* 2001; Dietz *et al.* 2007). In addition, interactions among climate, human populations, and disturbance agents, such as disease vectors, have both ecological and socioeconomic consequences (Yates *et al.* 2002).

Thus, connectivity across scales results from climate and land use as broad-scale drivers interacting with finer-scale patterns and processes that redistribute materials within and among linked terrestrial and aquatic systems (Figure 2). Thresholds and feedbacks associated with these dynamics often result in non-linear system behavior, as the rates of change vary discontinuously through time and across space (Peters *et al.* 2004a). Connectivity occurs via transport vectors (eg wind, water, animals, people) that move materials and resources (eg dust, soil, water, energy, nutrients, propagules, diseases, and chemical constituents) within and among terrestrial and aquatic systems across a range of spatial and temporal scales (Reiners and Driese 2003; Peters *et al.* 2006). Changes in drivers and pattern–process relationships through time and across space can alter ecosystem dynamics within particular locations, and can change dynamics across locations and large regions (Allen 2007; Peters *et al.* 2007). Although our framework shares some similarities with hierarchical systems theory (Allen and Starr 1982), this approach is designed to understand and predict the conditions when broad-scale drivers will overwhelm fine-scale variability, and when fine-scale processes propagate to influence broad spatial extents. This approach also needs to account for uncertainties in predictions that exist for large-scale systems (Ludwig *et al.* 1993).

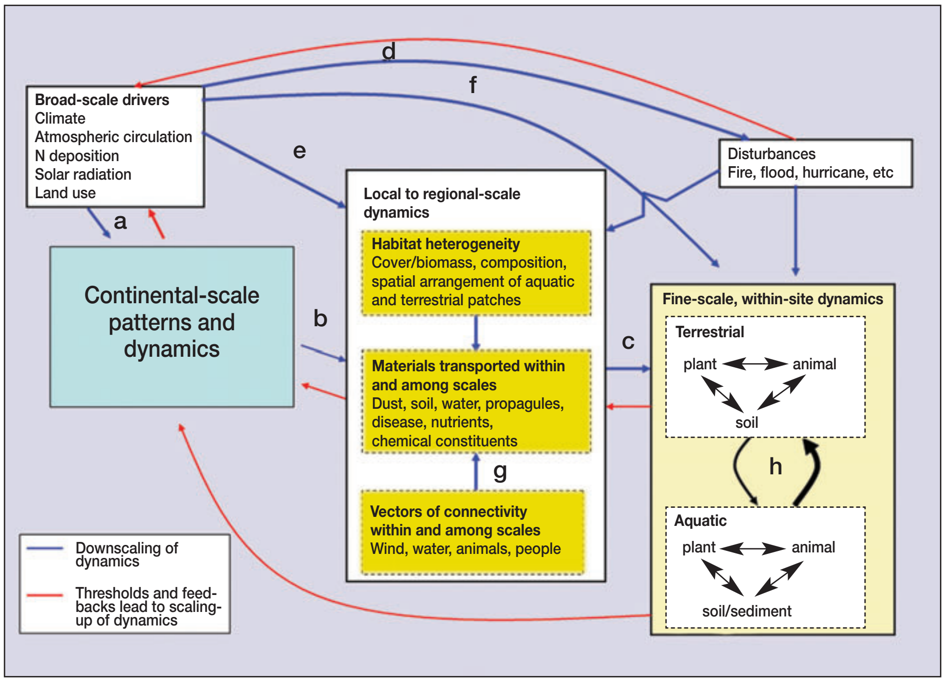

Figure 2. *Continental-scale patterns and dynamics result from climate and people as broad-scale drivers interacting with finer-scale vectors that redistribute materials within and among linked terrestrial and aquatic systems. Climate and land-use change interact with patterns and processes at multiple, finer scales (blue arrows). (a) These drivers can influence broad-scale patterns directly, and these constraints may act to overwhelm heterogeneity and processes at (b) meso-scales and at (c) the finer scale of local sites. Broad-scale drivers can also exert an indirect impact on broad-scale patterns through their interactions with disturbances, including (d) the spread of invasive species, (e) pattern–process relationships at meso-scales, or (f) at finer scales within a site. Connectivity imparted by the transfer of materials occurs both at (g) the meso-scale and at (h) finer scales within sites where terrestrial and aquatic systems are connected. These dynamics at fine scales can propagate to influence larger spatial extents (red arrows). Feedbacks occur throughout the system. The term "drivers" refers to both forcing functions that are part of the system and to external drivers.*

■ What can we expect in an increasingly connected world?

Globally, some materials and resources are becoming more concentrated over time (eg nitrogen), while others are becoming more broadly distributed (eg infectious diseases, invasive species). Some resources, such as those in freshwater, are becoming both more concentrated and more widely distributed, depending on the spatial and temporal scales of observation (Baron *et al.* 2002). In certain cases, connectivity in one vector can either increase or decrease connectivity in other vectors, with consequences for resource redistribution and ecosystem dynamics (Breshears *et al.* 2003). For example, human settlement patterns at fine scales can increase connectivity in non-vegetated areas through wind and water erosion (Nates and Moyer 2005), yet can decrease connectivity in wildlife movement and dispersal of infectious diseases by fragmenting landscapes (Haddad *et al.* 2003). Connectivity of a single resource can change in different ways at different scales. For example, at the continental scale, human activities are increasing connectivity between areas through increases in atmospheric nitrogen (N) deposition, yet N levels are increasing and becoming less connected among spatial units as population density and sprawl increase (Figure 4).

Our framework is particularly useful for focusing a suite of ecological questions on the key drivers of contemporary change at multiple scales. These questions were identified by the ecological community as critically important to forecasting future ecosystems at broad scales (eg NRC 2001; AIBS 2004 a,b; MacMahon and Peters 2005). Specific hypotheses can be tested, based on our connectivity framework (see WebPanel 1). These hypotheses are organized around two major issues: ecological effects of connectivity at local versus global scales, and the effects of increasing versus decreasing connectivity, as influenced by different transport vectors.

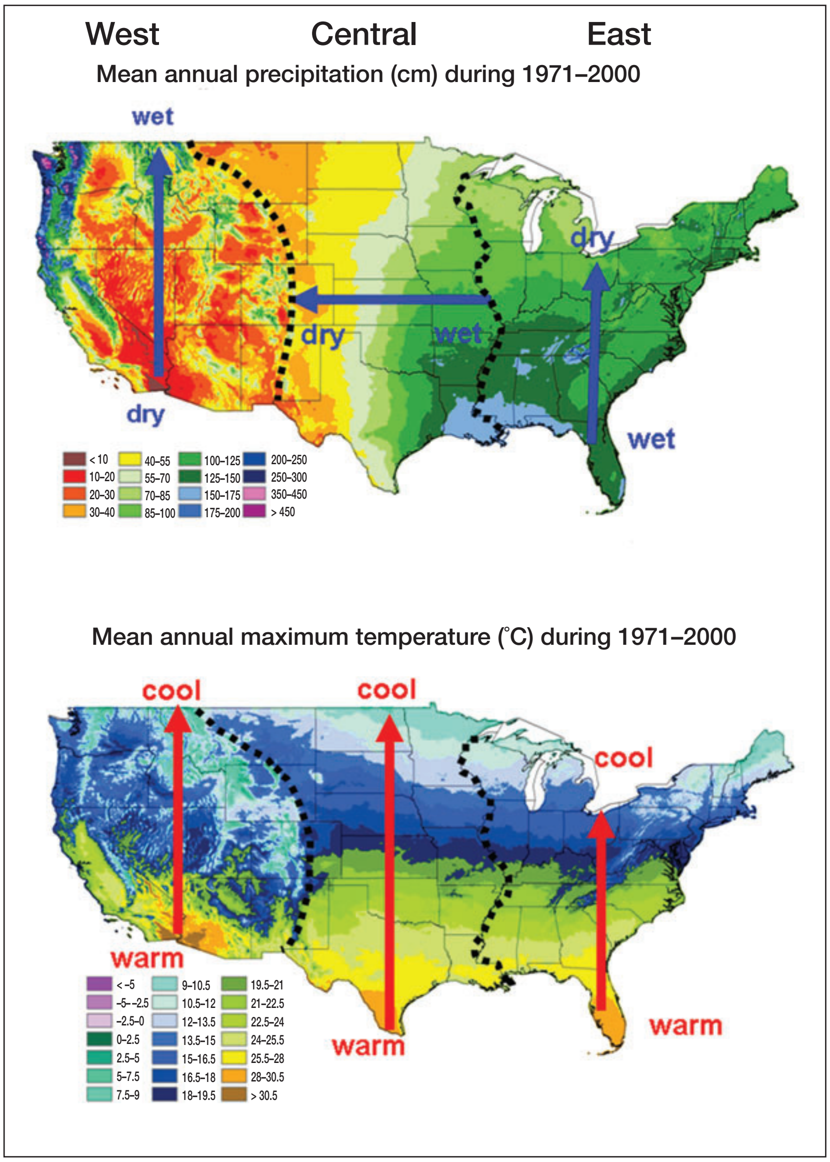

Figure 3. *The US can be divided into three general regions based on a combination of broad-scale patterns in (a) precipitation (annual total) and (b) annual maximum daily temperature. Shown are average annual values (1971–2000) from the PRISM model (http://prismclimate.org). Gradients for each climatic variable are shown in blue (precipitation) or red (temperature).*

Approach to conducting continental-scale research

Testing hypotheses and addressing questions from our framework (WebPanel 1) will require a new strategy for experimental design that includes a network of sites distributed across the US (as representative of North America) and the globe, and along the continental margins. Our design strategy consists of five steps, outlined below.

Step 1. Identify continental-scale patterns in broad-scale drivers

Spatial patterns in three broad-scale environmental drivers critical to our framework and relevant to ecosystems (precipitation, temperature, and N deposition) can be discerned using long-term data (> 30 years) collected from standard weather stations (www.nws.noaa.gov/) and sampling collectors of atmospheric chemistry (eg http://nadp.sws.uiuc.edu/) located throughout the US. Average seasonal and annual precipitation, and minimum, average, and maximum seasonal and annual temperatures are some of the most important climatic variables controlling ecosystem dynamics by influencing connectivity of resources across scales (Figure 3).

Step 2. Stratify a continent into regions, based on broad-scale patterns in drivers

The US can be roughly divided into Eastern, Central, and Western regions, based on a combination of broad-scale patterns in key climatic drivers. The Rocky Mountains and the Mississippi River provide general demarcations between regions to illustrate broad-scale patterns. Fine-scale variation exists within these general regions that may not follow the regional-scale pattern. Each region has contrasting patterns and correlations between precipitation and temperature (Figure 3), variable human population settlement and growth dynamics, and contrasting forecasts for climate change (IPCC 2007).

In the Eastern region of the US, the dominant climatic pattern is a positive correlation between temperature and precipitation, with both variables, in general, decreasing from south to north (Figure 3). Spatial variation in N inputs results mainly from nitrogen oxide (NO_x) emissions from agricultural regions, NO_x emissions from industrialized regions, and transport via wind and deposition as rain and snow (Figure 4). This region contains about 60% of the total US population, mostly living in coastal counties, which comprise only 17% of the land area. Most people are concentrated in the Northeast, which includes four large metropolitan areas (New York, Washington/Baltimore, Philadelphia, and Boston), and represents the most densely populated coastal region in the nation (Crossett *et al.* 2004). Most invasions of exotic plants and animals originate here, especially along the coastal flyway and major river systems (eg the Mississippi–Ohio and the St Lawrence), which serve as invasion corridors to the mid-continent. The Eastern region has a long history of intensive land use followed by abandonment (Foster and Aber 2004). Most of the forests are still regrowing and absorbing substantial amounts of carbon, and much of the land is privately owned. Older urban areas along the eastern seaboard are losing population as extensive residential developments continue to spread in suburban and exurban lands.

In the Central region, precipitation and temperature occur as orthogonal, linear gradients that result in natural experimental opportunities with almost completely independent driving variables (Figure 3). This region includes a climate threshold of historical relevance. The 100th meridian, the north–south precipitation isoline of approximately 63.5 cm average rainfall per year, marks the boundary between rain-fed cultivation and grazing-based agriculture. This threshold has shifted back and forth with climatic cycles, with disastrous consequences to humans and the economy. The relatively flat topography eliminates orographic effects (effects related to or caused by physical geography) and allows unimpeded north–south and west–east movement of weather fronts, including some of the most violent storms on the planet. This corridor includes the central migratory flyway for birds, and provides a clear path for invasion by southern plants, animals, and pathogens into the center of the country.

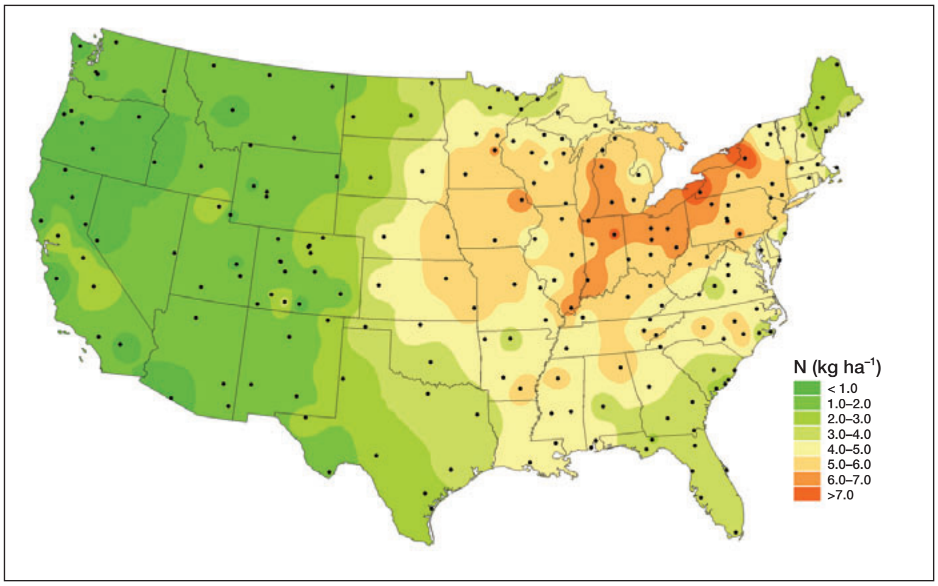

Figure 4. *Continental variation in N deposition (NADP 2007). The map depicts 5-year (2002–2006) annual weighted-average concentrations of ammonium and nitrate at National Trends Network (NTN) sites. To include sites with high proportions of snow, NADP data completeness criteria (http://nadp.sws.uiuc.edu/documentation/completeness.asp) were relaxed from 75% to 60%, except for the criterion requiring precipitation depth measurements at least 90% of the time.*

The Central region encompasses much of the Mississippi River watershed, which eventually drains into the Gulf of Mexico. Large-scale N-deposition gradients are related to human population density (Figure 4). This region also includes a gradient of human population density because the eastern portion has much higher densities than the western portion. The high proportion of private ownership of agricultural land has limited the impact of federal land management agencies, in contrast with the West. In warmer parts of the Central region, urban and suburban areas are experiencing large influxes of population, resulting in an emerging north–south gradient in population.

The Western region differs from both the Eastern and Central regions because of high topographic variability (Figure 3). A relatively uniform heterogeneity of elevation-driven temperature and precipitation gradients is associated with mountain ranges across the western US. Precipitation and temperature have a strong negative correlation at both the local scale (eg elevation gradients) and the sub-continental scale (from the warm, dry south to the cool, wet north). Strong seasonality in rainfall and snowmelt drives runoff characteristics in the region. Runoff can also be altered by water management; in California, reservoirs store spring snowmelt for use in the summer, when water demand for agriculture and power is highest, effectively truncating the normal spring peak in the hydrograph (Kimmerer and Schubel 1994). Dry deposition accounts for most spatial variation in N, and high N inputs are concentrated in, and upslope of, basins with either high human population densities or intensive agriculture (Fenn *et al.* 2003). Overall, portions of the Western region have the lowest precipitation rates and human population density, and greatest public ownership of land compared to the other two regions. Not surprisingly, human population density is strongly correlated with water availability along the continental precipitation gradient, and in areas where water is concentrated by either topography or engineering. Nevertheless, the West is experiencing rapid urbanization, and harbors some of the fastest-growing metropolitan regions in the country (eg Phoenix, El Paso, Las Vegas). California had the fastest growth in coastal population in the US between 1980 and 2003, increasing by 9.9 million people (Crossett *et al.* 2004).

Step 3. Define gradients and identify sites within and among regions

Fine-scale gradients nested within broad-scale drivers can be selected to answer the same questions in different parts of the continent with different environmental conditions. These gradients are often hierarchical and related to meso- and sub-continental-scale patterns in climate, atmospheric chemistry, resource quality and quantity (eg water, nutrients), and land use. River basins, in particular, provide a sub-continental gradient in water availability that connects adjacent and non-adjacent areas via the transfer of materials, organisms, and information (WebFigure 1). Other gradients nested within river basins can be connected by other transport vectors. Understanding the interactions among these vectors and ecological patterns across spatial and temporal scales can provide new insights to continental-scale dynamics.

In the Southwest, for example, a snowmelt gradient associated with the Rio Grande starts in southern Colorado and extends to southern Texas, where the river reaches the Gulf of Mexico (WebFigure 1). Associated with this snowmelt gradient and regional-scale transport by water are gradients in temperature and precipitation that are not necessarily linear along the river, which generally flows north to south. Mosaics of land use, invasive species, infectious diseases, and nitrogen deposition occur within these regional-scale gradients. Fine-scale patterns in land use (eg rural, exurban, suburban, urban) exist, and are similar to those in many parts of the country. Ecological systems now considered wildlands, as well as managed lands, are being encroached upon by growing urban areas (see Grimm *et al.* [2008] in this issue). These urban fringes may consist of suburban and exurban sprawl areas that are expanding and creating either barriers or corridors to connectivity in adjacent or embedded wildlands. Barriers disrupt migratory pathways of animals, while corridors increase rates of spread of exotic species from cities to natural areas. Land-use gradients of wildland–urban fringe–urban areas occur throughout the country, although the characteristics of each land-use type (eg housing density, wildland type), distances between types, and connectivity in terms of the rates of transfer among types differ regionally (Grimm *et al.* [2008] in this issue).

River basins in other regions, such as the Columbia, Colorado, San Joaquin, and Missouri, have similar hydrologic, climatic, and land-use gradients that can be used to evaluate the regional- to continental-scale consequences for ecosystem dynamics of connectivity in multiple transport vectors. In addition, repeated patterns of interacting gradients can be used to investigate continental-scale terrestrial and aquatic responses to drought and other extreme climatic events (Marshall *et al.* [2008] in this issue; Williamson *et al.* [2008] in this issue), spread of invasive species and infectious diseases (Crowl *et al.* [2008] in this issue), transfer of pollutants (Grimm *et al.* [2008] in this issue), coastal instability (Hopkinson *et al.* [2008] in this issue), and disturbances, such as fire and hurricanes (Hopkinson *et al.* [2008] in this issue; Marshall *et al.* [2008] in this issue). The nested gradients selected will depend on the specific questions and responses being addressed.

Site selection should capture key characteristics of the gradients being studied. Sites that are expected to exhibit state changes in the near future (decades) and those that are expected to be comparatively stable (centuries) should be included in the design.

Step 4. Sampling scheme for measuring importance of connectivity across scales

Measuring the importance of connectivity to ecosystem dynamics in adjacent and non-contiguous areas requires coordinated and integrated efforts to sample transport processes and spatial context as well as drivers and local processes at each site. Changing pattern–process relationships across scales need to be studied explicitly (Peters *et al.* 2007). Representative samples with adequate replication are required at each scale, along with standardized indicators of change and sampling techniques (eg Herrick *et al.* 2005). Coordinated sampling among sites is insufficient without integration and an understanding of the key connectors across space and through time. For example, the same set of investigators collected similar measurements at sites located throughout the Dust Bowl region, yet they were unable to predict the continental-scale consequences of locally high plant mortality and movement of dust (Weaver and Albertson 1940).

In general, there are three parts to the sampling scheme. First, patterns and processes need to be characterized at each spatial scale. Key transport vectors (water, wind, animals, people) that move materials among spatial units and processes that occur within spatial units (eg sedimentation, fertilization, denitrification, land-use conversions) should be identified. The sources and sinks of materials need to be determined for each transport vector at each scale. The initial patterns in biota, soils, and climate should be documented along gradients of sites with different broad-scale drivers and transport vectors.

Second, short- and long-term dynamics must be documented using observations, experiments, and simulation models. Changes in pattern need to be monitored through time as the broad-scale drivers vary naturally. Drivers or patterns can also be manipulated experimentally to observe ecosystem responses under altered, yet controlled, conditions (eg Cook *et al.* 2004). Realistic mechanistic models are needed to predict ecosystem dynamics as drivers and transport of materials change along gradients and across the continent. These dynamics must be compared statistically with historical trends, if possible, to determine if changes constitute natural fluctuations, directional dynamics, or heightened variability.

Third, information should be integrated and synthesized, both within and across scales. The relative importance of local and transport processes to ecosystem dynamics needs to be compared statistically as drivers change through time. The results must be synthesized among sites, both within and across gradients and within and across regions, to compare responses and seek generalities.

Finally, this information can be used to determine when and where fine-scale processes propagate to influence large areas (adjacent or not), and the conditions under which broad-scale drivers overwhelm fine-scale processes.

Forecasting future dynamics

Addressing continental-scale questions will require development of ecological, hydrological, climatological, and sociological models that are integrated and linked with one another. Some models will address questions at local to regional scales, whereas others will incorporate fine-scale patterns and processes to simulate regional- to continental-scale dynamics. Still other models will forecast a future with conditions that are unprecedented in Earth's history; an empirical extrapolation of responses based on current or past conditions is therefore impossible and a mechanistic modeling approach will be required. In addition, these forecasting models will need to be both spatially explicit and spatially interactive to project experimental results from plots to local, regional, and continental scales (Peters *et al.* 2004b).

Most models thus far have been developed for specific sites with defined spatial and temporal resolutions, are based on existing input parameters, and have been validated under current environmental conditions (eg Schimel *et al.* 1997). A new generation of models is needed to address cross-scale interactions such as those posed here. These new models can build on existing models, but will require advances in programming and cyberinfrastructure to simulate responses that change through time or across space, and to identify and forecast potential thresholds. Simulating coupled socioecological systems will require linking models after resolving differences in spatial and temporal scales (eg Costanza and Voinov 2003). For example, ecohydrologic models couple biogeochemical processes with hydrologic transport to describe connectivity by water for hillslopes and watersheds (eg Tenhunen and Kabat 1999). Coupling advanced fluid-dynamic models, population dispersion models, or human demographic models with ecosystem models would dramatically improve our understanding of connectivity via multiple interacting vectors.

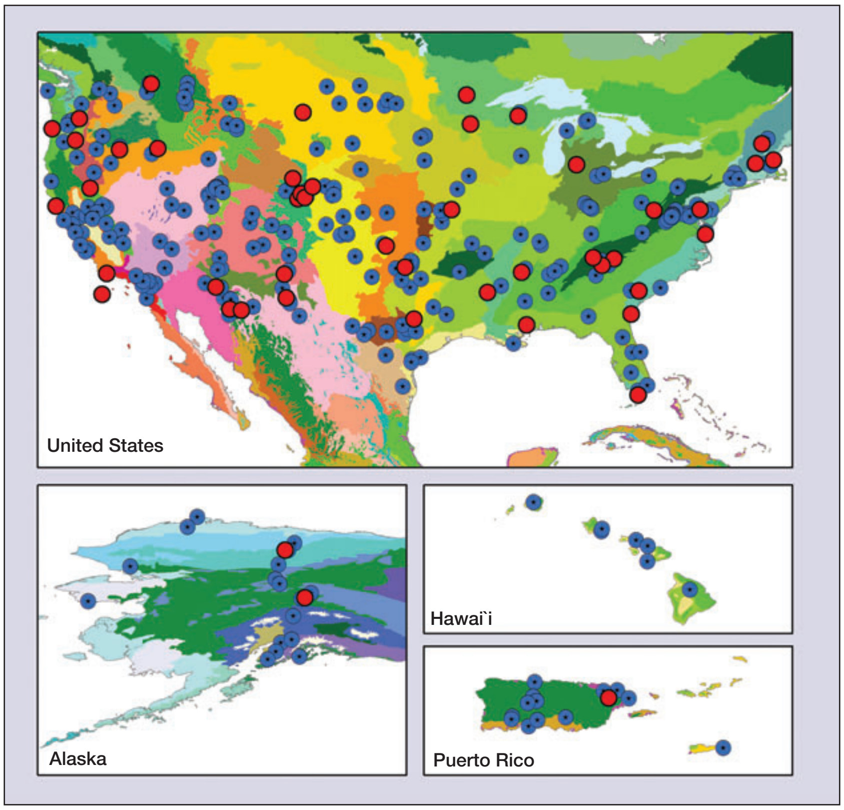

Figure 5. *Location of > 250 existing ecological research sites in the continental US, Alaska, Hawai'i, and Puerto Rico on a map of ecoregions. Red dots indicate sites in the EcoTrends project of long-term data (www.ecotrends.info); blue and red dots indicate sites in the Pole-to-Pole Ecological Lattice of Sites project (www.p2erls.net). See www.worldwildlife.org for ecoregion legend. Underlying ecoregions map downloaded from www.worldwildlife.org/science/data/terreco.cfm.*

Relationship with existing and emerging networks of continental-scale research

Understanding connectivity in the flow of materials, organisms, and information at the continental scale requires a network of ecological research sites that provides spatial breadth (eg comprehensive representation of the full range of climatic, ecological, and socioeconomic conditions) and temporal depth (eg sites with long-term records). The concept of creating an ecological "network of networks" to study global climate change and other broad-scale phenomena dates back to a 1991 workshop (Bledsoe and Barber 1993). The report called for the creation of a network that included the National Science Foundation's Long Term Ecological Research (LTER) Network and Land-Margin Ecosystem Research sites (now folded into the LTER Program), National Oceanographic and Atmospheric Administration Marine Sanctuaries, the Department of Energy Research Park Network, the US National Park Service, and the Man and the Biosphere Reserves. Today, such an ecological network of networks in the US would also include US Geological Service (USGS) and USDA Forest Service and Agricultural Research Service sites, biological field stations and marine laboratories (eg Organization of Biological Field Stations, National Association of Marine Laboratories), the AmeriFlux network, and emerging environmental observatories (eg National Ecological Observatory Network, WATERS, Oceans Observatories Initiative). This network would encompass sites in every major ecoregion (Figure 5) to include the full range of climatic and environmental conditions. The network would also encompass valuable, long-term observations from an array of research sites that are presently being compiled in EcoTrends (www.ecotrends.info), a collaborative effort, designed to make long-term ecological data accessible for science and education.

Achieving a continental-scale understanding of the multiscale connectivity interactions raised here necessitates international collaboration to include Canada's Environmental Monitoring and Assessment Network, Mexico's National Commission for the Knowledge and Use of Biodiversity (CONABIO), and other relevant research sites and networks throughout North America. The availability of data from a North American "network of networks" would substantially augment the knowledge base that is emerging from international research networks like FLUXNET, the International Long Term Ecological Research Network, the OCEAN Sustained Interdisciplinary Timeseries Environment Observation System, the Global Lake Ecological Observatory Network, and the International Geosphere–Biosphere Program. Cyberinfrastructure would provide the data and resources for understanding ecological connectivity at the global scale and would entail closer integration of US (eg USGS NBII, NASA DAACs, Knowledge Network for Biocomplexity) and global (eg Committee on Earth Observation Satellites International Directory Network, the Global Observing Systems Information Center, the International Oceanographic Data and Information Exchange) networks. An initial step toward networking ecological sites globally is being made with the development of a common web interface that allows information about sites to be made easily accessible to users (www.p2erls.net).

Conclusions

Given the availability of existing global networks, this is an exciting time for ecological research. Together, these networks provide a platform for continental-scale research with their legacy data, site-based knowledge and expertise, and, in many cases, shared concerns about the consequences of an ever-changing, increasingly connected world. A framework focused on connectivity provides a way to integrate the information being collected in a way that both facilitates and shows the necessity for collaborative research across multiple scales. The integrated understanding of an increasingly connected world derived from a global network of networks is essential for the continental-scale science needed to understand and forecast the causes and consequences of anthropogenic global environmental change.

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The spread of invasive species and infectious disease as drivers of ecosystem change

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Invasive species, disease vectors, and pathogens affect biodiversity, ecosystem function and services, and human health. Climate change, land use, and transport vectors interact in complex ways to determine the spread of native and non-native invasive species, pathogens, and their effects on ecosystem dynamics. Early detection and in-depth understanding of invasive species and infectious diseases will require an integrated network of research platforms and information exchange to identify hotspots of invasion or disease emergence. Partnerships with state and federal agencies that monitor the spread and impacts of invasive species and pathogens will be critical in developing a national data and research network that can facilitate a full understanding of the resulting effects on ecosystems and society. Citizen science can also play a role; individuals can report new invasions, record phenological changes associated with invasions or disease outbreaks, and can participate in efforts such as the Breeding Bird Survey, which may reveal long-term biotic change following species invasions and disease spread. The ecological and societal impacts of invasive species and pathogens differ across gradients of climate and land use, and in the presence of global climate change may exacerbate both their propagation and impacts. Understanding the interactions of invasive species, disease vectors, and pathogens with other drivers of ecosystem change is critical to human health and economic well-being.

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The increased connectivity of the global human population has amplified the frequency and effect of biological invasions and disease outbreaks. New trade routes among previously disconnected countries (Aide and Grau 2004) as well as enhanced transportation technology (eg airplanes and barges) have increased both the frequency and magnitude of invasions and potentially deadly disease outbreaks worldwide. In addition, land-use and climate change interact with human transportation networks to facilitate the spread of invasive species, vectors, and pathogens from local to continental scales (Dukes and Mooney 1999; Sakai *et al.* 2001; Benning *et al.* 2002; Patz *et al.* 2004; Smith *et al.* 2007). The introduction of non-native species and range expansions of native species with changing land use and climate may have profound consequences for the ecosystems they occupy. Invasive species drive ecological dynamics at multiple spatial scales and levels of organization, through local and regional extinctions of native species (eg chestnut blight; Mack *et al.* 2000) and entire communities, shifts in native species richness and abundance (Parker *et al.* 1999), and altered fire regimes, water quality, and biogeochemical cycles (D'Antonio and Vitousek 1992; Vitousek *et al.* 1996; Strayer *et al.* 1999; Bohlen *et al.* 2004). Invasive species are the second leading cause (after human population growth and associated activities) of species extinction and endangerment in the US (Pimentel 2002). An estimated cost of non-native species in the US alone is over $120 billion annually (Pimentel *et al.* 2005). Because climate change and land use can exacerbate the spread and effects of invasive species across scales (Dukes and Mooney 1999; Simberloff 2000), identifying invasion and curtailing the spread of invaders is an enormous ecological and societal challenge (Lodge *et al.* 2006).

In a nutshell:

- Invasive species and infectious diseases are becoming more prevalent and widespread with increased connectedness and globalization
- Alien species are the second leading cause of extinction in the US and cost approximately $120 billion annually
- Disease vectors and pathogens are spreading across continents due to human transport, land-use change, and climate change
- To adequately understand and predict the spread of invasive species and disease, we must coordinate the many existing networks at local, regional, continental, and global scales
- Both observational and experimental approaches are required to fully understand the effects and impacts of invasive species and diseases and, more importantly, to understand the biotic and abiotic factors that enhance or diminish their effects

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Several recent reviews of invasive species and disease focus on modeling spatial spread (Hastings *et al.* 2005), species interactions and ecosystem processes (Lovett *et al.* 2006), evolutionary change (Strayer *et al.* 2006), and policy recommendations (Lodge *et al.* 2006). The objectives of this review are (1) to frame questions and hypotheses for linking regional and continental-scale processes that govern the spread and impact of invasive species and disease and (2) to highlight the need for a continental-scale network of sites for monitoring and predicting the spread and impact of invasive species and disease.

To adequately address the environmental and societal problems of invasive species and the spread of diseases, such as avian-dispersed H5N1 avian influenza or severe acute respiratory syndrome (SARS), we must develop a continental-scale network to: (1) monitor changes in the local and geographic distributions of invasive species and infectious disease (Peterson *et al.* 2003; Drake and Bossenbroek 2004); (2) predict the processes and environmental conditions that promote the spread of invasive species and disease vectors from individual sites to regions and the continent (Hufnagel *et al.* 2004); and (3) understand the long-term ecological and evolutionary responses to ecosystem invasion (Mooney and Cleland 2001; Strayer *et al.* 2006). A coordinated cyber-infrastructure, along with improved data portals, would enable a more effective integration of databases from state and federal partner agencies that monitor invasive species or infectious diseases (including the US Department of Agriculture, US Geological Survey, Centers for Disease Control, US Environmental Protection Agency, US Fish and Wildlife Service, National Parks Service, and US Department of the Interior). A national database on invasive species and vectors, as well as key environmental features to identify potentially suitable habitat, would help scientists to forecast the spread and effects of invasive species and of diseases (Ricciardi *et al.* 2000). A number of such networks currently exist, including the Global Invasive Species Information network, the Inter-American Biodiver-sity Information Network, the Non-indigenous Species Network, and the Non-indigenous Aquatic Species Network. A complete description of these networks can be found in Meyerson and Mooney (2007).

Because exotic species and disease spread encompass multiple scales of interacting biotic and environmental factors (Figure 1), it is necessary to carry out large-scale monitoring while conducting fine-scale experiments and observations. Understanding new species and pathogen introductions and subsequent invasion success requires an understanding of the transport vectors, the local environmental conditions, organismal ecology, and the population and community ecology of the organisms (Figure 1). This framework can only be successfully employed if it is designed with scale-specific hypotheses and questions.

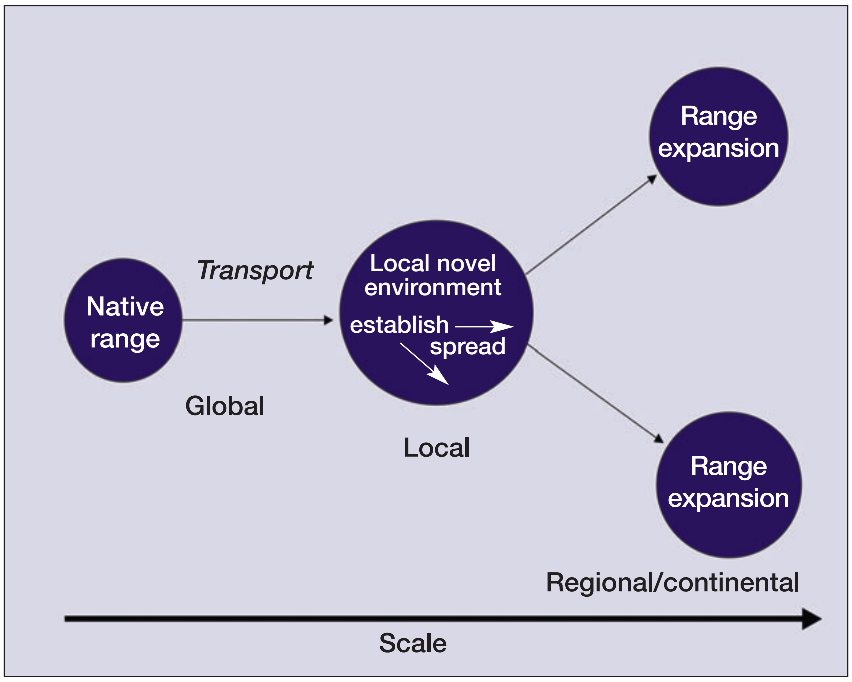

Figure 1. *Invasion sequence from left to right. Species and pathogens first move via a transport mechanism from their native range to a novel habitat (global scale). Once they have arrived in a novel environment, they may (1) not survive, (2) persist but fail to spread, or (3) begin to reproduce and expand their local distribution. Finally, as the population continues to increase due to available resources, and lack of competitors, predators, or parasites, the species or pathogen may begin to expand its distribution both regionally and continentally, resulting in multiple, discrete, expanding populations.*

Continental hypotheses and questions

The overarching questions that must be addressed include:

(1) What societal and environmental factors can we use to accurately forecast the spread of invasive species and infectious diseases globally and at continental and local scales?
(2) What are the population-, community-, and ecosystem-level causes and consequences of invasive species and infectious diseases, how do these vary across land-use and climatic gradients, and what suite of environmental variables predict these consequences?
(3) How will ecosystems and their components respond to changes in natural and human-induced effects, such as climate, land use, and invasive species, across a range of spatial and temporal scales? What is the rate and pattern of the responses?

Environmental measurements for invasive species and pathogens must be coordinated with continental-scale gradient initiatives on climate change (Marshall *et al.* [2008] in this issue), coastal instability (Hopkinson *et al.* [2008] in this issue), and land use/urbanization (Grimm *et al.* [2008] in this issue). Linking aquatic habitats (lakes and rivers) to terrestrial systems is essential, because invasive species are one of the most important drivers of

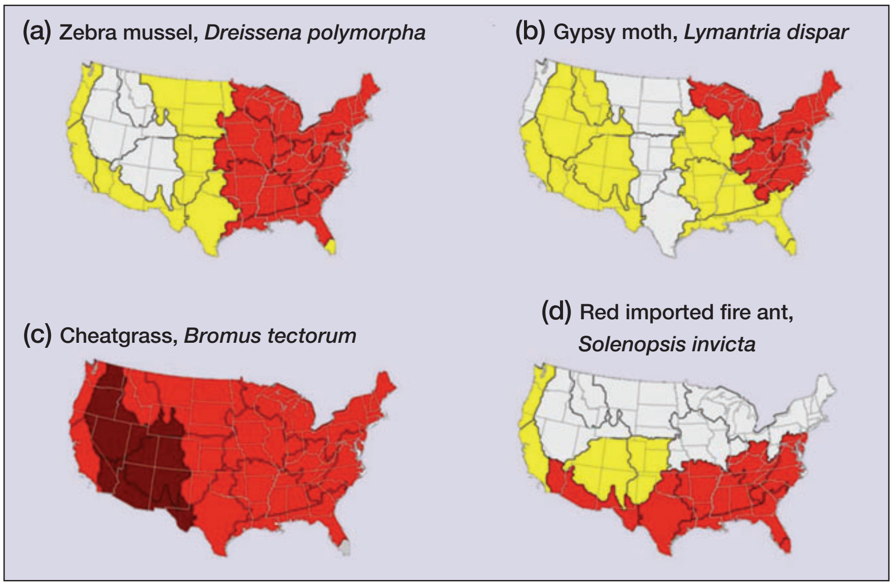

Figure 2. *Present (red) and potential (yellow) geographic ranges of four invasive species among NEON climate domains. (a) The potential range of* Dreissena polymorpha *includes southeastern Alaska. (b) Gypsy moths,* Lymantria dispar, *currently show a restricted range but are predicted to spread widely. (c)* Bromus tectorum *occurs in nearly all NEON climate domains, but its impact is greatest in three climate domains (dark red). (d) The potential range of* Solenopsis invicta *includes Hawai`i.*

biotic change in aquatic environments (Sala *et al.* 2000), and many terrestrial diseases and their hosts and vectors have links to aquatic systems (Williamson *et al.* [2008] in this issue). This is especially true as the connectedness among watersheds through human development increases the scale across which organisms can readily move (Peters *et al.* [2008] in this issue). Spatial coverage of monitoring will be greatly expanded through partnerships with several state and federal agencies.

New techniques for monitoring and forecasting the spread of invasions using remote sensing techniques will greatly extend the coverage of ground-based data (Asner and Vitousek 2005). Regional and continental-scale forecasting will also require data on human population densities, rates of land-use change, and the major transportation corridors connecting urban, recreational, and wildland areas. In addition, information on the pathways of species introductions and vectors of transport will be needed to prevent the introduction of non-native species and diseases (Kilpatrick *et al.* 2006). These include commerce in food and non-food plants and animals, shipping containers and ballast water, aircraft and shipping cargo areas, and intentional introductions by fish stocking, horticulture, and the pet trade (Lodge *et al.* 2006).

The general research questions listed above can be parsed into hypotheses that put infectious disease and the spread of invasive species into the context of increased connectedness, especially with respect to human development and climate change:

(1) Connectedness of plants, animals, goods, and people predict disease and invasive species emergence.
(2) Transportation vectors, land use, and climate interact to alter the mode, rate of spread, and effect of invasive species on natural and managed ecosystems.
(3) Diseases affect not only human health and welfare, but also ecosystem functions.

Testing these hypotheses requires two kinds of measurements to understand and forecast the occurrence and effects of invasive species and infectious disease: (1) population, community, and ecosystem effects, and (2) rates and modes of spatial spread. Given the wide range of possible responses to species invasions, several kinds of measurements at multiple spatial scales with nearly continuous data collection are needed. The development of the National Ecological Observatory Network (NEON) should go far toward fulfilling these needs.

A few examples of invasive species with current or potential continental-scale distributions serve to illustrate how each invasive species varies among climate regions (as defined by NEON) in terms of their potential spread and in their effects on local ecosystems. The invasion of the zebra mussel (*Dreissena polymorpha*) into the Great Lakes and its subsequent spread to major river systems of the Midwest has altered abiotic factors, such as water transparency, nutrient cycling, and benthic habitat structure, as well as biotic factors, such as food-web structure, the bioaccumulation of contaminants, and the diversity of native freshwater mussels (Strayer *et al.* 1999). The presence of this invader has also led to the introduction of a roundworm parasite (*Bucephalus polymorphus*), which is responsible for dramatic impacts on cyprinid freshwater fish, the parasite's intermediate host. Models that use abiotic variables to predict the potential range of zebra mussels project further spread into river systems in virtually all of the eastern climate domains, and distinct focal points of invasion in the Pacific and southwestern US (Drake and Bossenbroek 2004; Figure 2a). Recreational boating will probably act as the transport vector, linking geographically isolated mussel populations.

Outbreaks of the gypsy moth (*Lymantria dispar*) cause regional defoliation in eastern forests, especially in stands containing oak, aspen, or birch. Short-term impacts include effects on light penetration, nitrogen (N) cycling, and primary production; the long-term effects of defoliation are unclear, but could involve interactions with other stressors such as pathogens or atmospheric N deposition (Lovett *et al.* 2006). The potential range encompasses most forested regions of the US (Figure 2b);

spatial spread is characterized by slow diffusion coupled with pulsed, long-distance establishment via anthropogenic transportation, ahead of the invasion boundary (Johnson *et al.* 2006).

Cheatgrass (*Bromus tectorum*) has established in all 50 states and is invasive in arid and semi-arid shrublands and grasslands of the Intermountain West (Figure 2c). As with other annual-grass invaders, cheatgrass promotes fire, creating a positive feedback cycle favoring further invasion, the exclusion of native plants, and loss of carbon (C) to the atmosphere (D'Antonio and Vitousek 1992; Young and Allen 1997). Cheatgrass is also of low nutritive value, and its unpredictable and ephemeral primary production threatens livestock.

The red fire ant (*Solenopsis invicta*) is increasing its range in the southern US (Figure 2d). Fire ant invasion is especially important in disturbed areas, where it causes declines in invertebrate biodiversity and nesting success of birds (Holway *et al.* 2002). Fire ants affect pollination mutualisms, kill livestock, and affect human health, and lead to pesticide use in attempts to control the ants. Invasive ants alter ecosystem processes by displacing native ant species that construct deep, long-lived nests, rich in organic matter (MacMahon *et al.* 2000). Climate change will probably extend the range of fire ants northward (Morrison *et al.* 2004).

Many other consequences to ecosystem functions and services occur with regionally important species. The following are just a few examples. Invasion of the N-fixing tree, *Myrica faya*, into nutrient-poor soils in Hawai`i affects the trajectory of plant community development and biogeochemical cycling (Vitousek *et al.* 1996). Salt cedar (*Tamarix* spp) invasions of riparian zones alter stream flow, increase evaporative water loss and soil salinity, and negatively affect native stream invertebrates and riparian plants (Morisette *et al.* 2006). Non-native earthworms (*Lumbricus* spp) in northern temperate forests have accelerated decomposition and C flux from soil, altered N and phosphorus (P) cycling, changed soil micro-organisms and invertebrates, and even facilitated the invasion of understory plants (eg garlic mustard, *Alliaria petioloata*; Bohlen *et al.* 2004). The rapid invasion of the African tulip tree (*Spathodea campanulata*) into Puerto Rico has affected nutrient cycling and decomposition processes (Crowl *et al.* 2006; Abelleira Martínez and Lugo in press) and is predicted to spread throughout moist, subtropical, and warm temperate (sensu Holdridge 1967) areas in the southeastern US and the Caribbean. This species restores forest conditions on abandoned lands, thus promoting the re-establishment of native tree species (Abelleira Martínez and Lugo in press), and its dominance after invasion lasts about 50 years (Lugo 2004). The regional expansions of native species as a result of climate change or land-use change can also transform ecosystems. For example, desertification of perennial grasslands by the expansion of desert shrubs, such as mesquite (*Prosopsis glandulosa*) and creosotebush (*Larrea tridentata*), alters hydrologic and biogeochemical cycling, decreases biodiversity and range productivity, and facilitates invasions by non-native plant species (Peters *et al.* 2006). In Puerto Rico, mesquite restores forest conditions in degraded dry forest lands and promotes the re-establishment of native species on these lands (S Molina Colon pers comm).

An integrated network of ecological research sites spanning the North American continent would also allow us to develop a comprehensive understanding of the ecological effects of invasive or emerging disease vectors and pathogens. While the majority of initial "detections" of new regional pathogens will undoubtedly come from public health workers and wildlife specialists, a network of established, long-term research sites would provide the resources and "continuity" to increase our understanding of the life cycles and ecology of targeted vectors and pathogens. For example, Lyme disease was first discovered in the northeastern US in 1977 (Steere *et al.* 2004), but it took nearly 25 years of ecological research to develop an understanding of the complex interactions between the bacterium, vector, and hosts in the environment (Randolph 2004; Tsao *et al.* 2004; Ostfeld *et al.* 2006). In the American Southwest, a new strain of hantavirus (*Sin Nombre* hantavirus; Nichol *et al.* 1993) emerged in 1993, and once CDC scientists had identified the deer mouse (*Peromyscus maniculatus*) as the host (Childs *et al.* 1994), ecologists in New Mexico were able to immediately apply the results of ongoing studies to explain the ecological causes of the disease outbreak (Parmenter *et al.* 1993). Subsequent long-term research at sites in Montana, Colorado, New Mexico, Utah, and Arizona (Mills *et al.* 1999) have led to a detailed understanding of the evolution and ecology of rodent–virus dynamics (Yates *et al.* 2002) and the development of remote sensing-based predictive models (Glass *et al.* 2002, 2006, 2007).

How can measurements be used in predictive models for forecasting?

The actual spread of invasive species has been forecast using analytical models based on diffusion, network, and gravity models that incorporate human-mediated transport (Hastings *et al.* 2005; Johnson *et al.* 2006; Bossenbroek *et al.* 2007). Another approach is to use climate-based niche models that predict the suitable habitats and potential geographic ranges of invasive species (Peterson *et al.* 2003; Drake and Boessenbroek 2004; Morisette *et al.* 2006). For many species, airborne and satellite imagery can be used to parameterize models on the spatial spread of invasive species. Remotely sensed data and embedded sensor networks can provide the detailed environmental measurements that are needed for more predictive climate- or habitat-based niche models of potential species distributions across ecosystems, regions, and geographic ranges. Ground-based measure-

Figure 3. *(a) Operating out of a mobile laboratory, (b) field biologists sample blood and fleas from deer mice* (Peromyscus maniculatus) *for plague, hantavirus, and* Bartonella *in northern New Mexico.*

ments are also needed to provide information on prevalent abiotic and biotic conditions, data required for predictions of ecosystem invasibility and impacts. Measurements of the spread and ecosystem effects of invasive species must be obtained across gradients of climate, land use, and human population densities. Gradient-based measurements will be critical in developing models to predict the interacting effects of invasive species, climate change, and land-use change. Benning *et al.* (2002) show how landscape models can be used to predict changes in the distribution of native birds in Hawai`i, in response to the interacting effects of climate warming, deforestation, and invasion by avian malaria.

Models that forecast disease outbreaks require data on host, vector, and pathogen populations and their environments, including spatial distribution, demography, and behaviors. Data on abiotic and biotic environmental conditions are also needed, since host or vector populations may show time lags in response to climate or food supply (Jones *et al.* 1998; Yates *et al.* 2002). New modeling approaches incorporate climatic variability (Altizer *et al.* 2006), hydrologic dynamics (Shaman *et al.* 2002), or host diversity (Keesing *et al.* 2006) as drivers of disease risk. For this new generation of models, the goal will be to develop the predictive forecasting capability that will use past and current environmental information to assess future infection risks in plants, wildlife, and humans.

Multispecies approaches to monitoring invasive species and pathogens

The numbers of non-indigenous species of plants, birds, and fishes vary predictably across the US, according to native species richness and human population density (Stohlgren *et al.* 2006). Native plants and birds are characterized by high species richness in the eastern and southwestern US, with higher values in coastal and mountainous areas. Native fish species richness is highest in the large drainages of the Mississippi and Ohio River Valleys, which are also hotspots of diversity for other freshwater taxa, such as unionid clams. Areas of high native richness and high human population size and road densities are strongly associated with non-indigenous species occurrence and invasion success (Stohlgren *et al.* 2006). Broad-scale patterns lead to a continental-scale selection of sampling sites based on: (1) areas of high native and non-indigenous species richness, (2) gradients of urban to wildland areas within regions, and (3) areas with invasive species that have impacts over broad geographic ranges. The third criterion is important because the impacts of a particular invasive species or infectious disease may depend on local ecosystem characteristics and the presence of other non-indigenous species (Parker *et al.* 2005).

Collection of data on infectious diseases requires other considerations. Once an invasive or emergent disease has been identified, sampling locations should be selected within suitable habitats for hosts, vectors, and pathogens. Additional vertebrate and invertebrate species, as well as aquatic fauna and terrestrial plants, will need to be monitored at the appropriate sites to adequately quantify pathogen transmission. Sampling must include inter-site locations across continental-scale gradients of temperature, elevation, and latitude. At local sites, appropriate habitats should be sampled by rapid mobile units (Figure 3) to assess pathogens in particular vectors and reservoir host species. For example, mosquitoes will need to be sampled across North America, as their distributional ranges cover vast regions of latitude, longitude, and elevation (Figure 4); however, at the local site, mosquitoes should be sampled along river and stream corridors, ponds and lakes, and in selected wetlands, irrigated fields, and urban drainage fields at core sites and along inter-site gradients.

Migratory birds, which represent a major reservoir hosts for some human diseases, can be live-captured during both breeding seasons and migratory movements and sampled for introduced viruses such as H5N1 influenza, West Nile, or other potential invasive pathogens. Mosquito populations can be assayed for potential invasive pathogens that cause human disease, such as malaria, Rift Valley fever, and dengue. Pathogens and hosts of aquatic fauna (eg shellfish, fish, amphibians) will also need to be sampled with both regional and continental patterns in mind. Similarly, field-sampling efforts for targeted plant diseases will necessarily be directed toward locations along gradients where host plants exist. The continental-scale approach will provide comparative data on disease dynamics among and within different ecosystems under varying environmental conditions, which will allow the further refinement of predictive models.

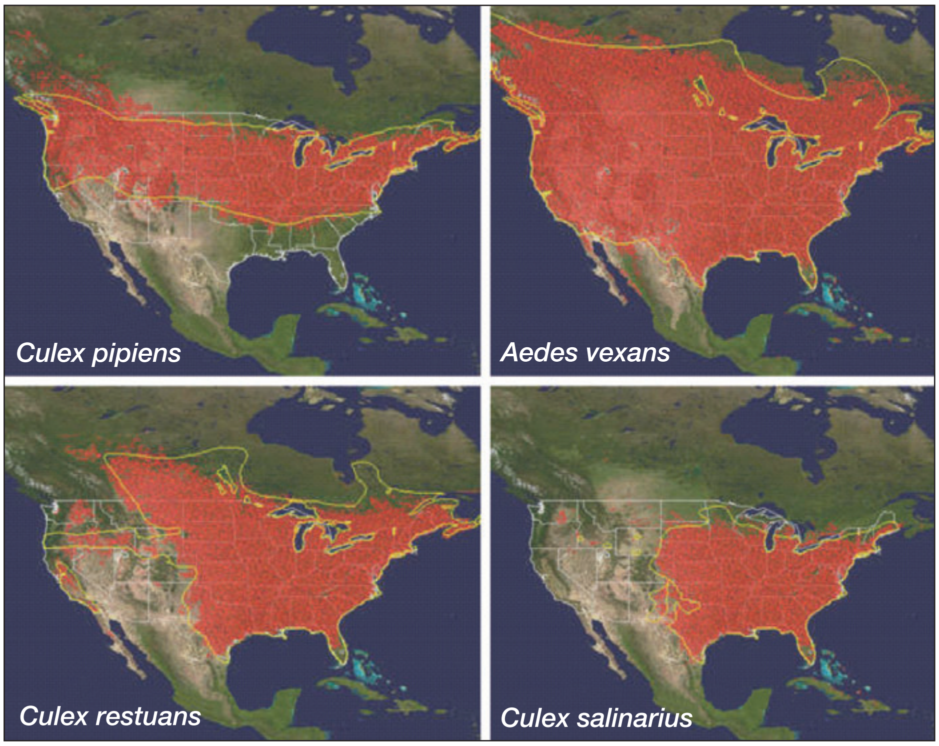

Figure 4. *The geographic distribution of mosquito disease vectors,* Culex *spp and* Aedes vexans*, in North America.*

Conclusions

Invasive species and new diseases pose the same problem; each is a new species with the potential to modify the existing structure and function of ecosystems and the ecosystem services upon which people rely. Furthermore, some new pathogen species can directly impact human health. Thus, the addition of new species (invasives or diseases) to an ecosystem can affect the well-being of people, whether through economics or health. Many species already present influence human well-being positively or negatively, and we must be concerned that the introduction of new species may result in novel biotic interactions and modify existing ones in the current ecosystems (natural and managed; Figure 5).

Whether introduced species impact ecosystem services, the economy, or human health, we need to understand species interactions and the consequences to local ecosystems. Traditional epidemiology has often ignored the ecological perspective, but it largely corresponds to host–pathogen or host–vector–patho-gen population ecology. There-fore, local biotic understanding is necessary to assess (and reduce) the impacts of invasive species and disease.

While new species exert their impacts at the local biotic scale, we know that, in many cases, their establishment, their effects, and the success of countermeasures can vary from one location to another. We therefore need to examine the problem at much greater geographical scales (Figure 5), using networks of study sites to address a series of questions.

First, what causes the variability between locations in the establishment of, impact of, and success of countermeasures against new species? This knowledge will im-prove our ability to predict which locations will be susceptible to invasion by a particular species, the potential effect on the local ecosystem and people, and what the most effective local countermeasures will be. Detailed ecological study will be required at a variety of locations selected a priori, to address how specific species characteristics (eg growth, reproduction, survival) under different local "driver" values (eg gradients of temperature, moisture, elevation, human activities) influence biotic interactions and, thereby, human well-being. Too often in the past, answers to these questions have emerged slowly or not at all, because sampling has been implemented in limited locales, based on specific observations, and are not adequate to measure landscape-level patterns.

Second, how do new species' propagules arrive at a location? This requires knowledge at regional and global scales, so we can assess how a particular new species becomes available for invasion, what controls invasion rates, and how preventative measures can be developed. Only at this larger scale can invasion fronts and their movements be monitored and studied (Hengeveld 1989). This requires specific biotic information such as species characteristics related to propagule numbers emerging from surrounding populations and vagility, but today this may largely be a function of external "drivers" such as markets (eg plant and animal trades) and transportation systems (eg regional connectedness and modes of transportation providing "friendly" transient environmental conditions for propagules). Compared to the previous question, above, the network of study sites addressing this question needs to contain a greater number of uniformly distributed sites, because proximity to propagule sources, rather than "driver" differences, is the key factor.

Finally, how might invasibility change in the future, and among different classes of species? Obviously, answers to

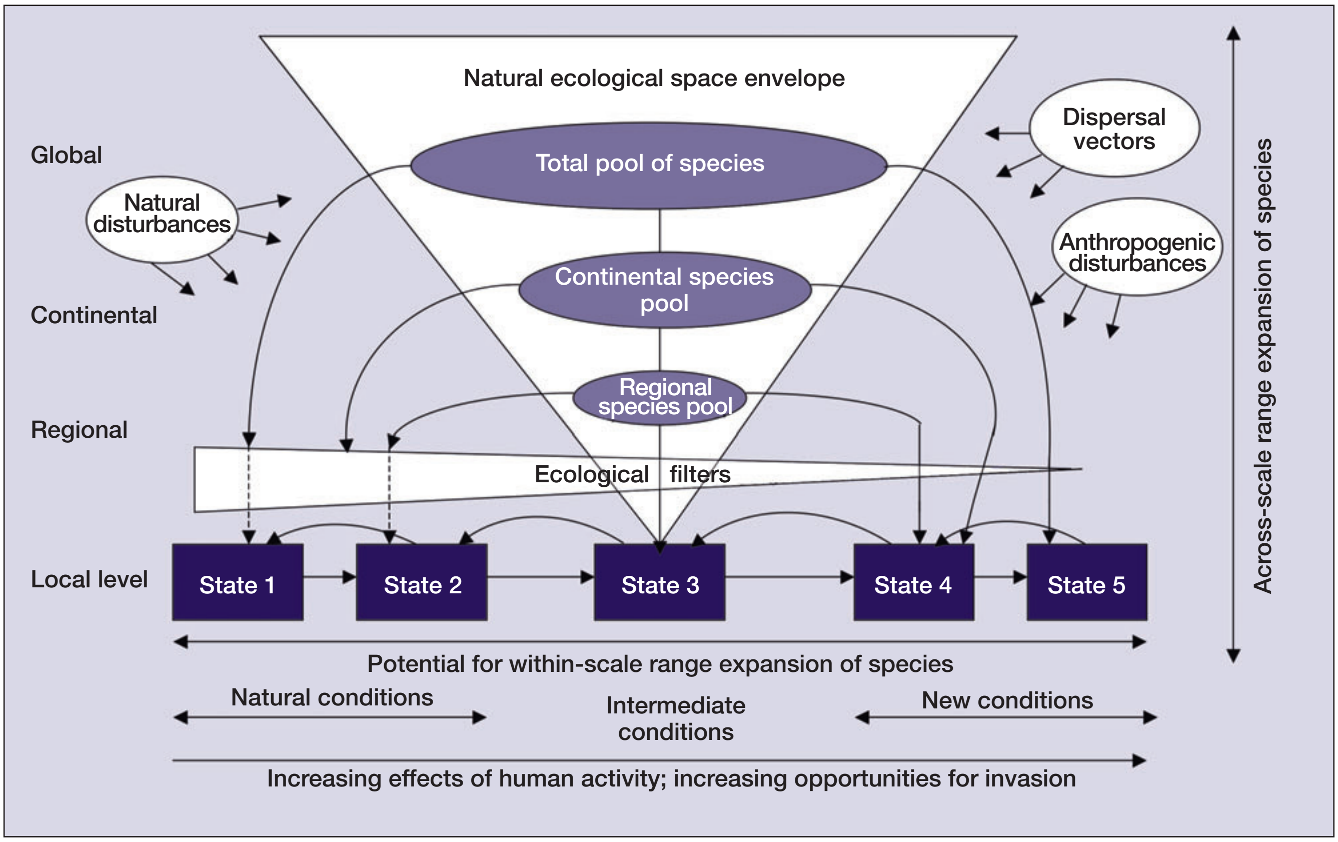

Figure 5. *Summary diagram illustrating the factors that influence the spread of invasive species and diseases across geographic and ecological space and their interaction with native species in the formation of new species assemblages (novel ecosystems sensu Hobbs* et al. *2006). The lines with arrows represent the movement of species and dashed lines represent negligible rates of species movement. Geographic space is represented vertically from global to local scales, while ecological space is represented by the inverted triangle. There are more species and diversity of ecological conditions at global than at local scales. However, natural and anthropogenic disturbances, as well as many other vectors, disperse species across geographical and ecological space. For a species to actually invade an ecosystem (represented at the local level by boxes, each at a different state of maturity along a gradient of human activity: states 1 and 2 without measurable human effects, states 4 and 5 exposed to heavy human activity, and state 3 an intermediate level of anthropogenic impact), it must pass through an ecological filter. We expect that the ecological filters that determine the success of an invasion are weaker to the right of the diagram and, thus, are conducive to greater invasion success in ecosystems of states 4 and 5 than in ecosystems of states 1 and 2. Under extreme anthropogenic impact, new conditions develop, which in turn select for novel ecosystems dominated by invasive species.*

this question require knowledge from the previous two questions. The first question provides insight into how future conditions may influence which species are able to invade, how their presence could affect ecosystems and human well-being, and how best to develop countermeasures. The second question provides insight into where and when these invasions might take place. However, additional information is required to assess how the spatial matrix and "drivers" are changing over time in terms of, for example, climate and human activity. Therefore, a network of locations needs to be distributed across the landscape in a manner that allows us to assess not only current conditions, but how they may change in the future. It is the combination of information from the first and second question, in the spatial context of temporally changing conditions, that will provide us with the ability to forecast.

Each hierarchical level of question presented above poses different challenges to the number, spacing (location), and measurements considered in network design. Consequently, a network designed to address one hierarchical level is useful, but only slightly greater design effort may permit all hierarchical levels to be addressed and synergisms to emerge when cross-hierarchical questions are simultaneously addressed. These considerations will allow network construction to better address issues in invasion and disease ecology, and better enable networks to predict and forecast emerging threats.

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Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes

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Recent advances in our understanding of the importance of continental- to global-scale connectivity among terrestrial and aquatic ecosystems make consideration of aquatic–terrestrial linkages an urgent ecological and environmental issue. Here, we describe the role of inland waters as sentinels and integrators of the impact of humans on terrestrial and aquatic ecosystems. The metabolic responses of lakes and streams (ie the rates at which these systems process carbon) are proposed as a common metric to integrate the impacts of environmental change across a broad range of landscapes. Lakes and streams transport and alter nutrients, contaminants, and energy, and store signals of environmental change from local to continental scales over periods ranging from weeks to millennia. A carefully conceived and well-integrated network that includes monitoring and experimental approaches to terrestrial–aquatic connectivity is critical to an understanding of basic ecosystem-level processes and to forecasting and mitigating future environmental impacts at the continental scale.

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Aquatic ecosystems are particularly vulnerable to environmental change and many are, at present, severely degraded. Ironically, this vulnerability makes aquatic ecosystems good sentinels and integrators of environmental change at scales ranging from local (eg extinctions of endemic species) to global (eg climate change).

In a nutshell:

- Inland waters supply essential ecosystem services to human populations by providing water for drinking, bathing, industry, and recreation; they are also a hotspot of biodiversity, but their integrity is threatened
- Inland waters are sentinels and integrators of terrestrial and atmospheric processes, because they are integrally linked with changes in the terrestrial landscape and are highly connected through the transport and storage of water, nutrients, contaminants, and energy
- The metabolism of inland waters provides a fundamental metric of cross-ecosystem connectivity that responds to natural and human disturbances across scales, from changes in riparian zones to global-scale climate change
- A continental-scale network, involving both observational and experimental research in inland waters, is necessary to understand human impacts on terrestrial and aquatic ecosystems and the critical services that they provide

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Freshwater fish, mussels, and crayfish are among the most highly endangered groups of animals on the planet (Ricciardi and Rasmussen 1999), and rates of decline in biodiversity are higher for freshwater than for either terrestrial or marine organisms (Jenkins 2003). Even some of the most pristine alpine lakes and streams, which provide drinking water supplies for much of the world, are threatened (Figure 1). As a result, Americans spend billions of dollars annually to avoid consumption of tap water – over 5 billion gallons of bottled water were purchased in 2000 (US EPA 2003). "No swimming" signs warn of unsafe waters and harmful algal blooms along beaches that border lakes, rivers, reservoirs, and coastal oceans. Consumption warnings have been issued for fish in 44 states in the US, due to levels of mercury contamination that can cause neurological and developmental problems in children (Driscoll *et al.* 2007). Oxygen depletion in both lakes and coastal environments has caused extended anoxic "dead zones", where fish kills and mortality of other benthic organisms are common (Dybas 2005). Water-borne pathogens, including the bacterium that causes cholera (*Vibrio cholerae*), have been found in recreational waters such as the Chesapeake Bay (Huq *et al.* 1983), and severe and potentially fatal intestinal parasites such as *Cryptosporidium parvum* are estimated to be present in up to 55% of surface waters and 17% of drinking water supplies in the US (Rose *et al.* 1991). This vast array of largely human-induced problems in lakes and streams necessitates a continental-scale network to effectively address such environmental challenges.

Concurrently, global climate change is transforming aquatic ecosystems (Poff *et al.* 2002). The period of winter ice cover on lakes and rivers is a week or two shorter

Figure 1. *Arikaree Glacier and its meltwater alpine lake in the headwaters of a protected watershed in the Rocky Mountains of Colorado. This watershed serves as a municipal water supply for the Boulder metropolitan area. Such alpine lakes have very short ice-free growing seasons, low nutrients, and very little vegetation in the surrounding terrestrial watershed, making them very vulnerable to contaminants entering from the surrounding airshed. Such high elevation environments are also experiencing some of the most rapid responses to climate change.*

than it has been in the past (Magnuson *et al.* 2000) and, within a few decades, the Arctic Ocean is likely to be completely ice-free, with potentially severe feedbacks for global climate regimes (Johannessen *et al.* 1999). All of these are signs that the aquatic ecosystems on which we depend are undergoing serious changes at local, regional, and continental scales.

The most important questions are: how do we begin to understand the causes of such large-scale changes in aquatic ecosystems, and how can we forecast and prepare for those changes? These shifts in our aquatic ecosystems are driven largely by human impacts on terrestrial and atmospheric systems. While human hydraulic modifications, channelization, water abstraction, and impoundments also contribute greatly to the alteration of inland waters, here, we address ecological issues related to three primary large-scale environmental forcings: changes in climate, land use, and nitrogen deposition (Peters *et al.* [2008] in this issue). We use these three major forcings as a framework to outline the role that inland waters play as sentinels and integrators of environmental change in terrestrial and atmospheric processes. For clarity, we refer collectively to flowing waters (eg streams, rivers, wetlands) as "streams", and to standing waters (eg ponds, lakes, reservoirs) as "lakes". Thus, we use "lakes and streams" to include all continental inland waters except groundwater. While there are a number of water-quality networks that monitor inland waters in the US, these networks focus on pollutants and primary nutrients. Long-term estimates of metabolism in streams indicate seasonal, daily, and annual changes in rates (Roberts *et al.* 2007). Thus, occasional measures of concentrations do not provide enough information to protect the integrity of the process-based ecosystem services provided by lakes and streams on continental scales (Dodds 2006b).

The role of lakes and streams as sentinels and integrators

Just as the circulatory and respiratory systems give medical doctors critical information on personal health, the metabolic and other ecosystem characteristics of streams and lakes that supply and receive water from the surrounding landscape provide critical information on the health of terrestrial and atmospheric processes. The most integrative signals of environmental change are likely to be found at the lowest points in the landscape (WebFigure 1). Whether it is the cycling or fate of nutrients, organic carbon, contaminants, or pathogens, the water that drains these systems provides critical signals of past and present disturbance that, in turn, provide the foundation for forecasting future impacts. In addition to being the most critical resource for human civilization, water is also one of the primary conduits transporting contaminants and pathogens across the landscape. Water is the lifeblood of the biosphere, and lakes and streams are central to any continental-scale approach designed to understand environmental change.

We argue that metabolism should be a primary response variable if we are to understand the impacts of climate change, land use, and nitrogen deposition (Table 1). Metabolism refers to the rates at which whole ecosystems, or their component parts, process carbon through primary production and respiration (WebFigure 2). Metabolism is perhaps the most fundamental of ecosystem processes and is influenced directly by changes in climate, land use, and atmospheric deposition. Lakes and streams consume carbon dioxide and produce oxygen through photosynthesis, and reverse this process through respiration and fermentation of organic carbon. The majority of the respired carbon in many streams and lakes derives from the surrounding terrestrial ecosystems (Cole *et al.* 2006). Climate change, land use, and nitrogen deposition can alter ecosystem metabolism in fundamental ways: lakes and streams are integrators, sentinels, and, to some extent, regulators of environmental change. For example, whole-lake metabolism is directly influenced by the relative balance of external loadings of nutrients and dissolved organic carbon (Hanson *et al.* 2003). Changes in these loadings due to alterations in climate, land use, or atmospheric deposition will influence the metabolic balance of lakes. Understanding the resistance, resilience, and directional responses of lakes and streams to environmental change is also crucial to effective management.

Aquatic ecosystems integrate local watersheds that vary across the landscape. Even within the same geographic region, lakes and streams in nutrient-poor watersheds are unproductive, oligotrophic, blue-water systems, while those nearby, containing numerous wetlands and forests, may be heterotrophic, stained, brown-water systems, and those in enriched watersheds are productive, autotrophic, green-water systems. This variation gives lakes and streams a wide range of potential responses. Not only do they signal environmental change at local scales, but also at regional to continental scales. For example, acidification of lakes and streams in the northeastern US is driven by mineral acids released into the atmosphere in the Midwest. Similarly, the Mississippi River transports nutrients, contaminants, and sediments from the northern edges of the US to the Gulf of Mexico (Figure 2). Watersheds provide a convenient unit with relatively well-defined boundaries to compare responses across the continent, and a common set of experimental approaches can be used to understand aquatic processes across diverse systems (Peterson *et al.* 2001; Webster *et al.* 2003).

Lake and stream metabolism can help us to understand climate-change impacts

Temperature

Climate change is complex, but one of the most fundamental metrics is temperature. Temperature controls many ecological processes, including ecosystem metabolism. Generally, an exponential increase in metabolic rates occurs with increasing temperature until inhibiting temperatures are reached (Brown *et al.* 2004). One of the best integrators of regional temperature is the timing of ice cover on lakes and rivers, because long-term records are available for this metric. A 1.2˚C warming of air temperatures in northern temperate regions has led to freeze dates that average 5.8 days later and ice-breakup dates that average 6.5 days earlier per 100 years (Magnuson *et al.* 2000). These temperature changes alter lake phenology in ways that may upset aquatic food webs by causing a mismatch between the seasonal timing of populations of primary consumers and their food resources (Winder and Schindler 2004). Reductions in ice cover also create a positive feedback mechanism that accelerates warming, due to the greater absorbance of solar radiation by open water in comparison to snow and ice. A connected network that provides continuous measurements of temperature, including the timing of ice cover, will provide us with a powerful metric of climate change and of ecosystem function at regional scales.

Carbon cycling

Understanding the fate of organic carbon in aquatic ecosystems is central to understanding the dynamics of climate change. Terrestrial carbon enters streams and is altered and transported by streams. Some carbon is metabolized (respired or altered chemically), additional carbon may be added by photosynthetic organisms, and some may be deposited in stream and river sediments (Hall 1995; Mulholland 1992). Streams move both organic and inorganic carbon into lakes, where there is substantial additional processing. Although lakes and reservoirs comprise less than 2% of the surface area of the planet, more organic carbon is deposited in their sediments than in the world's oceans (Dean and Gorham 1998) and lakes receive about twice as much terrestrially derived C as do the oceans (Cole *et al.* 2007). The terrestrial subsidies of organic carbon make most lakes net heterotrophic: ecosystem respiration exceeds gross primary production and, as a result, these lakes release more CO_2 to the atmosphere than they consume (Cole *et al.* 1994). Most organic carbon in the water column of lakes and streams is in the form of dissolved organic carbon (DOC). In lakes, DOC influences metabolism by decreasing water transparency and reducing the amount of sunlight available for photosynthesis, as well as altering thermal structure by decreasing the mixing depth. DOC provides a source of fixed carbon for microbial food webs, driving microbial respiration and fermentation in lakes and streams. DOC also absorbs potentially damaging UV radiation, resulting in photobleaching and release of more bio-

Table 1. Examples of sentinel responses of lakes and streams to three primary environmental forcings

Environmental forcings	*Sentinel response variables*	
Climate	***Specific responses***	***Responses to all three forcings***
Temperature	Period of ice cover Mixing of depth (L)	Water transparency (ultraviolet radiation [UVR], photosynthetically active radiation [PAR])
Precipitation	Water level	
		Temperature
Land use		
Erosion	Suspended solids Sedimentation rates (L)	Oxygen profiles
Nutrients	Nutrients (N, P, Si)	Conductivity, pH
Contaminants	Contaminants (PAH*, PCB**, atrazine)	DOC, DIC
		Algal pigments
Nitrogen deposition	Nitrogen concentrations	Chlorophyll (algal biomass) Phycocyanin (cyanobacteria)
	Nitrogen cycling rates	
		Paleolimnological (eg diatoms)
		Palynological (ie pollen)
		Indicators of anoxic metabolism (generation of methane and nitrous oxide)

Notes: Forcing is largely through the effects of the independent variables on terrestrial and atmospheric systems. In addition to the listed response variables, weather stations would monitor incident UVR, PAR, air temperature, relative humidity, and wind speed and direction. (L) = lakes only; (S) = streams only; * = polycyclic aromatic hydrocarbons; ** = polychlorinated biphenyls.

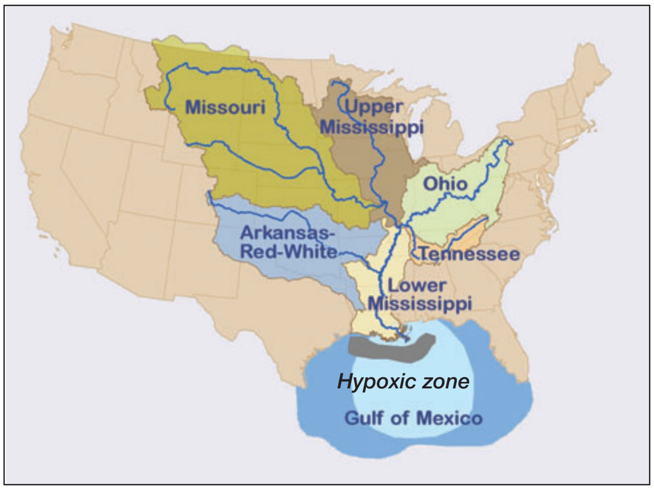


Figure 2. *Map showing how the Mississippi River interconnects the majority of states in the US. Continental-scale approaches to examine environmental impacts of this important river will require a network of monitoring and experimental sites, coordinated at the local (state), regional (major watershed basins shown), and continental (whole Mississippi River) scales.*

logically available carbon and CO_2. All of these processes connect terrestrial, atmospheric, and aquatic processes in ways that alter freshwater metabolism.

DOC concentrations in lakes and streams have changed dramatically in recent decades. Through the early 1990s, anthropogenic acidification and drought drove trends of decreasing DOC and increasing UV transparency in lakes in Europe and North America (Yan *et al.* 1996; Schindler *et al.* 1997). In recent years, even more striking increases in DOC have been observed in rivers draining peatlands (Freeman *et al.* 2004). DOC concentrations have doubled over the past 16 years in New York's Hudson River (Findlay 2005) and, in the past two decades, DOC has increased by an average of 91% in lakes and streams in the UK (Evans *et al.* 2006).

The prevailing hypothesis for recent increases in DOC in Europe and North America holds that human-dominated landscapes are beginning to recover from acidification following the passage of clean air legislation (Evans *et al.* 2006; Monteith *et al.* 2007). In contrast, more remote aquatic systems, such as those in the Yukon, have shown trends of decreasing DOC export that may signal destabilization of organic carbon stored in soils, potentially contributing to increased atmospheric CO_2 (Striegl *et al.* 2005). Human activities in riparian zones and immediate watersheds can also alter the carbon balance, nutrient inputs, and extent of heterotrophy through effects on the metabolism of lakes and streams (Carpenter *et al.* 1998b). Net biomass accumulation has ceased in forests of the northeastern US in recent decades (Likens 2004), but we do not know whether this is connected to observed trends in DOC. A continental- to global-scale observatory that monitors metabolism in lakes and streams and their connectivity with terrestrial systems is needed. Changes in dissolved oxygen, DOC, DIC, nutrients, and other variables can be used to address the causes and consequences of these widespread changes in terrestrially derived organic carbon (Table 1). Concurrent experimental manipulations of streams and lakes will allow us to better understand mechanisms that underlie the critical regulatory processes and thus mitigate problems ranging from acidification of inland waters to climate-change impacts.

Lake and stream metabolism can help us to understand land-use impacts

Land-use changes alter the metabolism of lakes and streams through the loading of sediments, nutrients, and contaminants, and can be measured in lakes with sediment traps. Anthropogenic loading of nitrogen and phosphorus to lakes and streams leads to eutrophication and degradation of water quality, including harmful algal blooms in coastal as well as inland waters (Smith *et al.* 2006). Nutrient loading can have considerable economic and ecological effects in freshwaters (Carpenter *et al.* 1998a; Dodds 2006a), one of the most serious being depletion of oxygen in deeper waters and the consequent development of "dead zones" in both lakes and coastal regions, often resulting in extensive fish kills (Dybas 2005).

While commonly used pesticides and herbicides may affect lake and stream metabolism through their effects on primary producers (Seguin *et al.* 2001), they also cause endocrine disruption in humans and wildlife. For example, atrazine, the most commonly used herbicide in the US, can induce sex changes in frogs at levels 30 times lower than EPA's safe drinking water standards, and 40 times below levels found in rainwater in agricultural regions of the US (Hayes *et al.* 2002). Thus, both streams and rainfall can transport these contaminants across the continent. Effects may be even more serious with exposure to multiple pesticides (Hayes *et al.* 2006). Water-borne pathogens, including the human protozoan parasites *Cryptosporidium parvii* and *Giardia lamblia*, are also widespread due to increased activity of humans, livestock, deer, geese, and other wildlife in the watersheds that drain into lakes and streams (Jellison *et al.* 2002; Brookes *et al.* 2004). Connectivity is thus provided not only by streams, but also by wildlife migration. Many of the receiving waters serve as municipal drinking water supplies. These toxic contaminants and pathogens may influence lake metabolism indirectly by altering primary production or the activities of consumers, including discouraging human recreational use and fishing.

Metabolism of lakes and streams is also altered by changes in the large regional- to continental-scale airsheds that deposit nutrients and contaminants to downwind areas (Likens and Bormann 1974). Atmospheric deposition can lead to nitrogen enrichment, acidification, and accumulation of mercury and toxic organic compounds. Atmospheric deposition of mercury derived from coal-burning power plants accumulates in aquatic food webs, leading to fish consumption advisories, such as those that have been implemented in most of the US

(Driscoll *et al.* 2007; Evers *et al.* 2007). One of the most insidious mechanisms of contamination is the "alpine distillery" – the atmospheric fractionation by which toxic compounds produced at low elevations are concentrated in seemingly pristine alpine lakes and streams (Figure 3). The toxicity of many of these contaminants may be mitigated by the presence of DOC (Oris *et al.* 1990; Weinstein and Oris 1999), but alpine lakes and streams are notoriously low in DOC due to the sparse vegetation within their watersheds. Atmospheric deposition further highlights the importance of landscape position in determining the effects of natural and human disturbances on inland waters (Kratz *et al.* 1997; Webster *et al.* 2000). For example, in Wisconsin, neighboring lakes sharing the same geological and climatic setting can differ substantially in size, color, and metabolism because of subtle differences in the lakes' positions in the local to regional hydrologic system. Lakes high in the flow system receive most of their water directly from the atmosphere, whereas those lower in the flow system receive additional water and solutes from streams or groundwater (Kratz *et al.* 2006).

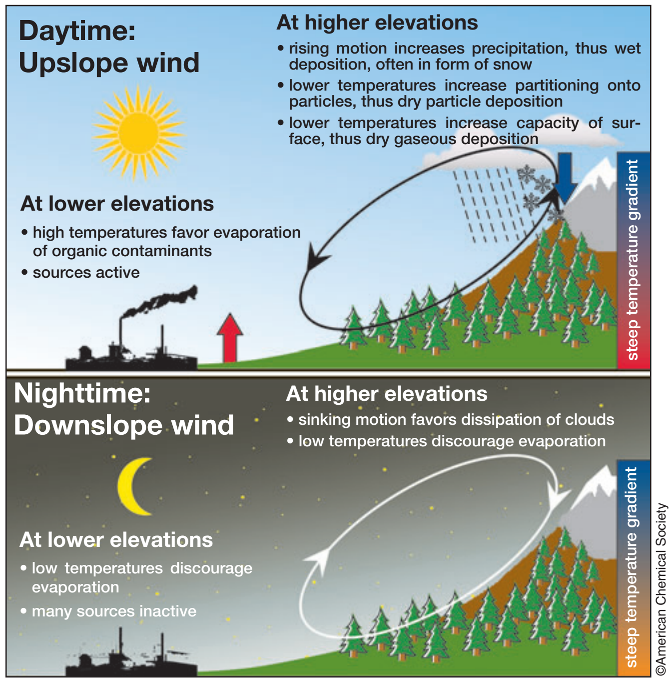


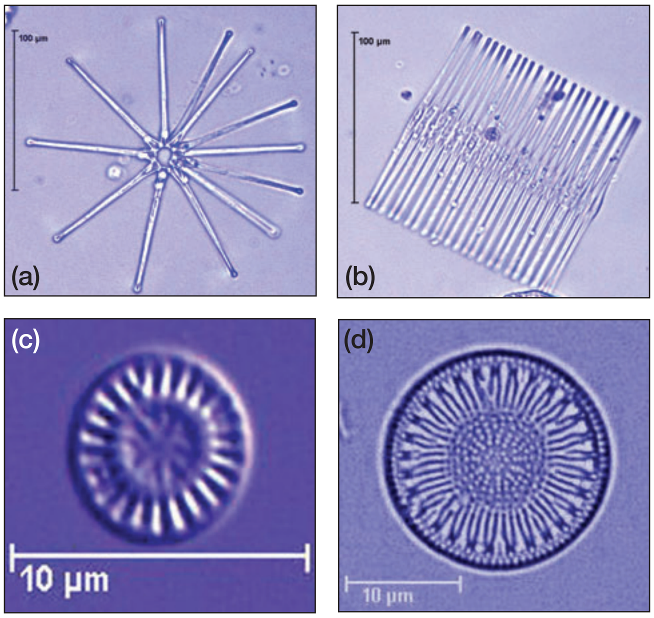
Figure 3. *The alpine distillery by which atmospheric fractionation concentrates contaminants in the pristine alpine lakes and streams that often provide drinking water supplies for major populations around the world. Modified with permission from Daly and Wania (2005).*

■ Lake and stream metabolism can help us to understand nitrogen deposition

Human activities have now more than doubled the input of fixed nitrogen to the world's ecosystems, with severe consequences for nutrient cycling, acidification, and biodiversity of terrestrial and aquatic ecosystems, as well as human health (Vitousek *et al.* 1997; Driscoll *et al.* 2003; Townsend *et al.* 2003). On a global basis, fixed nitrogen is one of the most important nutrients limiting primary productivity in both terrestrial and marine ecosystems, although phosphorus is often co-limiting (Vitousek *et al.* 1997; Elser *et al.* 2007). Heterotrophic metabolism is important in many freshwater systems (eg Dodds 2006a), and can also be limited by nitrogen (Tank and Dodds 2003). When nitrogen deposition exceeds about 7 kg ha^{-1}, some soils become saturated (Aber *et al.* 2003) and nitrogen is exported into streams, lakes, and coastal oceans. There is a direct correspondence between human population within a watershed and nitrogen output into rivers (Peierls *et al.* 1991). Lakes and streams are thus sentinels of nitrogen saturation in terrestrial systems, as well as important sites of nitrogen retention (Peterson *et al.* 2001), and can themselves become saturated with nitrogen (Bernot and Dodds 2005). Fertilization of experimental plots has shown that nitrogen deposition can stimulate increases in DOC export from soils to aquatic systems (Schmidt *et al.* 2004), and metabolic processing of DOC inputs in streams is tightly linked to nitrogen availability (Bernhardt and Likens 2002). Deposition of fixed nitrogen can also induce changes in diatom community structure in inland waters (Saros *et al.* 2005). The US Clean Air Act Amendments of 1990 have helped to reduce sulfate-induced acidification, but nitrogen deposition, which is less well regulated, continues to increase, and will likely replace sulfates as the primary source of anthropogenic acidification within the next decade (Likens 2004). Thus, measurements of nitrogen (and phosphorus), as well as DOC, pH, and dissolved oxygen, can provide information on N deposition-induced metabolic changes in lakes and streams (Table 1).

■ Connectivity between lakes, streams, and terrestrial ecosystems

Peters *et al.* (2008, in this issue) argue for integration of measurements and understanding of ecological connectivity over space and time. In all but the most xeric landscapes, lakes and streams are sentinels, providing a spatially connected framework that ties together the terrestrial landscape. Streams transport water and materials to and from the surrounding landscape, while the metabolism of lakes and streams integrates the consequent signals of environmental change over time. In contrast, migratory fish, such as salmon, can bring nutrients up from marine environments into rivers and other low-nutrient aquatic and terrestrial ecosystems at higher elevations (Naiman *et al.* 2002; Schindler *et al.* 2005). In addition to the integration and spatial connectivity provided by metabolic responses of these inland waters to changes in climate, land use, and nitrogen deposition, lakes provide integration and connectivity over longer time periods, through signals deposited in their sediments, such as shifts in tree pollen, diatom frustules, and organic carbon content (Table 1). The extensive connectivity of lakes and streams also provides a conduit for



J Erickson and J Saros, University of Maine Climate Change Institute

Figure 4. *Diatoms are microscopic algae that serve as primary producers and food for consumers in many lakes and streams. Diatoms also provide signals of environmental change, through the silica cell walls (frustules) they leave behind after they die, in the sediments of lakes. With their differential sensitivity to environmental change, diatom species present in sediments help scientists to estimate historical changes in a wide range of environmental conditions, including acidification, temperature, and drought. Time intervals that can be resolved range from as short as a decade to thousands of years. For example, (a)* Asterionella formosa *and (b)* Fragilaria crotonensis *are increasing in abundance in alpine lakes, due to increases in nitrogen deposition. (c)* Discostella stelligera *and (d)* Cyclotella bodanica *have shown rapid changes in abundance in the sediments of alpine and Arctic lakes for as yet unexplained reasons. Combining such paleolimnological records with palynological (pollen) records permits us to extend the timeline of our understanding of environmental change in not only lakes and streams, but in terrestrial ecosystems as well.*

both waterborne pathogens and invasive exotic species to enter the landscape, with consequences that translate to costs in billions of dollars per year (Crowl *et al.* [2008] in this issue).

Peters *et al.* (2008, in this issue) also emphasize the need for making connections between short- and long-term dynamics, as well as for a mechanistic level of understanding to enable the prediction of future conditions never before experienced in Earth's history. This requires linking experimental and modeling approaches with long-term dynamics, as assessed by a spatially connected network. Lakes and streams have particularly well-defined boundaries and their metabolism is usually driven by populations of microscopic organisms with very short generation times. These characteristics make freshwater systems unusually responsive to environmental change and amenable to experimental manipulation. When short-term ecological experiments and long-term paleoecological and palynological (pollen) records are used in concert, inland waters can link ecosystem dynamics across time scales ranging from days to millennia and simultaneously elucidate the mechanisms of change (Saros *et al.* 2003, 2005; Figure 4). These long-term records provide critical information on the resistance and resilience of ecosystems to human-induced change.

Table 2. Questions and hypotheses for two complementary approaches to using lakes and streams as sentinels and integrators of changes in response to the three primary environmental forcing variables: climate, land use, and nitrogen deposition

Question	*Core hypotheses*
Based on interaction scales: How will chronic nutrient inputs (N or P), higher probabilities of extreme events (eg droughts and floods), and simplification of food webs (eg loss of consumers) impact the resistance and resilience of metabolism, nutrient cycling, and nutrient retention by lakes and streams?	**H1: Resistance and resilience of ecosystem functioning** Productivity, respiration, nutrient cycling, and retention are jointly determined by frequency of extreme hydrologic events (droughts, floods), rate of nutrient loading, and food web structure.
	H2: Time scales of ecosystem feedbacks and regime shifts Long-term nutrient loading and increased frequency of hydrological disturbance interact to promote irreversible "regime" shifts that alter resistance and resilience of ecosystem function to droughts and floods (hydrologic disturbance).
	H3: Spatial scales of response Resilience and recovery of ecosystem functioning over large (continental) scales will vary with regional context, including local species composition and diversity, climate, and hydrological disturbance regime.
Based on environmental forcing: How do changes in climate, land use, and invasive species alter lake and stream metabolism and, consequently, ecosystem services, through biogeochemical, biodiversity, and hydro-ecological responses?	**H1: Climate change** Alters ecosystem metabolism and phenology by altering organic matter loading in lakes and streams, as well as the thermal structure and extent of anoxia in lakes.
	H2: Changes in land use Alter ecosystem metabolism by changing nutrient, contaminant, sediment, and organic matter loading.
	H3: Invasive species Alter ecosystem metabolism by changing aquatic community structure and biomass and, hence, water transparency.

Where do we go from here?

Both observational and experimental approaches must be driven by core questions and hypotheses that can be addressed with common metrics across a wide variety of landscapes. We propose that lake and stream metabolism is a key metric (Table 2). To date there is little systematic, ongoing measurement of aquatic ecosystem metabolism across North America or any other continent. While this single ecosystem property is unlikely to provide information on subtle ecosystem effects, such as extinction of already rare species, sub-lethal toxic effects, and alterations in community structure, it is the most basic measurement of ecosystem function. Strong continental gradients in precipitation, temperature, nitrogen deposition, and human land-use patterns (Peters *et al.* [2008] in this issue) will guide the design of observational work. Long-term, networked sites located strategically across these gradients can be used to assess the responses of lake and stream metabolism and to monitor transport of contaminants, pathogens, and invasive species (Crowl *et al.* [2008] in this issue). Episodic weather events, including hurricanes, floods, and droughts will provide "natural experiments" to help tease out the causes and consequences of change.

Conclusions

Lakes and streams are key sentinels and integrators of environmental change in the surrounding terrestrial landscape. In addition to providing water for drinking, bathing, recreation, and commercial and industrial use, inland waters provide many other ecosystem services to both humans and wildlife. Lakes and streams are the arteries and veins of the surrounding landscape. While current, long-term monitoring programs have provided key insights that would not otherwise have been possible (Lovett *et al.* 2007), they are not in and of themselves adequate for the task at hand. A more sophisticated and interconnected continental-scale network is essential to address the rapid, large-scale environmental changes that we are experiencing across the planet.

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Forecasting effects of sea-level rise and windstorms on coastal and inland ecosystems

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We identify a continental-scale network of sites to evaluate how two aspects of climate change – sea-level rise and intensification of windstorms – will influence the structure, function, and capacity of coastal and inland forest ecosystems to deliver ecosystem services (eg carbon sequestration, storm protection, pollution control, habitat support, food). The network consists of coastal wetland and inland forest sites across the US and is representative of continental-level gradients of precipitation, temperature, vegetation, frequency of occurrence of major windstorms, value of insured properties, tidal range, watershed land use, and sediment availability. The network would provide real-time measurements of the characteristics of sea-level rise and windstorm events and would allow an assessment of the responses of wetlands, streams, and inland forests at spatial and temporal scales associated with sustainability of ecosystem services. We illustrate the potential of this approach with examples of hypotheses that could be tested across the network.

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Two components of climate change likely to have a disproportionate effect on the biosphere are rising sea level and increased frequency and intensity of windstorms (eg hurricanes, typhoons, extra-tropical storms). Within the context of ecosystem connectivity, the effects of climate change will extend from the coastal zone throughout much of the continent and will vary regionally. These regional effects will be modified by human activities, particularly those that influence the delivery of sediments and nutrients from watersheds. They will, in turn, affect the functioning of coastal wetlands and barrier islands and their capacity to buffer continental landmasses from the ravages of intense windstorms and sea-level rise (Bortone 2006; Cahoon 2006; Greening *et al.* 2006; Stanturf *et al.* 2007).

In a nutshell:

- We identify a continental-scale network of coastal and inland sites to evaluate how two aspects of climate change, sea-level rise and intensification of windstorms, will influence the structure, function, and capacity of coastal and inland forest ecosystems to deliver services
- The network is representative of continental-level gradients of precipitation, temperature, vegetation, frequency of occurrence of major windstorms, value of insured properties, tidal range, watershed land use, and sediment availability
- The precision and extended scale of this network would enhance our capacity to model climate-change scenarios in association with other landscape changes that disrupt ecosystem services for long periods, including land use, soil movements such as landslides, sediment delivery to the coast, forest fragmentation, and flooding

Globally, sea level has risen between 10 and 25 cm over the past century, primarily because of a net input of water (ie eustatic sea-level rise or ice melt; Rahmstorf *et al.* 2007) and thermal expansion (ie steric sea-level rise or water warming). This rate of rise is an order of magnitude greater than that of the past several millennia (Douglas *et al.* 2001). Observed trends in relative sea level (level of the sea relative to local landmass) vary across the North American continent (Figure 1), however, from very large increases along the Gulf coast (exacerbated by tectonic subsidence, sediment compaction, and oil and gas extraction; eg Morgan 1970; Penland and Ramsey 1990; Morton *et al.* 2003) to decreases in parts of the Pacific Northwest (plate subduction and uplift). Changes in Alaska are thought to be the result of tectonic uplift (eg Aleutians) or crustal rebound following glacial melting. The projected sea-level rise for the mid-Atlantic is 10–31 cm by 2030 and 40–102 cm by 2095 (IPCC 2001); the rate of rise for the past 20 years (to 2006) is 25% faster than the rate in any 20-year period over the past 115 years (Rahmstorf *et al.* 2007).

Coastal wetlands and upland forests are also impacted by intense, ocean-originating storms. These are mainly hurricanes and typhoons that build on energy from the release of heat stored in seawater, but also include more

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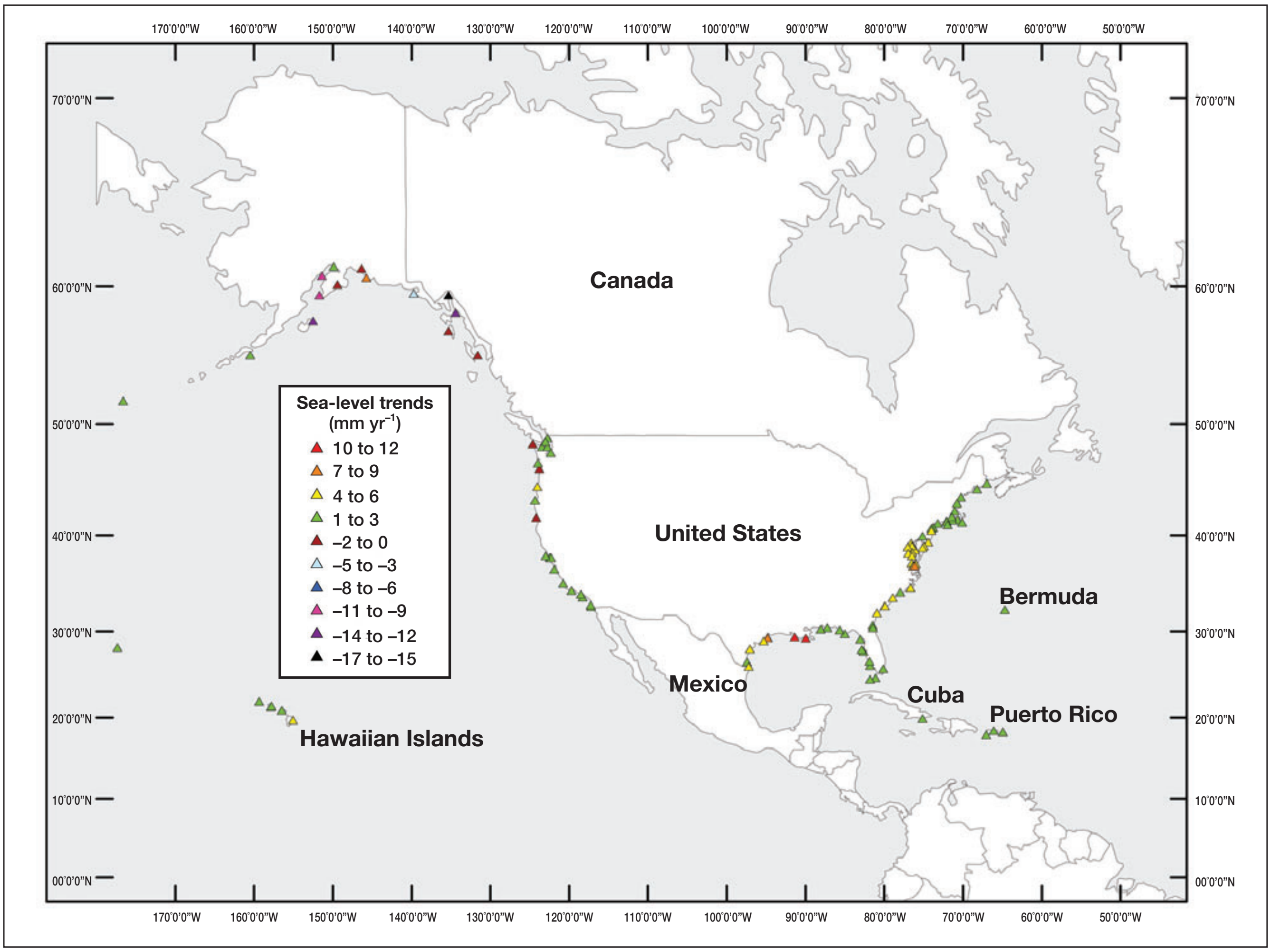

Figure 1. *Sea-level trends around portions of North America (http://tidesandcurrents.noaa.gov/sltrends/slrmap.html). Modifications courtesy of J Carpenter.*

frequent extra-tropical cyclones that affect both the east and west coasts of the US. Extra-tropical cyclones form from poleward-moving tropical systems or from strong temperature gradients between air masses (baroclinic storms, such as nor'easters). Hurricanes control climate by dissipating energy from low latitudes to high latitudes and can move enormous quantities of water from the low latitudes into the middle and high latitudes. Much is known about the characteristics and forecasting of hurricanes and extra-tropical storms (Diaz and Pulwarti 1997; Goldenberg *et al.* 2001; Webster *et al.* 2005; Holland and Webster 2007). Both types of storms, and the surf they create, are predicted to increase in intensity due to global warming (IPCC 2007). Hurricane frequency in the North Atlantic basin may also increase (Holland and Webster 2007), but a scientific consensus for this prediction has still not developed (IPCC 2007; Bengtsson *et al.* 2007 a,b; Boissonnade *et al.* 2007; Vitart and Doblas-Reyes 2007). Hurricanes change in character with geography, typically becoming weaker as they move northward or inland, but historic hurricane tracks have shown effects as far inland as the Great Lakes (Neumann *et al.* 1978). A large fraction of the US mainland, all of Puerto Rico, and the US Virgin Islands are currently exposed to 4- to 35-year return periods for hurricanes (Figure 2; Neumann *et al.* 1978), which translates to 2–16% probabilities of being in the direct path of a hurricane in any given year (Crossett *et al.* 2004). Storm events vary from year to year, with interannual and decadal oscillations associated with El Niño–Southern Oscillation (ENSO; El Niño/La Niña sea-surface warming) and other climatic oscillations.

Climate exerts broad-scale control on coastal intertidal wetlands (marshes and mangroves) that varies through interactions with local-scale processes (Michener *et al.* 1997; Figure 3). Sea level sets the minimum elevation for an emergent wetland, but land use and ocean use, as well as storm disturbance, can affect the physical and biological processes that deliver sediment to the coasts and allow material to accumulate. Although inland forests are not directly affected by sea-level rise (SLR), there is a connection in that coastal wetland loss increases the vulnerability of inland ecosystems (and humans) to storm disturbance. It is therefore critical to develop a predictive understanding of the ability of coastal wetlands to persist in the future, particularly in light of the continental-scale processes and feedbacks that control this response.

The wind and rain generated by ocean-originating storms affect upland forests in multiple ways. The immediate effects of hurricanes on forest structure and nutrient cycling have been described (eg Everham and Brokaw 1996). However, the ecological, hydrological, geomorphological, and geochemical effects of hurricanes, intense rainfall, and related windstorms are not well understood (Walker *et al.* 1991, 1996). There is even less knowledge about inland impacts and long-term continental effects of hurricane passage, particularly under a regime of increased storm intensity (eg Gerald *et al.* 2006; Slutzman and Smith 2006; Knight and Davis 2007; Stanturf *et al.* 2007).

Predicted alterations to coastal wetlands and inland forests will affect their ability to provide ecosystem services in the future. Coastal intertidal wetlands provide services unrivaled among natural environments, including waste assimilation, food-web support for fish and shellfish, and wildlife habitat. Ecosystem services derived from inland forest habitats, such as carbon sequestration, nutrient retention, maintenance of water quality, and prevention of sediment erosion, can be severely affected by storm events. Addressing questions of climate effects is important because, over the long term, these events shape the structure, function, and species composition of coastal ecosystems at local to regional scales. These changes will also affect the habitability of the coastal zone, which is one of the most developed areas on Earth; more than 53% of the US population now lives in coastal counties, which comprise only 17% of the total land area of the US (Crossett *et al.* 2004). In addition, we do not have a good understanding of the connection that exists between storm events and disease vectors (not limited to human diseases), in terms of the numbers of individuals transported, changes in strains, transmission rates, virulence, and the possibility of spread of invasive non-native species.

Here, we provide a conceptual framework and guidelines for development of a network of coastal observatories to understand and predict the effects of SLR and major storms on coastal wetlands and forests. Monitoring programs have been proposed previously to explore the relation between SLR and barrier island erosion (Leatherman *et al.* 2003). A predictive understanding can be reached through a comparative analysis, across major continental gradients, of climate, topography, geology, pollution, land use, latitude, biogeographic province, tidal range, human habitation, SLR, and hurricane frequency. By combining observations from across a continental network of sites with experimentation and modeling, we would be able to address the following types of scientific questions:

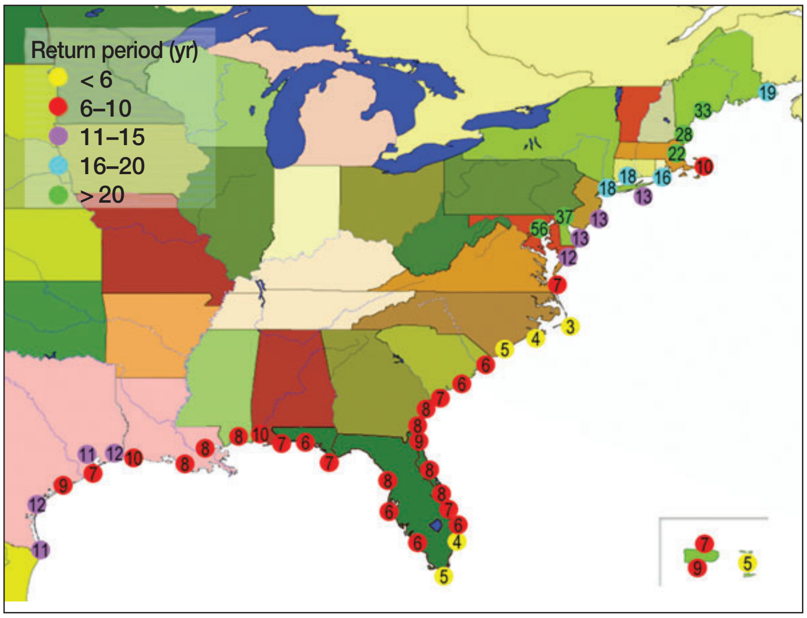

Figure 2. *Return period for a Category 1 or stronger hurricane on the US east coast and the Caribbean (Blake* et al. *2006, with data for Puerto Rico and US Virgin Islands courtesy of C McAdie, National Hurricane Center).*

Status and trends: What are the continental-scale trends and predictions for SLR and coastal wetland persistence? What are the transcontinental effects of, and responses to, hurricanes and other intense storms? How will the vulnerability of human property and institutions to wetland loss and intense storms in the coastal zone compare and change across gradients in population density, geology, and topography?

Ecosystem processes: What ecosystem attributes affect the ability of an area to withstand changes in storms or sea level, and how do these feed back into climate cycles? What factors control the limits to vertical accretion of coastal wetlands and the rate and type of regeneration in forests? How do changes in intensity, spatial distribution, and frequency of intense windstorms affect ecosystem attributes? How do changes in sea level and storm dynamics interact with the spread of invasive species?

Ecosystem services: How will changes in sea level and storms alter the capacity of coastal wetlands and inland forests to deliver ecosystem services to humans and contribute to sustainability? What are the continental-scale implications of coastal wetland loss for carbon sequestration, commercial fisheries production, and wildlife habitat? How will storm damage in inland forests (soil erosion, water retention, nutrient export) affect coastal systems?

Human interactions: How will regional changes in the export of water, nutrients, and sediments interact with climate change to affect the ability of

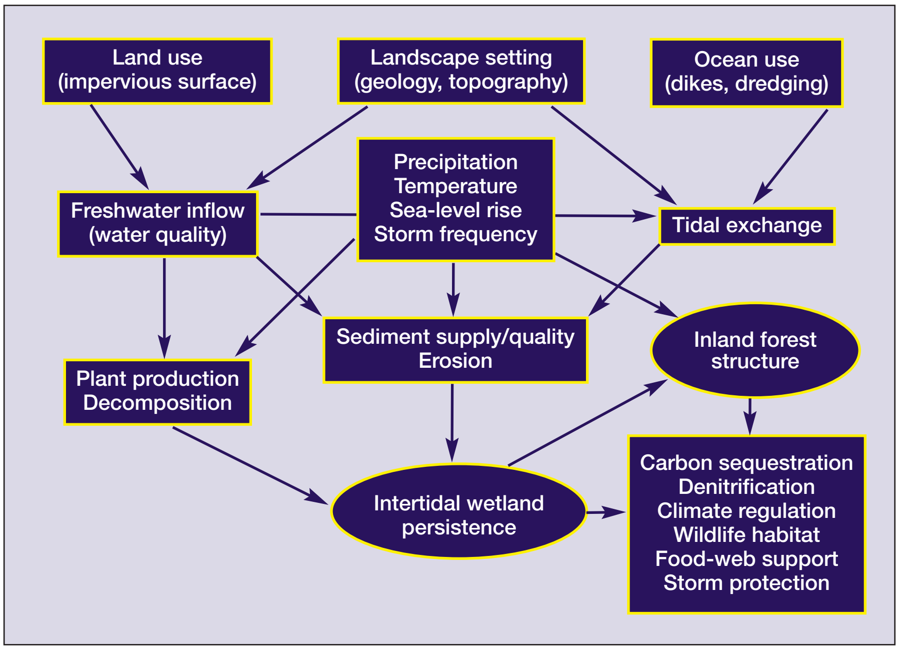

Figure 3. *Conceptual model of factors influencing the persistence of coastal wetlands, the ecosystem services they provide, and their link to inland forests.*

intertidal wetlands to maintain areal extent and elevation relative to SLR? How will wetland loss, increased frequency of intense windstorms, and increased destruction of human property affect the displacement of people and their settlement patterns at the continental scale? Will SLR and storm dynamics render currently settled coastal areas uninhabitable or uninsurable?

■ Why a continental-scale analysis is required

At present, we lack the knowledge needed to predictively map responses of coastal and upland systems to SLR and intense windstorms. The controlling factors do not vary linearly along the coast or across the country; rather, most factors vary at regional and even local scales. In addition to variations in the rate of SLR, there are also strong spatial variations in other drivers, including tidal range, marsh flooding frequency, and sediment delivery. While the frequency of storm occurrence follows a relatively smooth gradient, forest stature and structural complexity differ greatly across the continent. Thus, we can expect tremendous variability in ecosystem response at all spatial scales. It is not enough to study one site and thereby understand outcomes across the country: a doubling of the hurricane probability in Massachusetts would equal the current probability in Puerto Rico, but there is no reason to expect that New England temperate forests would respond in the future in the same way that subtropical moist forests respond at present.

Patterns at broad scales can be driven by fine- to broad-scale processes, so that understanding and predicting continental-scale dynamics requires analysis across a range of scales. For example, the deltaic wetlands of the Mississippi River are influenced by broad-scale patterns of climate (including hurricanes), topography, geology, and land use that control sediment erosion and transport to the coastal zone. They are also influenced by a combination of small-scale patterns, such as channelization and levee construction along the river and through wetlands, which control the distribution and deposition of sediments. The present and future condition of Louisiana's wetlands at the mouth of the Mississippi will reflect the interaction of these broad- and fine-scale processes. We can develop this example further from the perspective of hurricanes, where the spatial extent of coastal wetlands and their condition will directly influence the potential storm damage to inland regions. There are feedbacks as well: the greater the disruption of this coupled human–natural system along the Gulf coast, the greater the disruption at broader scales (eg as people are evacuated and oil refineries shut down). Thus, to fully understand the effects of SLR and intense storms on coastal systems, we must examine patterns and processes across a range of spatial scales.

■ Approach to developing a continental-scale network

Here, we apply a new strategy for experimental design (Peters *et al.* [2008] in this issue) to address the effects of SLR and storm disturbance. The design strategy consists of three steps.

Step 1: Identify continental-scale gradients

We advocate establishing a network of sites across four gradients within 200 km of the continental margin of North America. The four gradients include two latitudinal gradients (one along the east coast and another along the west coast) anchored by tropical and Arctic regions, and two coast-to-inland gradients (one on the east coast and one on the Gulf of Mexico coast; Figure 4). For coastal wetlands, these gradients subsume the standard coastal biogeographic provinces of the US.

Step 2: Define gradients for key ecosystem drivers and identify sites spanning these gradients

Coastal gradients

A combination of several gradients dictates coastal wetland characteristics and their likely response to SLR. The coastal sites network must therefore include the full range of conti-

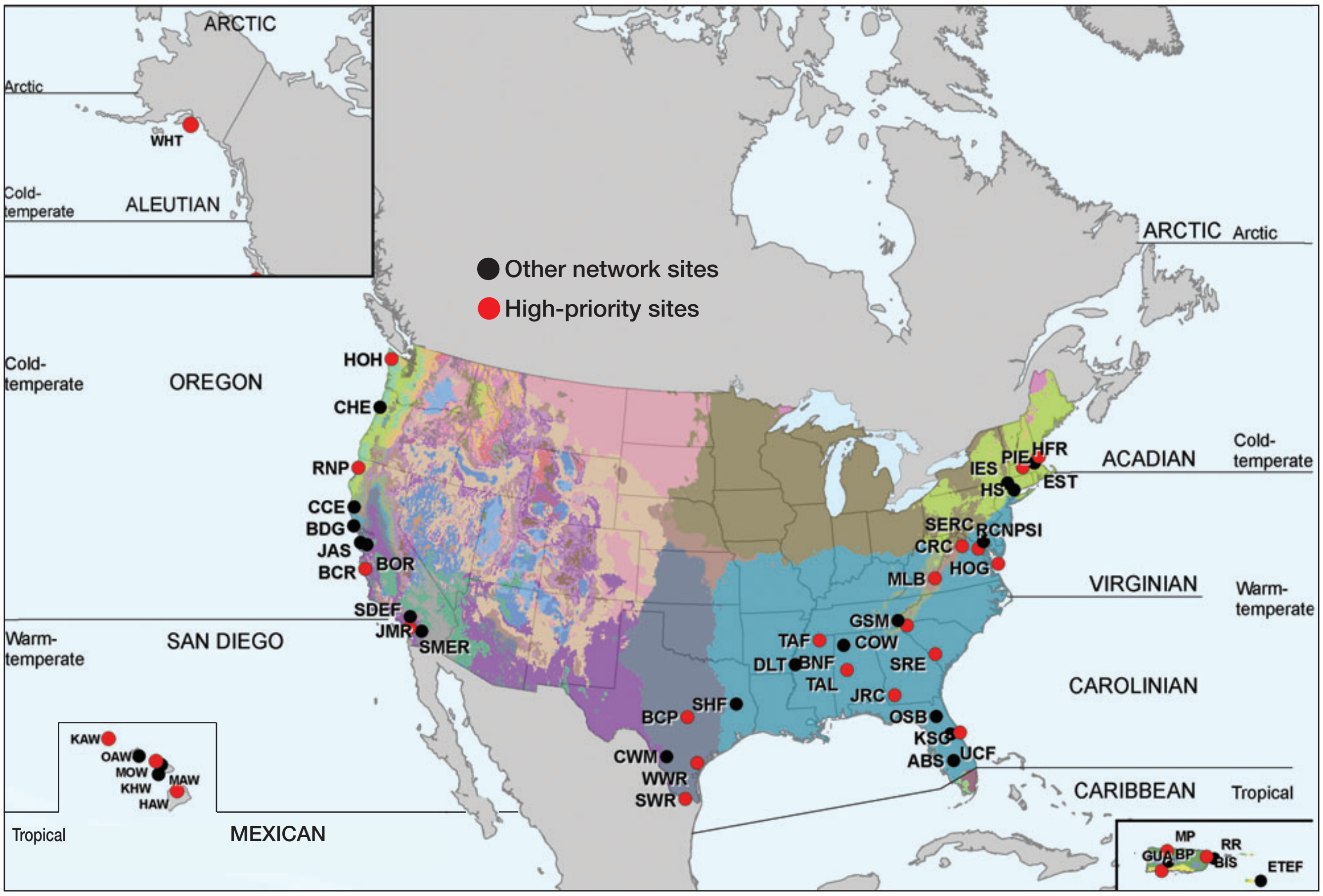

Figure 4. *The distribution of continental ecoregions and coastal biogeographic provinces and climates of North America, showing several of the major gradients that must be included in a continental-scale network. Potential inland forest sites are shown as red dots, along with other sites from several existing networks, which are shown as black dots. Potential coastal wetland sites are not shown here but would extend across all coastal biogeographic provinces and climate zones. Biogeographic provinces and climates from Briggs (1974) and Hayden and Dolan (1976).*

nental gradients in sediment export and supply (reflecting continental patterns in geology, topography, climate, and land use/land cover), tidal range (0.3–8 m), precipitation (20–182 cm yr^{-1}), temperature (4–26°C), and salinity (20–90 practical salinity units). These gradients result in wetlands dominated by marsh grasses in temperate areas (eg *Spartina patens* in the northeast and *Spartina alterniflora* in the southeast) and by mangrove trees (eg *Rhizophora*, *Avicennia*, and *Laguncularia*) in the tropics. This broad coverage will allow a rigorous assessment of the status and trends of wetland response to SLR across the full spectrum of factors that control wetland accretion or erosion. Data from these observatories will be critical for developing and testing predictive simulation models of the effects of SLR on coastal wetlands.

Inland forest gradients

To study the effects of windstorms, one must be in the right place at the right time. A network of inland forest sites should be arrayed across regions where the passage of windstorms is likely to occur. The network must address local and regional gradients in climate, topography, geology, and land use (eg rural to urban and wild to managed). Given the probabilities of storm occurrence computed from return periods shown in Figure 2, a network of 25 sites spread over the eastern US will likely experience 75 storm and 23 hurricane events over a 30-year lifespan. This sample size will permit development of a database capable of addressing a wide range of questions about hurricane effects, which can then be used in predictive models. We expect a similar probability for severe windstorms on the west coast.

Step 3: Observational infrastructure and spatial configuration

We envision a network of sites monitored with a combination of in-situ sensors, discrete samplings, and remote sensing. We suggest a "catchment" layout of instrumentation, to facilitate examination of both vertical and horizontal biogeochemical flowpaths.

■ Coastal wetlands

The basic geographic unit of study for coastal wetlands should be a tidal marsh "creekshed", which includes a first- or second-order tidal creek and the marsh platform flooded

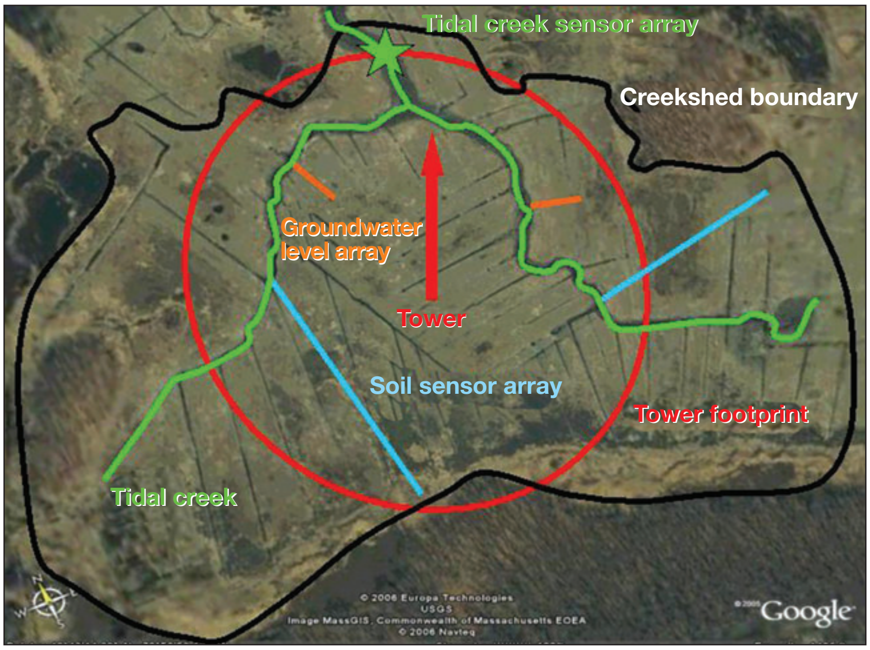

Figure 5. *Physical layout of infrastructure in a generic tidal creekshed. Such a layout, including remote sensors based on a tower, can provide the framework for developing a predictive understanding of the factors contributing to coastal wetland condition over time.*

by that creek's tidal water at mean high tide (Figure 5). The study unit should include adjacent uplands, if present locally. Detailed observations and experiments at these sites can facilitate examination of land–water linkages and land–atmosphere and internal fluxes. Thus, instrumentation and sampling should be laid out to capture mass fluxes of water, sediment, nitrogen, and carbon between marsh/water and the atmosphere, between the creek bank and inland marsh, between the marsh platform and its tidal creek, and between the marsh surface and buried sediments. A mass balance augmented with remote sensing will enable us to fully characterize the net accretion of a marsh and the processes contributing to its gain or loss. Real-time hyperspectral remote sensing from a tower at the site can provide temporal information on plant species composition, plant condition, and plant biomass. Aerial remote sensing can be used to extend the results to broader regions, to define the change in extent of intertidal wetlands and estuaries, to examine boundary conditions (eg human infrastructure and coastal armoring, coastal distribution of sediment), and to test predictions spatially.

■ Coastal inland forests

Because the passage of a windstorm is a probability event, we need sufficient instrumentation capacity to assess expected changes in forest structure and functioning over large land areas and long time periods. Measurements should include a complete suite of environmental characteristics, gas exchange, hydroecology, and telemetry of organisms before, during, and after events. Key processes and systems to examine include: plant and soil respiration, plant photosynthetic rates, primary productivity, whole ecosystem gas exchange, and alterations to the water budget and dry deposition. Rapidly deployable instruments would be placed in the likely path of oncoming storms to obtain real-time and site-specific measurements of storm intensity at a landscape scale. High-resolution remote sensing data for the whole path of the storm (coast to upland forests) collected at intervals of weeks to months to years after the storm will complete the assessment of effects and recovery patterns, and extend the understanding gained from site-level measurements. From these sources, we can develop landscape change maps to assess recovery after each major event.

■ Hypotheses

We offer examples of the types of hypotheses that could be addressed with a continental-scale network as described here.

Hypothesis 1: Areas with limited ability for wetland migration will see marked reductions in the provision of ecosystem services and will be increasingly vulnerable to intense storm damage in the future. By extension, human communities that have the most limited potential for migration will incur the greatest structural, cultural, and economic losses from SLR and storms.

In the absence of humans and their engineering works, it might be relatively straightforward to predict future shorelines and wetland distribution, but the ability of humans to modify coastal topography greatly complicates predictions. We expect that coastal regions with steep topography (eg west coast) or with high population densities (eg urban centers such as Charleston, South Carolina), will see a marked decrease in both estuarine and wetland areal extent as sea level rises, because transgression will be restricted. This will reduce the storm buffering service provided by coastal wetlands and thereby increase the vulnerability of human systems, which will, in turn, have continental-scale ramifications, as resources are expended to protect, repair, and distribute people and their infrastructure following storms.

Hypothesis 2: The capacity of coastal wetlands to maintain elevation relative to sea level will decrease as the rate of SLR increases, as climate warms and droughts become more severe and frequent, and as continental sediment and nutrient inputs change.

Primary factors controlling wetland accretion are vegetative sediment trapping, sediment availability, and peat accumulation. These factors, in turn, are controlled primarily by climate, continental land use, and SLR. We expect that areas likely to experience the most severe wetland degradation and loss are situated where sediment supply is reduced as a result of reforestation and erosion control management in the continental interior and where the wetland balance between gross primary production and respiration is shifted toward respiration due to climate, nitrogen deposition, and runoff (ie less root and peat production). Drought will greatly contribute to wetland loss, as it can kill wetland vegetation (peat production), while only temporarily slowing decomposition (peat decomposition and negative accretion). Shifts in vegetation structure induced by climate change (eg northward expansion of mangrove trees) have the potential to decrease wetland sediment trapping ability. Regional differences in the levels of change expected for factors controlling wetland accretion will result in varying rates of wetland loss at continental scales.

Hypothesis 3: Windstorm strength, duration, and capacity to impose ecosystem change will diminish with latitude, but windstorm effects will increase.

Energy dissipation per unit area and time will be less at high latitudes than at low latitudes. Therefore, given the same storm frequency and forest structure, we would expect forests at higher latitudes to incur less damage. However, we know that ecosystem structure is at least partially determined in response to disturbance regimes. Increased intensity and/or frequency of windstorms may therefore result in increased damage at higher latitudes, given a lack of adaptation to high winds among most native species, a greater time since last occurrence of high-wind disturbance, and greater dominance by non-sprouting conifer species. In contrast, resilience may be greater at lower latitudes, due to the greater capacity of native species to recover rapidly and adapt to avoid long-term damage.

Hypothesis 4: The capacity of forest ecosystems to support human activities will change with increasing windstorm frequency and magnitude, and rainfall intensity, because of directional changes in species composition and ecosystem structure. Increasing storm frequency will also accelerate the rate of ecosystem change.

Long-term changes in storm frequency and intensity represent fundamental changes in the conditions that shaped modern forests. Rainfall from tropical hurricanes has increased over much of the Southeast, while non-tropical hurricane rainfall has remained largely unchanged (Knight and Davis 2007). Forest responses to gradual change in these major drivers will involve shifts in species composition and vegetation structure, which will cascade downward to phenological patterns, biogeochemical characteristics, and watershed dynamics (Batista and Platt 2003; Boutet and Weishampel 2003; Zhao *et al.* 2006). Such changes will probably affect the rates and types of services that humans derive from modern forests, rivers, coastal wetlands, and riparian ecosystems. For example, the economic costs associated with these recent cumulative disturbances can exceed $3 billion in diminished supplies of timber, lost protection of watersheds that provide essential water resources to society, reduced sequestration of carbon by old-growth forests, and extensive loss of property and human lives (Sturdevant-Rees *et al.* 2001; McNulty 2002; Stanturf *et al.* 2007).

Cyberinfrastructure and modeling for synthesis and outreach

The observational network advocated here will result in the collection of large amounts of data; this will require building capacity for data acquisition, management, and curation. We can look to several existing or proposed large-scale programs for guidance along these lines, including the Long Term Ecological Research network (LTER), the National Center for Ecological Analysis (NCEAS), and the National Ecological Observatory Network (NEON).

Modeling should play an integral role in evaluating the effects of SLR and intense windstorms on ecosystems. There are already numerous coastal models, ranging from fine-scale plant growth to coarse-scale geomorphology models (eg Morris 1982; Sklar *et al.* 1985; Gardner 1990; Konisky *et al.* 2003; van de Koppel *et al.* 2005; Lightbody and Nepf 2006) and models that describe hurricane winds, wind interactions, and forest community and population dynamics (eg EXPOS and HURRECON, Boose 2004; JABOWA, Botkin 1993; or SORTIE, Pacala *et al.* 1993). The challenge will be to link these models with newer, continental-scale models (eg land-use change and landscape models) and ocean and atmospheric models. The combined models should make use of data from the continental network to synthesize the various data sources into a single, internally consistent representation of the monitored ecosystems and to project the results in both space and time (Rastetter 1996). New visualization techniques will help to convey long-term forecasts and display landscape-change scenarios that are normally challenging to communicate to the general public.

At the national level, climate change was recently identified as a major research priority by the National Science and Technology Council Joint Subcommittee on Ocean Science and Technology. The scientific knowledge to be gained through data analysis and predictive modeling will be of value for analyzing ecosystem properties and determining risk and response to sea-level rise, marsh degradation, and storm events. What makes this network initiative unique is its emphasis on ecological feedbacks and its continental-scale scope, which will allow observations in coastal wetlands and inland forests to be evaluated in the context of broad-scale drivers, such as global climate cycles and upstream land-use decisions.

Useful products will include real-time data on the inland extent of storm damage, remote sensing imagery that can be used to visualize the effects of SLR on coastal wetlands, risk-assessment models, and simulations that explore the linkages between upstream management decisions and coastal wetland processes.

Conclusions

Inland forests and coastal wetlands provide important ecosystem services, which will be compromised given the predicted increases in sea level and the severity and frequency of intense windstorms. The development of a continental-scale network of sites is necessary to document trends and better understand the mechanisms whereby SLR and intensification of windstorms alter the structure, function, and capacity of these systems to deliver services. New models and visualization techniques will be required to transfer scientific knowledge gained from the network of observatories to the public at large, resource managers, and policy makers. The network's strength and promise lies in its focus on ecological and land-use feedbacks and its continental-scale scope, which will allow observations in coastal wetlands and inland forests to be evaluated in the context of broad-scale drivers, such as global climate cycles and upstream land-use decisions.

Acknowledgements

We thank J Franklin and E Shulenberger for helpful conversation on the subject of windstorm effects on ecosystems and J Carpenter for help in assembling a figure illustrating sea-level trends. The research that led to this paper was supported in part by grants to CSH (NSF BCS-0709685, DEB-0614282, OCE-0423565, GA Sea Grant NA080AR4170724), AEL (NSF BIR-8811902, DEB-9411973, DEB-9705814, DEB-0080538, DEB-0218039), MA (NSF OCE-0620959, GA Sea Grant NA08OAR4170724, GA Coastal Management Program NA07NOS4190182), APC (NSF DEB-0218039), and SJVB (USDA CSREES PR00NRI001, McIntire Stennis PR014). We thank the NSF LTER program for its support.

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The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients

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Urbanization, an important driver of climate change and pollution, alters both biotic and abiotic ecosystem properties within, surrounding, and even at great distances from urban areas. As a result, research challenges and environmental problems must be tackled at local, regional, and global scales. Ecosystem responses to land change are complex and interacting, occurring on all spatial and temporal scales as a consequence of connectivity of resources, energy, and information among social, physical, and biological systems. We propose six hypotheses about local to continental effects of urbanization and pollution, and an operational research approach to test them. This approach focuses on analysis of "megapolitan" areas that have emerged across North America, but also includes diverse wildland-to-urban gradients and spatially continuous coverage of land change. Concerted and coordinated monitoring of land change and accompanying ecosystem responses, coupled with simulation models, will permit robust forecasts of how land change and human settlement patterns will alter ecosystem services and resource utilization across the North American continent. This, in turn, can be applied globally.

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Beyond climate, land use – and its manifestation as land-cover change and pollution loading – is the major factor altering the structure, function, and dynamics of Earth's terrestrial and aquatic ecosystems. Urbanization, in particular, fundamentally alters both biotic and abiotic ecosystem properties within, surrounding, and even at great distances from urban areas (Grimm *et al.* 2008). Around the world, rates of land change will increase greatly over the next 20–50 years, as human populations continue to grow and migrate (Alig *et al.* 2004; Theobald 2005). The nature, pattern, pace, and ecological and societal consequences of land change will vary on all spatial scales as a result of spatial variation in human preferences, economic and political pressures, and environmental sensitivities (Carpenter *et al.* 2007). To respond, we must determine how variables influence land change and ecosystem properties at multiple interacting scales, and understand feedbacks to human behavior.

Human social and economic activities drive land change at all scales, and may enhance or hinder the movement of materials via wind, water, and biological and social vectors, sometimes in surprising ways that cut across scales (Kareiva *et al.* 2007; Peters *et al.* [2008] in this issue). For example, individual human decisions can influence regional dynamics within a continent when many people respond similarly to the same economic or climatic driver; the Dust Bowl in the North American prairies during the 1930s is a historical example of such cumulative effects (Peters *et al.* 2004). Individual decisions can also influence broad-scale land-change dynamics on other continents; for example, a switch to soybean production in South America is being driven by market demand from China. In turn, the changes wrought by humans produce ecosystem dynamics that feed back to influence resource availability and human well-being. Human responses may ameliorate or exacerbate these effects. Thus, there are complex interactions and feedbacks between the direct manifestations of human activ-

In a nutshell:

- Land changes associated with urbanization drive climate change and pollution, which alter properties of ecosystems at local, regional, and continental scales
- Urbanization alters connectivity of resources, energy, and information among social, physical, and biological systems
- A continental research program across multiple gradients, within and radiating out from both small and large cities, is needed to advance understanding of urbanization beyond individual case studies
- Research should include spatially continuous information on land-cover change, monitoring of land change and accompanying ecosystem responses, and development of simulation models capable of producing robust forecasts of land change
- Forecasting land change will show how changing human settlement patterns alter ecosystem services and resource utilization at the continental scale

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ity and their diverse ecological consequences, across a range of interacting spatial and temporal scales (Figure 1).

Here, we consider land change (especially urbanization) and pollution arising from human activities. Ecosystem responses to these "press" events (ie continual or increasing stresses on ecosystems over relatively long time frames) occur on local, regional, and continental scales, as a consequence of connectivity among resources, energy, and information in social, physical, and biological systems (Peters *et al.* [2008] in this issue; Figure 1). For example, urban areas are both sources and recipients of atmospheric and aquatic pollutants. Eastern landscapes of the US receive depositions of air pollutants from the industrial Midwest, and small streams across the country receive pollutant loads (eg nitrate, ammonium) from intensive agriculture and concentrated feedlots (Mulholland *et al.* 2008). Meanwhile, the entire continent receives particulate and chemical inputs, borne in the upper atmosphere from distant global sources, including China and northern Africa(http://visibleearth.nasa.gov/view_set.php?categoryID=4831). Urban areas are also foci for species introductions (Hope *et al.* 2003; Crowl *et al.* [2008] in this issue).

There are many important two-way interactions between urban processes and climate that further complicate responses at multiple scales. The specter of sea-level rise and more frequent and severe hurricanes resulting from regional and global climate change is particularly important for urban ecosystems, as they tend to be located near coastlines (Crossett *et al.* 2004; Hopkinson et al. [2008] in this issue; WebFigure 1). Locally, changes in albedo, evapotranspiration, and surface energy balance in developed areas may exacerbate global warming through urban heat island and oasis effects (Arnfield 2003; Kalnay and Cai 2003). Dust generation from construction within urbanizing areas may be enhanced by drought. These urban dynamics may contribute to meso-scale and global climate change, through massive greenhouse-gas emissions and radiative forcing of non-greenhouse gases (Pielke *et al.* 2002), and by alteration of rainfall patterns (Cerveny and Balling 1998). Profound structural modification of streams and rivers, coupled with changes in impervious surfaces, affect hydro-ecology in, and downstream from, cities and suburbs (Paul and Meyer 2001).

Panel 1. Key research questions to guide development of continental and regional observation networks for understanding the interactions of urbanization, pollution, and climate change

- Q1: What are the ecological and socio-ecological consequences of local land-use changes at regional and continental scales?
- Q2: Does urbanization increase or decrease social, physical, and biological connectivity at local, regional, and continental scales?
- Q3: How will varying patterns of urbanization interact with climate change across continental gradients in climate and land cover to affect ecosystem processes and services?
- Q4: How are pollutant source and deposition regions (connected through air and water vectors) related to patterns of land use, and how do ecosystem structure, function, and services respond to changes in pollutant loadings resulting from changing land use?

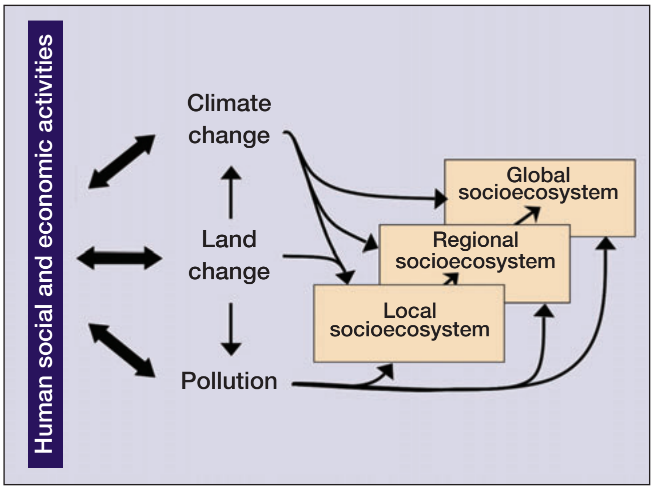


Figure 1. *Interactions among land change, climate change, and pollution, driven by human social and economic activities, in affecting local, regional, and global socioecosystems.*

The goals of this review are: (1) to demonstrate that interactions among component parts of landscapes (eg urban, rural, wildland), and interactions across scales from local to continental, are mediated by vectors of water, wind, organisms, and people, and (2) to provide an operational framework for conducting continental-scale research on land change and pollution in social–ecological systems. Key scientific questions that can be addressed by this framework relate to the ecological consequences of land change and human–environment dynamics, both as drivers and responders, as well as the origins and fates of pollutants at multiple, interacting scales (Panel 1).

■ Urbanization and pollution at the continental scale

Regional variation in ecosystems arises as a result of different combinations of climate, vegetation, and geomorphology. Both today and over the course of human history in North America, this variation is perceived and responded to by people who make choices about where to settle and how to use the land. There are therefore recognizable regional differences in settlement density, current types and intensities of land use, land-use legacies, and rates and patterns of urban–suburban growth (Figure 2; WebFigure 1). As a further consequence of these continental-scale differences, diffuse, "non-point" pollution coalesces into distinct hotspots or source regions, such as large urban agglomerations (or megapolitan areas; Panel 2; Figure 3) or zones of intensive agriculture (eg Figure 4).

In addition to the background template of natural systems, economic and cultural drivers influence human settlement patterns. The first wave of European settlers migrating across North America brought introduced Eurasian species and agricultural methods, initiating conti-

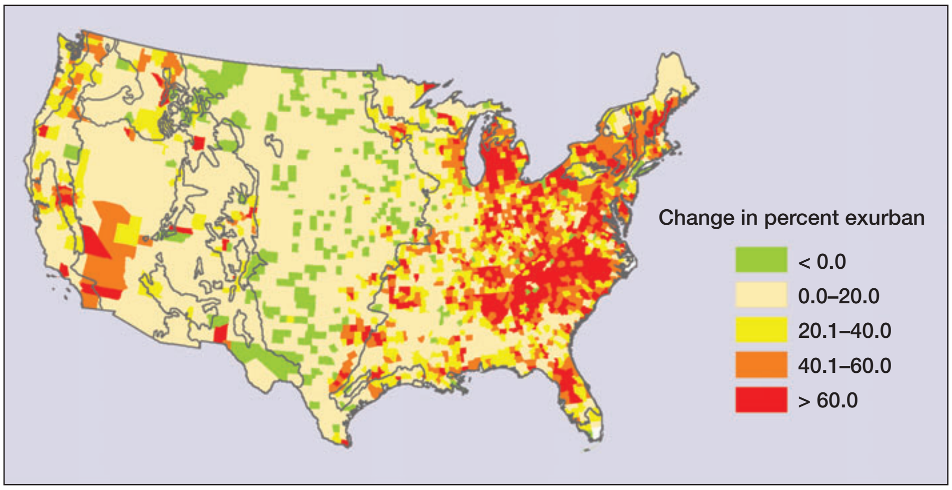


Figure 2. *Percentage change in exurban land use (defined as housing density of between 0.06 and 2.5 units ha^{-1}), between 1950 and 2000. From Brown* et al. *(2005).*

These changes include both the agglomeration of major US cities into megapolitan regions and the spread of housing into rural areas and wildlands. This land-use change will be geographically uneven and disproportionately associated with the southern and western regions of the US (Panel 2), requiring large appropriations and redistributions of limiting resources such as water and nutrients. However, even in areas experiencing low population growth, the spatial expansion of urban and suburban land uses is much greater than the rate of population increase, due to a continuing pattern of declining developmental density and increasing land appropriation per capita (Theobald 2005).

> ***Hypothesis 2.*** *Human activities, their legacies, and the environmental template interact with gradients of air pollution and nitrogen (N) loading to produce substantial variation in ecosystem patterns and processes, from sub-continental to regional scales.*

We expect pollution from urban and agricultural areas to influence ecosystem structure in profound ways. Emissions of nitrogen oxides, ozone, volatile organic compounds, other reactive gases, and aerosols derive from combustion sources (eg vehicles, power plants) in urbanized and urbanizing areas. Ammonia emissions are high in intensively fertilized agricultural and urban regions. Dust and aerosols are produced both from agricultural and urban construction activities, and as secondary products of reactive atmospheric chemistry. The impacts of these pollutants will occur both near emission sources and many hundreds to thousands of kilometers away, as a result of long-range transport and atmospheric chemistry. For example, excess ammonium and nitrate emissions from combustion and fertilization in the Midwest are implicated in chronically elevated reactive N-loading to sensitive ecosystems (such as high-elevation forests) in the Northeast and mid-Atlantic states (Driscoll *et al.* 2003; WebFigure 2). Nitrogen loading and ozone exposure cause changes in plant chemistry, photosynthesis, and ecosystem carbon balance in sensitive ecosystems (Aber *et al.* 1991). As transport and deposition of emissions continues, high N loading and air pollution (especially ozone exposure) may produce similar changes in less sensitive systems. Additional responses at these and larger scales may include shifts in dominant plant species (Arbaugh *et al.* 2003; Fenn *et al.* 2003; Stevens *et al.* 2004), export of nitrates and acidity to streams, rivers, and estuaries (Caraco and Cole 1999; Boyer *et al.* 2002; Donner *et al.* 2004), coastal eutrophication and

nent-wide ecological transformations. Today, the Southwest is a particularly important recipient region for Mexican immigrants, owing to geographical proximity and cultural and environmental similarities. Over the past century, the upper Midwest has been a magnet for northern Europeans, due to historical timing and the similarity of the region to these immigrants' native lands and climate.

Given biophysical and social influences on urbanization, ecosystem responses are likely to exhibit regional differences (see Panel 2). Classifying urbanizing regions based on both social and biogeophysical variables could form the basis for continental-scale comparisons of urbanization and resulting ecosystem responses. We expect that the nature and strength of feedbacks among urban–suburban land-use change and ecosystem biogeochemistry, hydroecology, and biodiversity will vary across the climatic, societal, and ecological settings that characterize these strongly contrasting regions.

Understanding atmospheric and aquatic transport processes and pollution generation has given atmospheric and aquatic scientists a strong working knowledge of the patterns of pollutant distribution at continental and subcontinental scales (eg Figures 2, 3). Yet, the ability to predict how connectivity across widely separated regions will lead to ecosystem responses to these patterns hinges upon a coordinated observation network distributed across pollutant gradients, coupled with experiments to identify mechanisms. At the continental scale, two hypotheses could be tested with such a network.

> ***Hypothesis 1.*** *Human sociodemographic changes are the primary drivers of land-use change, urbanization, and pollution at continental and sub-continental scales; in turn, these patterns are influenced by a continental template of climate and geography.*

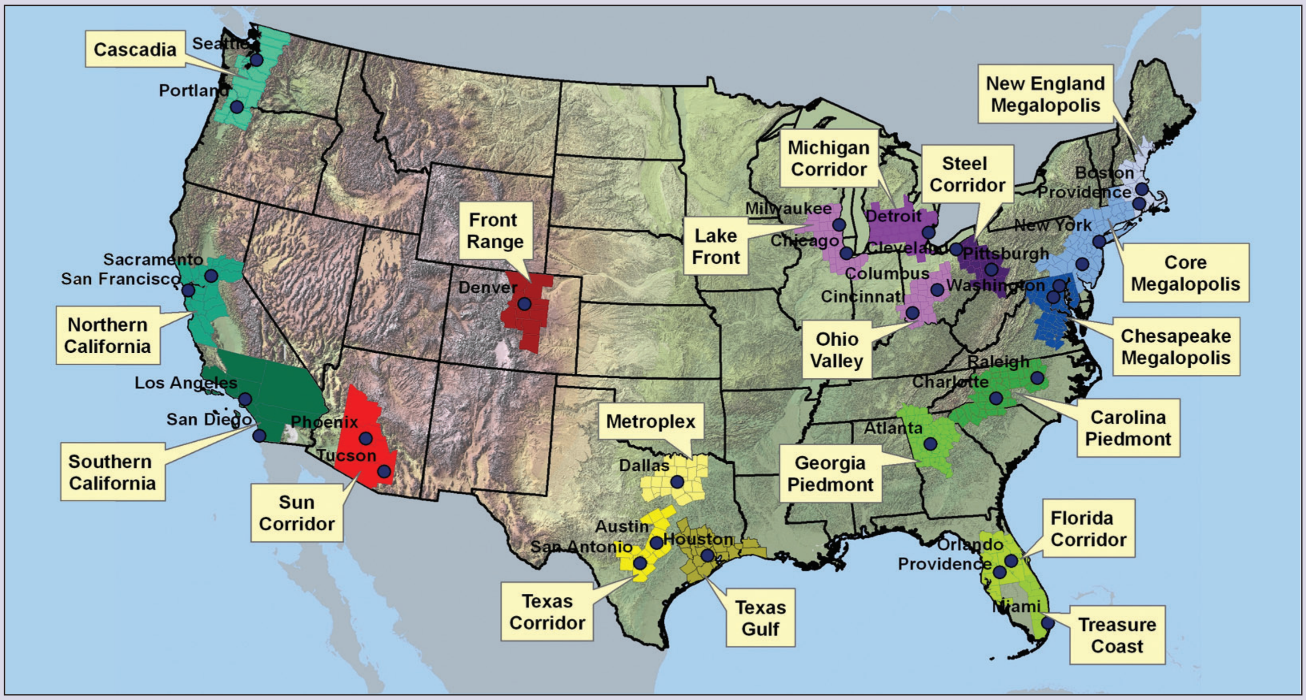
We expect major land-use changes associated with urbanization and suburbanization, leading to spatial redistribution and transformation of energy and material resources.

Panel 2. Megapolitan regions of the continental US

Seven megapolitan regions, each containing two or more megapolitan areas, have been identified for the continental US (Lang and Nelson 2007). In a megapolitan area, two or more large cities anchor the ends of a large corridor that is anticipated to fill with housing and other urban land uses over the early part of this century. This concept presents an exciting opportunity for ecologists, because regions differ markedly with respect to their social characteristics – history, current growth rate, density, and so forth (growth rate for 2000–2030 shown in the table below) – and can be superimposed on environmental gradients, such as that of climate (Marshall *et al.* [2008] in this issue) or topography (Figure 3).

Region	*Megapolitan area*	*Major cities*	*Growth rate*	*Color*
Megalopolis	New England	Boston/Providence	20	
	Core	NYC	20	
	Chesapeake	Baltimore/Washington	40	
Midwest	Steel Corridor	Cleveland/Pittsburgh	4	
	Ohio Valley	Cincinnati/Columbus	24	
	Michigan Corridor	Detroit	15	
	Lake Front	Chicago/Milwaukee	24	
Piedmont	Carolina Piedmont	Charlotte/Raleigh	45	
	Georgia Piedmont	Atlanta	55	
Florida	Florida Corridor	Tampa/Orlando	59	
	Treasure Coast	Miami	58	
Texas Triangle	Texas Gulf	Houston	51	
	Texas Corridor	San Antonio/Austin	62	
	Metroplex	Dallas/Oklahoma City	66	
Mountain West	Front Range	Denver	59	
	Sun Corridor	Phoenix/Tucson	81	
Pacific	Cascadia	Portland/Seattle	46	
	N California	San Francisco/Sacramento	43	
	S California	Los Angeles/San Diego	37	

Figure 3. *Megapolitan areas overlain on the topography of the continental US.*



harmful algal blooms (NRC 2000), and, possibly, increased invasiveness by N-demanding species (eg hybrid cattails, Eurasian *Phragmites* genotypes, winter annual grasses; Ehrenfeld 2003; Fenn *et al.* 2003).

Urbanization and pollution at regional and local scales

The megapolitan concept (Panel 2) provides an operational framework for predicting urbanization at the broadest scale. The phenomenon of urbanization is not restricted to the largest cities, however; although most people live in large cities (UNEP 2006), there are many more small cities than large ones. Diverse patterns of human settlement prevail across North America, from highly urbanized islands to sparsely populated forestland at high latitudes. Many gradients expressing these differences can be identified: cities from small to large, variable housing density, differences in the size of urban footprints (Folke *et al.* 1997; Luck *et al.* 2001), a shift from older cities to more suburban landscapes – all represent contexts that will affect the way that urbanization plays out. By studying contrasts or gradients between urban and wildland areas within regions and at local scales, scientists can develop a more comprehensive understanding of the ecosystem effects of urbanization and its feedbacks to society and management. The gradients we propose in this paper differ from the origi-

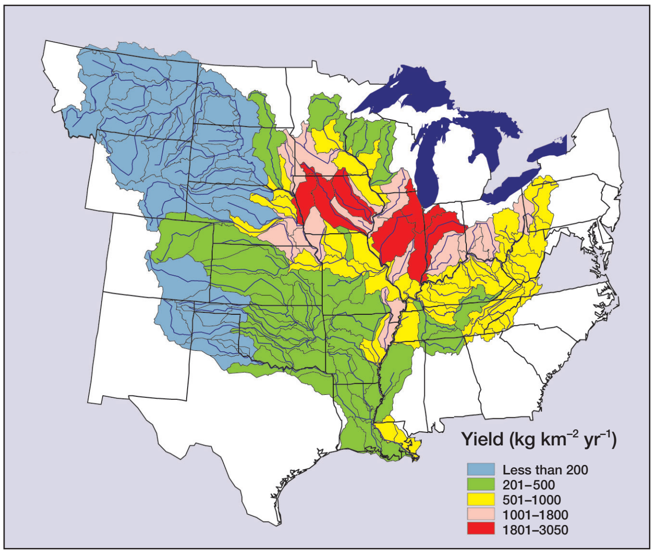


Figure 4. *Variation in N yield to the Mississippi River, illustrating the potential for specific regions to be "hotspots" of non-point-source pollution.*

nal urban–rural gradient paradigm described by McDonnell and Pickett (1990). A useful way to conceptualize the difference is to view the continental gradients as a collection of urban–rural gradients, each associated with individual metropolitan areas. Understanding the extent to which differences in human–ecosystem interactions along this collection of urban–rural gradients can be attributed to their contexts will advance urban ecology.

Generation and transport of pollutants at local to regional scales are well studied because of requirements for compliance with national air- and water-quality standards (see www.epa.gov/safewater/ and www.epa.gov/air/criteria.html). However, we do not know how the effects of air and water pollution from different human activities vary according to spatial context. For example, the concept of N saturation was developed for forest ecosystems (Aber *et al.* 1998) and is less frequently evaluated in grasslands, deserts, polar and alpine ecosystems, or lakes and streams (but see Wolfe *et al.* 2003; Bernot and Dodds 2005). The connectivity framework provides a useful context for understanding, within regions or even in local areas, how land change and pollution-generating activities affect nearby ecosystems. Hypotheses at this scale reflect connectivity both within and between urban areas, and with recipient ecosystems that are linked to them via wind or water vectors. We suggest three hypotheses that draw attention to differences and similarities across gradients in urban ecosystem structure and function and connectivity with the surrounding local–regional environment.

> ***Hypothesis 3.*** *Within urbanizing regions, landscape alteration and management result in a relative homogenization of form and function of urban land cover across climate zones.*

Regardless of setting, urban ecosystems are strongly engineered by their inhabitants and may share similarities, despite great geographical or climatic differences (eg Walsh *et al.* 2005). For example, similar horticultural species are introduced in contrasting urban regions across North America. Redistribution of water and nutrients in urban landscapes may reduce differences between xeric and mesic regions, relative to the dramatic differences between corresponding wildland ecosystems. New conceptual models of social–ecological processes are needed to integrate causes and effects of development patterns and management choices on urban ecosystem function (see Panel 3).

> ***Hypothesis 4.*** *Urbanization will generally increase connectivity via wind and animal vectors, but will disrupt connectivity via water vectors, especially at local to regional scales.*

Urbanization generates air pollutants that connect human settlements to adjoining wildland ecosystems. We therefore expect to see increased deposition of pollutants downwind and at potentially large distances from urban areas (Cooper *et al.* 2001). In addition, urban areas are a major source of the greenhouse-gas emissions underlying global changes in climate (Pataki *et al.* 2006). Wind transport of nitrogen, dust, and ozone from cities to outlying areas will alter plant productivity, ecosystem nutrient retention, and plant and microbial communities (Fenn *et al.* 1999). People also move both plants and animals. Comparison of species invasions and extinctions among land uses will show increased connectivity associated with human settlement for some species, although cities can also affect migration patterns by fragmenting habitat. Finally, because humans drastically modify water delivery and supply systems (eg streams, groundwater), connectivity via water will be disrupted, with dramatic consequences for aquatic ecosystems (see Panel 3). Some hydrologic connections will be increased as a result of urbanization (eg transport of water from source areas to cities, dispersal of invasive species along water corridors, sheet flow on impervious surfaces), while other hydrologic connections will be reduced (eg instead of long, slow flow paths from uplands to streams via groundwater, urban stormwater infrastructure creates new, short, fast flow paths that decrease ecological coupling between terrestrial and aquatic components of the landscape; Grimm *et al.* 2004).

> ***Hypothesis 5.*** *Humans fundamentally change biogeochemical inputs, processing, flow paths, and exports in areas undergoing development.*

Research on urban ecosystems has expanded over the past decade and has seen some synthesis (Grimm *et al.* 2000; Pickett *et al.* 2001; Alberti *et al.* 2003; Grimm *et al.* 2008), yet

Panel 3. Urbanization in a water-limited region

In Phoenix, Arizona, the site of the Central Arizona–Phoenix LTER program, urbanization has produced wholly new environments with different thermal and hydrologic characteristics than the ecosystems they replaced (Figure 5). Understanding ecological consequences of these changes relies on an understanding of their impacts on social systems and, indeed, the reciprocal interactions that characterize an urban socioecological system. For example, the urban heat island in Phoenix presents a challenge both to trees (which show reduced growth in response to high temperature) and people (who increase their water use to cope with high temperature). But there are further interactions between heat, water, plants, and people that provide excellent examples of the need for integration. An unequal distribution of high summer temperatures disproportionately affects the poor and non-white residents, whose neighborhoods also have lower plant diversity. Detecting this pattern requires access to remote-sensing methods from the geosciences and social distribution data from the social sciences, as well as eco-physiological studies of thermal responses of trees and spatially referenced measurement of plant diversity. In terms of water systems, major hydrologic modification and redistribution of water resulting from over 100 years of human decisions have greatly enhanced plant productivity throughout the urban area at the expense of a major pre-settlement river–riparian ecosystem. Since 1938, the region's major river has not supported streamflow, except during floods. Recent riparian restoration projects along the Salt River have involved school children in low-income South Phoenix, who have created signage and built owl boxes, to name a few activities. One outcome of this educational program has been the transfer of knowledge about rivers and riparian ecosystems throughout families and communities.

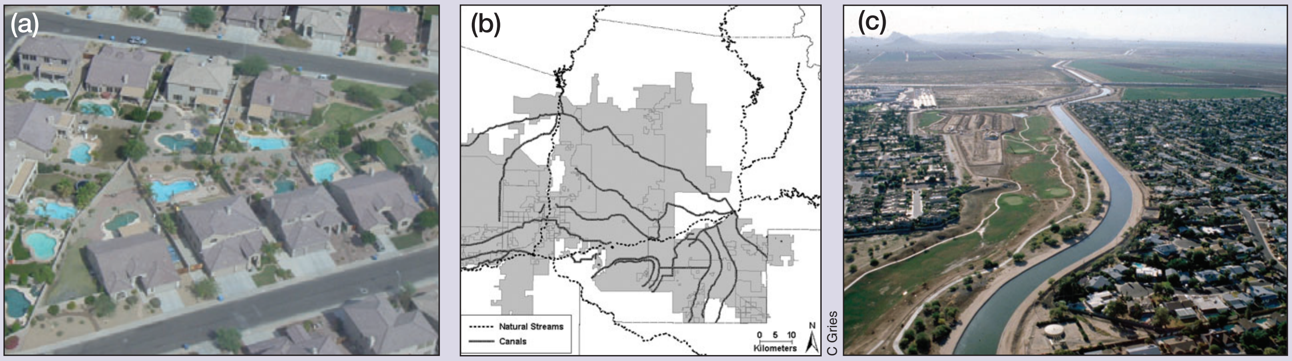


Figure 5. *Extensive modification of hydrologic systems, motivated by human desires for flood protection and water delivery, have replaced the historical broad river floodplain with a distributary canal system. Aquatic ecosystems no longer function like the streams they replace. (a) Swimming pools are a common feature of the hot, desert city of Phoenix. The urban heat island has worsened summer heat. For more information, see http://caplter.asu.edu. (b) The modern canal system and (c) a canal with riparian retention basin.*

this body of research consists largely of a collection of case studies. A continental network of urban sites would reveal how the major biogeochemical cycles are being altered by human activities (eg Kaye *et al.* 2006). We expect new, scaled models of biogeochemistry to emerge from observations of suburban, urban fringe, and exurban terrestrial and aquatic ecosystems. The fact that we have insufficient data on too few cities has precluded comparison of patterns of resource imports and their transformations within cities, which would allow us to test this hypothesis. At expanding urban fringes, we expect to observe changes in hydrologic balance and nutrient export as urban residents modify matter and energy fluxes through fuel, water, and fertilizer use, and as build-out increases impervious surface cover and modifies flow paths. Mercury, volatile organic compounds, endocrine disruptors, antibiotics, and nitrogenous pollutants released into streams from wastewater treatment plants or storm drainage will change species composition, nutrient retention capacity, and productivity of aquatic ecosystems. These processes have not been comprehensively evaluated across cities.

■ Cross-scale interactions

The influence of human land use and management on connectivity and ecosystems varies with spatial scale and region. Gradients in atmospheric deposition of N and sulfur at continental scales (eg WebFigure 2) result from prevailing air-transport patterns between source regions (eg industrial corridors, transportation hubs, agricultural regions) and sink regions (eg rural regions, wildlands, natural areas). Coastal and freshwater eutrophication can be traced to upland agricultural activities (particularly N and P fertilizer use; Figure 4) in the Midwest and Gulf of Mexico, and to urbanization and atmospheric deposition in the Northeast (NRC 2000; Driscoll *et al.* 2003). Urban thermal regimes vary compared to their surroundings, owing to the increased heat capacity of the infrastructure coupled with altered evapotranspiration, which is reduced in eastern cities relative to natural ecosystems, and enhanced in irrigated, semi-arid cities. However, the cross-scale interactions of urban heat islands with regional and global climate change are unknown. Sharp regional gradients in atmospheric and aquatic pollutants originating at urban point sources are superimposed on broader continental gradients of climate and long-range atmospheric or riverine transport of materials.

Perhaps most importantly, the scales at which human decision-making and actions occur are often inconsistent with the scales at which ecosystems are changing (Cumming *et al.* 2006). This mismatch in scale may be true both for causative action (eg automobile use by individuals and global atmospheric forcing of increased CO_2) and corrective action (eg amelioration of eutrophication by point-source wastewater treatment). We offer the following hypothesis.

> ***Hypothesis 6.*** *(a) Urbanizing regions will be less vulnerable than wildland ecosystems to many broad-scale, directional changes in climate due to the capacity of humans to modify their environment, and cities' access to political power and resources. However, (b) urbanizing regions will be more vulnerable than rural and wildland ecosystems to extreme events, because of the greater concentration of people and infrastructure that cannot be moved or modified over the short term. In addition, (c) efforts by urbanizing regions to adjust to change will place added stress on rural and wildland ecosystems that are connected to cities due to greater resource exploitation.*

Because the vast majority of the North American population lives in urban areas, the impacts of climate change on cities are of great interest. Urban areas and their institutions are able to adjust to directional and even some relatively abrupt changes, for example by increasing water supply during droughts or by strengthening infrastructure in response to the threat of hurricanes or sea-level rise. In addition, urbanization has a profound effect on local climatic conditions. Large urban areas essentially create their own climate: lighter winds, less humidity, more or fewer rainstorms compared to surrounding rural areas. Moreover, urban engineering, conservation, and landscaping alternatives allow urban residents to limit the variability of the climate that they experience (McPherson and Biedenbender 1991; Taha *et al.* 1999; Akbari 2002; Akbari and Konopacki 2005; Harlan *et al.* 2006; Stabler *et al.* 2006). In wildland ecosystems, climate mitigation options are more limited. We expect that human actions will, in general, degrade ecosystem services of linked wildlands (relative to those outside the influence of the urbanizing region), by resource extraction and air and water pollution.

■ Testing hypotheses at continental, regional, and local scales

Understanding how ecosystems respond to urbanization and pollution drivers requires accurate long-term tracking of land-use and land-cover change. In order to assess and interpret the dynamics of land change across scales, "wall-to-wall" (ie spatially continuous) continental coverage is necessary. Sub-continental and regional analyses would benefit from focused digital retrieval and analysis of more detailed data sources; such sources are not completely available today. At all scales, acquiring and analyzing historical records, human demographic data, resource consumption and transformation statistics, and imagery is requisite to testing hypotheses (eg Hypothesis 1) regarding drivers of land change in all regions of the continent. These data sources are used locally by individual investigators, but are not yet synthesized over larger areas. Historical resources are of particular value, as many current dynamics and future responses are conditioned by ecological legacies (eg soil, vegetation, biotic patterns and processes) resulting from past human or natural changes (Foster *et al.* 2003; Lewis *et al.* 2006). The tools needed for geographical analysis of land-cover changes and ecological responses will be essential for testing the hypotheses presented above.

Testing hypotheses at multiple scales will require a concerted and coordinated monitoring effort (ie direct observation of land change and accompanying ecosystem responses). Changes in atmospheric and hydrologic connectivity caused by urbanization (Hypothesis 4) might be assessed using atmospheric tracers that are incorporated into biota (eg Zschau *et al.* 2003; Hsueh *et al.* 2007) or by comparing stream discharge patterns before and after urbanization (eg Rose and Peters 2001). Measurements of ecosystem responses to urbanization and pollution at sites distributed continentally across various gradients would address Questions 1–3 (Panel 1) and, most specifically, test Hypothesis 4. At each site, scientists should measure the changes that ensue as an urban fringe area experiences increased housing and transportation system development, including those related to pollution. Intensive work within megapolitan regions would enable comparisons across major urbanizing regions of the continental US, addressing Questions 1–3 (Panel 1) and Hypotheses 2 and 4–6. These are complementary rather than competing approaches, which will ensure a more complete understanding of the urbanization phenomenon when applied simultaneously.

To answer Question 4 (Panel 1), sensors capable of measuring atmospheric and aquatic pollution should be established at a national network of wildland sites, such as an expansion of the current NADP sites to include greater spatial coverage (http://nadp.sws.uiuc.edu). Drought effects on dust emissions are expected to be greatest over the mid-latitude continental interior (IPCC 2001), and will combine with land-cover change throughout the continental US to increase fugitive dust emissions from suburban and urban locations. Because dust is often carried long distances (up to thousands of km) from its point of origin, the impacts of urbanization-induced dust emission should be observed across the continent.

A research infrastructure is needed to enhance our ability to track changes in emissions, transport, and deposition of N and other pollutants as they relate to changes in land use and human activities, and to assess the effects of these processes on ecosystem structure, function, and services. Such an infrastructure may be provided to some extent by existing networks and research programs, such as the Long Term Ecological Research Network (www.lternet.edu) and the National Atmospheric Deposition Program, in combination with networks coming on line, such as the planned National Ecological Observatory Network.

Networking observations, conducting syntheses, and forecasting

An important goal is predictive understanding of how human settlement patterns will alter ecosystem services and resource utilization at the continental scale. This predictive capacity is essential for a wide range of social, economic, and environmental national policy making, and for management efforts at local to national levels. A new generation of simulation models – spatially explicit socioeconomic and demographic models of human settlement, consumption, and land management dynamics that are integrated with hydrological–biogeochemical–land-use–invasion models – is needed to address these new questions across scales. Advances in cyberinfrastructure will be required to allow real-time input to be provided to these new, coupled models. Furthermore, a large-scale, networked research program has the potential to catalyze a move from empirical modeling, based on statistical extrapolation of historical trends, toward a forecasting foundation based on general principles governing land change. This theory development will arise from an iterative cycle of forecasting, observation, and change detection, refinement of theory and guiding principles, and repeated forecasting. Feedbacks from science to society should result in major changes in long-term forecasts as we witness human system responses to the recognition of its own impacts on the environment.

Conclusions

Urbanization is a globally important land-use change that is closely associated with climate change and pollution. Yet knowledge of ecosystem responses to urbanization and of the urban socioecosystems themselves is based, at present, on individual and often idiosyncratic case studies. Spatially contiguous observation of land-cover change coupled with a continental-scale network of observations of ecosystem responses, supplemented with historical and demographic data, will enable a transformation in our understanding of these complex, interactive processes and how they may be expected to change under future climate and human population scenarios. New, coupled ecosystem models and forecasting will play a key role in this transformation of the science.

In addition to the clear benefit to scientific knowledge, providing timely information on land change, urbanization, and pollution has the potential to enhance decision making on many levels. In turn, urbanization, pollution, and human influences on land change represent highly visible and comprehensible elements of human interactions with their environment. Establishing urban and urban-fringe sites for scientific investigation will thus offer unparalleled opportunities for outreach and educational activities.

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Predicting and understanding ecosystem responses to climate change at continental scales

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Climate is changing across a range of scales, from local to global, but ecological consequences remain difficult to understand and predict. Such projections are complicated by change in the connectivity of resources, particularly water, nutrients, and propagules, that influences the way ecological responses scale from local to regional and from regional to continental. This paper describes ecological responses to expected changes in four key meso-scale drivers that influence the ecosystems of the North American continental interior: drought, warming, snowpack disappearance, and altered fire regimes. Changes in these drivers will affect, for example, atmospheric smoke, dust, and reactive nitrogen concentrations; stream discharge; nitrate concentrations; sediment loads; and the vector-borne spread of invasive species and infectious diseases. A continental network of sensors and simulation models is required to detect changes in the transport vectors – atmospheric, hydrologic, and mechanized – that connect spatial scales. Knowledge of these downwind, downstream, and down-corridor effects will be critical if we are to understand and forecast responses to climate change at regional to continental scales.

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Climate influences ecological phenomena by limiting the distribution and activity of organisms (Pearson and Dawson 2003), the development of soils (Dahlgren *et al.* 1997), the availability of surface and sub-surface water (Vörösmarty *et al.* 2000), and the spatial and temporal dynamics of virtually all ecosystem processes (Bachelet *et al.* 2001). Climate also acts on connections among ecosystems, by altering rates and patterns of transport of materials through the movement of air masses, surface waters (Vörösmarty *et al.* 2000), migratory animals, and vegetative and microbial propagules (Brown and Hovmøller 2002). In addition, climate drives the spread of disturbances such as fire (Miller and Urban 2000). These effects on transport vectors are increasingly recognized as critical to our understanding of the way that local processes cascade to influence regional- and continental-scale patterns (Peters *et al.* 2007). These broad-scale climate effects on ecosystems also feed back to modify future weather patterns (Rosenfeld *et al.* 2001). Only by understanding the effects of climate change on transport processes and climate feedbacks can we predict future system dynamics as climate continues to change (IPCC 2007).

In a nutshell:

- Continued increases in mean temperature and drought severity will influence species interactions, phenology, snowmelt dynamics, and dust emissions
- Earlier melting of snowpacks will alter hydrologic fluxes, community composition, and the timing and rates of biogeochemical processes in snow-dominated areas and in streams and lakes that depend on them
- Fire regimes will be altered by climate change through effects on fuel accumulation, combustibility, and rates of ignition and spread; these changes will influence downwind ecosystems as smoke is redistributed according to local, pyrogenic, and synoptic patterns of air flow
- The transport vectors (air, water, migration, and human transportation) will themselves be influenced by climate change and variability in ways that are currently difficult to predict; this difficulty complicates forecasting of large-scale ecological effects
- Scaling from meso-scale to continental effects will require a continental-scale network of linked research sites, providing data to test our understanding of the connectivity of ecological processes

Climate also influences human population distribution and human land-use practices (Peters *et al.* 2006). For example, changes in land use, driven by government policies and technological change, interacted with long-term, extreme drought to result in one of the most serious regional- to continental-scale catastrophes in US history: the Dust Bowl of the 1930s (Peters *et al.* 2004, 2007). The Dust Bowl had major impacts on ecosystems of the Central Plains through high plant mortality and local loss of soil and nutrients; the resulting dust was redistributed across the continent. The Dust Bowl also had clear effects on human migration patterns, and caused substantial economic disruption and human health problems.

The goals of this paper are: (1) to identify sensitive ecological phenomena that are likely to be altered by changes in climate at local to continental scales, (2) to discuss how

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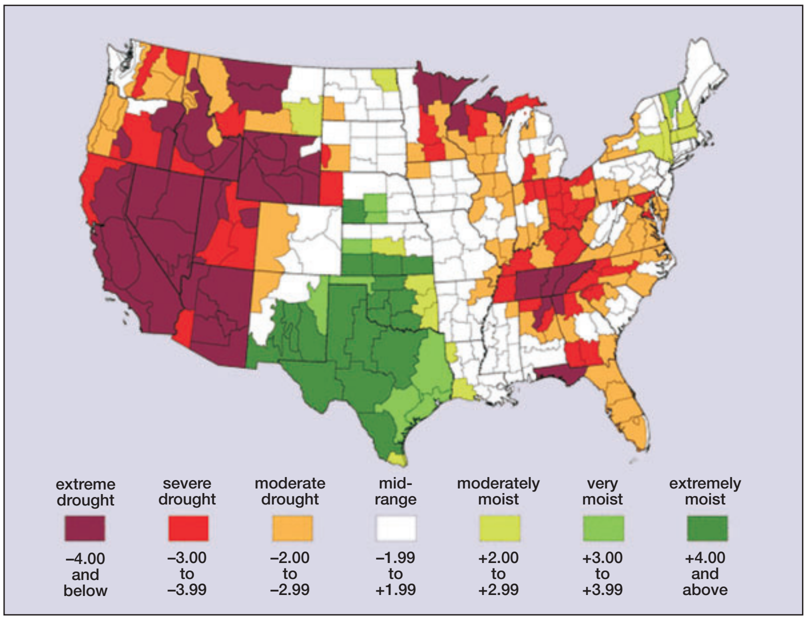

Figure 1. *The Palmer drought severity index (PDSI) for the period July 8–14, 2007, shows extreme drought (purple) and severe drought (red) for large portions of the West and parts of the Midwest and Southeast (www.ncdc.noaa.gov/oa/climate/research/drought/palmer-maps/index.php).*

these phenomena will influence and be influenced by climate-driven changes in connectivity across the continent, and (3) to highlight the need for an integrated network of research sites, located across the continent, to understand and predict the consequences of these changes.

Multi-scale patterns in climate drivers

The Earth's climate system can be understood as the result of external influences (forcings) and the mutual interactions between the atmosphere, hydrosphere, lithosphere, and biosphere. The mutual interactions include physical, chemical, and biological processes that transport and transform energy and matter. These processes are often described in computer simulation models over cells representing a portion of the Earth's surface (eg Fournier *et al.* 2002). The cells are then linked by mathematical descriptions of transport to and from adjacent cells. This view of the climate system includes multiple processes at fine spatial scales and builds to predictions of climate – and the transport of atmospheric contaminants – at continental and global scales (Eder and Yu 2006). The approach moves beyond traditional notions of cause and effect, as the climate system both drives and responds to key processes in adjacent cells. Connectivity across the globe, therefore, is increasingly recognized as an important component of climate and ecosystem dynamics. These cross-scale interactions of drivers and processes influence connectivity among resources in interesting and important ways, with consequences for ecosystem dynamics and feedbacks to the climate system.

Connectivity results from vectors of transport (eg wind, water, animals, people, disturbances), moving materials (eg dust, soil, water, nutrients, propagules, diseases, nutrients, chemical constituents) and energy (especially heat), within and among linked terrestrial and aquatic systems, across a range of spatial and temporal scales (Peters *et al.* [2008] in this issue). Changes in the drivers, the exchange processes within cells, and the transport processes among cells can alter climate and resulting ecosystem dynamics in unpredictable ways.

There are three major scales of climate drivers:

(1) Global circulation patterns influence long-term climate means, with effects on broad-scale patterns in vegetation.
(2) Meso-scale climatic phenomena are driven by regional patterns in climate. Three major patterns are now recognized (Kerr 2004): the Northern Annular Mode (NAM), which includes the North Atlantic Oscillation (NAO); the Pacific–North American (PNA), which includes the Pacific Decadal Oscillation (PDO); and the El Niño–Southern Oscillation (ENSO).
(3) Local topography and sub-continental-scale climate influence site-level variation (eg in precipitation).

An exhaustive review of the interactions among drivers, processes, and transport vectors is beyond the scope of this paper. Instead, we identify four major broad-scale drivers that we believe will be profoundly affected by climate change and will have their own downstream or downwind effects on other ecosystem variables.

Change in frequency and intensity of drought

Climate is a major control on the structure and function of terrestrial ecosystems worldwide. Climatic means are expected to change, but climatologists also predict an increase in climatic variability and the occurrence of extreme weather events, resulting in increased frequency of both droughts and heavy rainfall events (Woodhouse and Overpeck 1998). We focus first on droughts.

In 2007, severe droughts occurred across much of the western US, the upper Great Lakes, and parts of the Southeast (Figure 1). Predicting the ecological impacts of future droughts has been identified as a national research priority. Droughts restrict biological activity and therefore change ecosystem processes (Woodhouse and Overpeck 1998). Drought has obvious impacts on dryland agriculture and productivity in natural ecosystems (Schlesinger *et al.* 1989), timing of growth (Reynolds *et al.* 1999), plant mortality (Breshears *et al.* 2005), and organic matter dynamics (Connin *et al.* 1997). Although change in rates of ecosystem processes may be the initial response, longer-term responses may include transformations in species composition or vegetation structure (Albertson and Weaver 1942). Examples of vegetation changes include threshold responses to drought conditions (eg directional shifts in species distributions; Gonzalez 2001; Peters *et al.* 2006) and synchronous tree mortality across the southwestern US following extended drought (Breshears *et al.* 2005). Of course, the magnitude of these responses varies with the frequency, intensity, and duration of drought, as well as the resilience of the community or ecosystem and other local conditions, but in instances of severe drought, the ability of ecosystems to provide goods and services may be hindered.

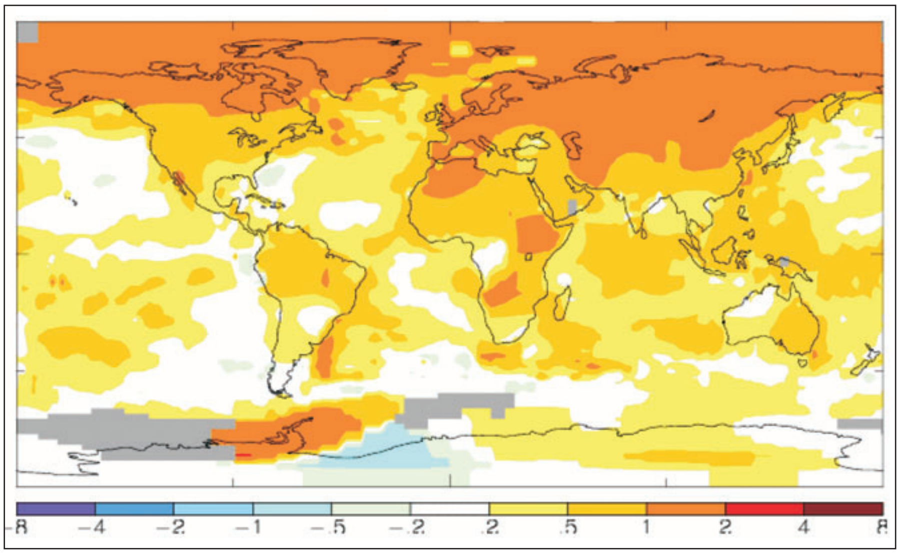

Figure 2. *Mean annual temperature anomaly, 2000–2006 versus 1951–1980. The orange regions, which are mostly at high northern latitudes, have increased by 1–2°C compared to the base period (1951–1980). Data from http://data.giss.nasa.gov/gistemp.*

As vegetation structure is altered, we expect that susceptible sites will display a threshold increase in dust production and redistribution (Gillette and Hanson 1989). These effects will be especially severe when drought is combined with marked human disturbance (eg tillage), low vegetation density, erodible soils, and high wind speeds (Gillette 1999). Such conditions contributed to the Dust Bowl in the early 1930s, which produced several dust storms of such intensity that airborne soil from Texas and Oklahoma was carried all the way to the eastern seaboard. Dust emitted from drought-stricken areas can have substantial impacts on downwind ecosystems; for instance, dust that falls on alpine snow as a result of upwind soil disturbance darkens the surface of the snowpack, leading to earlier melting and more rapid delivery of water to streams (Painter *et al.* 2007). These changes will have important impacts on downstream water consumers and on water-use planning. The input of dust has important effects on terrestrial ecosystems over short to long time scales (Chadwick *et al.* 1999; Okin *et al.* 2004), and often has immediate effects on ocean biogeochemistry and CO_2 uptake (Duce and Tindale 1991). In addition, dust poses a health hazard to humans (Griffin *et al.* 2001).

Finally, severe drought and attendant changes in ecological responses will influence the movement of people to other regions, as evidenced by the mass migrations during the time of the Dust Bowl. These responses may be especially acute if they are associated with reduced availability of groundwater due to declining aquifers. The consequences of such changes, especially those affecting the human population, will be difficult to predict.

Although this section has emphasized drought, it seems likely that increased climate variability will also manifest as increased frequency and intensity of high rainfall events in some areas (Easterling *et al.* 2000). Rainfall patterns with fewer but larger rain events can substantially alter ecosystem processes (Knapp *et al.* 2002), and if storm events become more common, they will erode disturbed soils, increase flooding, reduce water quality, deposit sediment in floodplains, and deliver sediment and nutrients downstream (Wainwright *et al.* 2002).

Increased mean annual temperatures

Perhaps the clearest manifestation of climate change thus far is the rise in mean temperatures since the early 20th century. Historical temperature records show this change most clearly in daily minima, with the steepest increase beginning in the early 1990s, particularly in northern latitudes (Figure 2). Climate models predict that the trend will continue.

Such warming will almost certainly influence ecosystem processes and community composition across North America. In particular, we expect warming to increase the drying power of the atmosphere (ie the vapor pressure deficit), which will, in turn, increase the frequency and severity of both drought and wildfire. Either drought or wildfire could lead to threshold changes in vegetation type, consumers, and ecosystem function.

Temperature also plays a key role in controlling phenology, the seasonal timing of events such as leaf-out date, the commencement of photosynthesis, and flowering date (Bradley *et al.* 1999). Such changes will favor some species over others, leading to changes in species composition. They will also induce changes in the seasonality of ecosystem processes controlling the transport of carbon, water, and nutrients within ecosystems and export of these beyond ecosystem borders. The National Phenology Network has been organized to observe changes in phenology within the US (www.uwm.edu/Dept/Geography/npn).

Increased temperatures will also influence the behav-

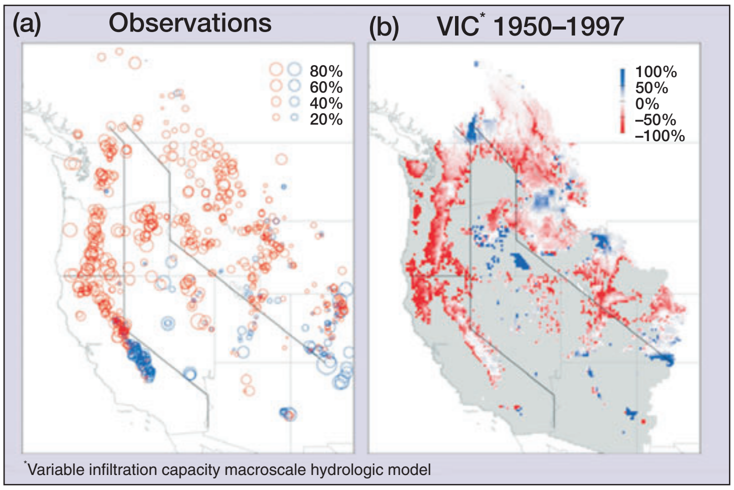

Figure 3. *(a) Measured and (b) modeled changes in the amount of water stored in the April 1 snowpack (snow water equivalent) in western North America. (a) Red circles show declines and blue circles show increases; size of the circle denotes the magnitude of the change during the period 1950–1997. (b) Trends in snow water equivalent over the same period, estimated by a physically based hydrologic model (Mote* et al. *2005).*

ior of undesirable species. For example, warmer temperatures will increase insect activity and shorten generation times, which may lead to more frequent outbreaks of harmful species, such as bark beetles (Hicke *et al.* 2006), and increased pathogenic fungal activity (Kiesecker *et al.* 2001). Finally, warmer temperatures may remove geographic barriers to the spread of pathogens, including those affecting human health (Epstein 1999).

Altered snowpack depth, duration, and distribution

Warming will almost certainly reduce the depth, duration, and distribution of the continental snowpack, as well as perennial cryosphere features such as glaciers (Vergara *et al.* 2007) and permafrost. There is good evidence that warming has already modified snowpack (Figure 3), especially at elevations where the snowpack is maintained at a relatively high temperature (Mote *et al.* 2005; Nolin and Daly 2006). In fact, snow cover decreased during the interval from 1966 to 2005 across the entire northern hemisphere, except in November and December (IPCC 2007).

Likewise, the temperature at the top of the Arctic permafrost layer has warmed by up to 3°C since the 1980s. In Alaska, the permafrost base has been thawing by up to 4 cm per year since 1992 (Osterkamp 2003). Simulations with the snowmelt runoff model (SRM; Martinec *et al.* 1998) of warming in glacial basins predict more rain, less snow, and increasing glacial meltwater until the glaciers disappear altogether (Rango *et al.* 2007).

We highlight these snowpack effects because they are, in one sense, a climate response and, in another sense, an ecological driver. The disappearance of the snowpack is a threshold phenomenon that will have clear effects on species composition and biogeochemistry from local to continental scales. The importance of snow and related cryosphere processes as an ecological factor has been recognized at least since the beginning of the 20th century (Chernov 1985), but much of the work remains anecdotal, making it difficult to predict the ecological responses to changes in snowpack, permafrost, and glaciers. Nonetheless, we speculate on its likely effects below.

The earlier disappearance of the snowpack will result in earlier commencement of biological activity in the spring, which is often delayed until the disappearance of snow, when temperatures can rise above 0°C to become more suitable for rapid metabolism. This phenological effect will result in an earlier commencement, for example, of photosynthesis and transpiration by plants (Monson *et al.* 2006), which will, in turn, dry soils down earlier in the summer, and possibly lower water contents. This will probably worsen the drought effects described above. However, snowpack disappearance will also eliminate the insulation that prevents soils from freezing during winter cold snaps, which might modify plant and microbial metabolism and perhaps distributions (Lipson *et al.* 2002).

At low elevations and latitudes, warming will lead to a change from a snow- to a rain-dominated winter precipitation regime. For example, in central Chile, air temperature data from 1975 to 2001 show an increase in elevation of the 0°C isotherm (the line on a map linking points at which the mean temperature is 0°C) by 122 m in winter and by 200 m in summer (Carrasco *et al.* 2005). The snowline of the European Alps is predicted to rise by about 150 m for each 1.0°C increase in winter temperature. A switch from snow- to rain-dominated watersheds would increase winter runoff and cause seasonal hydrograph peaks to occur earlier (Rango and Martinec 2000). Large changes in biogeochemical processes, such as the patterns of storage and release of reactive nitrogen, would be expected as well. Such changes will be particularly important downwind of cities, agricultural areas, and polluted regions, where atmospheric deposition rates are highest.

Warming would also change stream flow and lake dynamics. Magnuson *et al.* (2000) found that the freeze-up date for lakes and rivers in the northern hemisphere has been occurring later in the year, at a rate of 5.8 ± 1.6 days per century; meanwhile, ice breakup has occurred an average of 6.5 ± 1.2 days per century earlier. These changes will probably result in downstream changes in lake and stream biota, flooding, and the provision of water to satisfy human demands.

Altered fire regimes

Wildfires are dominant forces shaping terrestrial ecosystems, including embedded and adjacent urban areas and aquatic systems, throughout the US (Pyne 1997).

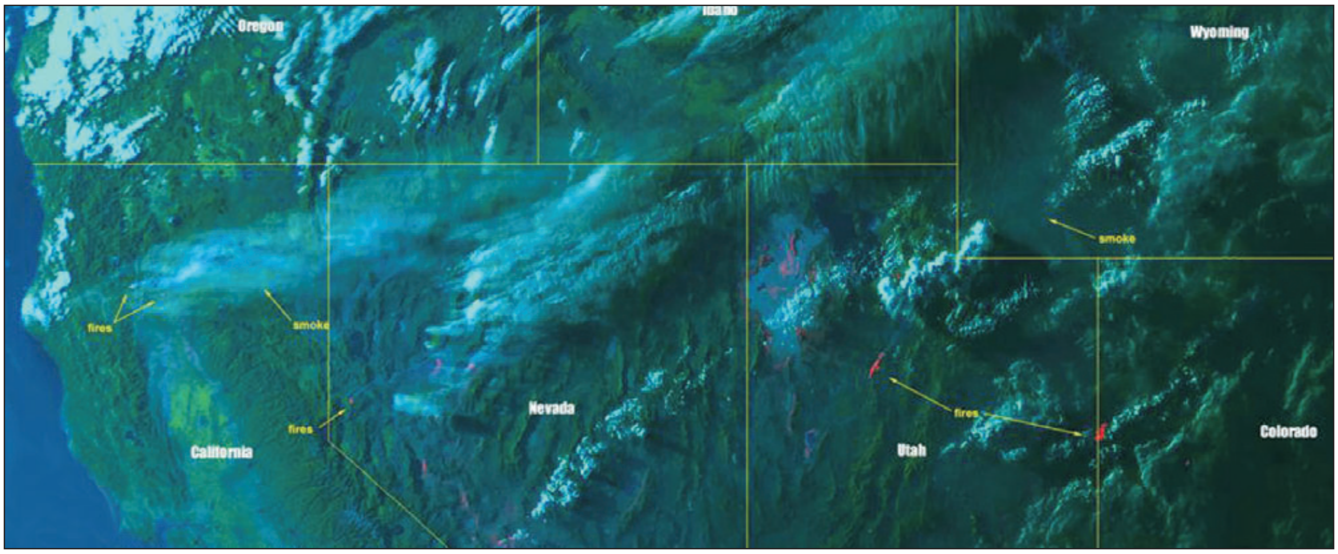

Figure 4. *Heat signatures and smoke plumes from fires burning in the western US in 1999. From NOAA-15 POES AVHRR HRPT.*

Wildfires, like other disturbances, interact with external drivers of climate, land use, and invasive species to influence patterns and dynamics of biodiversity, biogeochemical and hydrological cycles, and infectious diseases (D'Antonio and Vitousek 1992). The costs of wildfires are substantial: annual suppression costs now routinely exceed $1 billion per year in the US alone. In addition, the impacts of wildfires occur across a range of scales; for example, wildfires affect atmospheric carbon monoxide and fine particulates, with consequences for human health, over extensive downwind areas (Figure 4). Multiple fires burning at the same time can coalesce to influence broad-scale atmospheric circulation patterns.

Although research has been conducted on the ecological and economic impacts of individual wildfires, very little is known about: (1) how to forecast the rate and direction of fire spread across spatial and temporal scales for individual and multiple, coalescing fires; (2) how to forecast the regional, continental, and global impacts of wildfires; and (3) how to minimize the ecological impacts and maximize restoration potential under the full range of climatic and ecological variability inherent across the country.

Wildfires often start with a single ignition point, yet can increase rapidly to affect large spatial extents. Fire behavior across scales (rate, direction, intensity) is difficult to predict because of positive feedbacks among local and regional weather (eg wind speed and direction, relative humidity), vegetation (eg fuel quality, quantity, spatial distribution), and landscape features (eg topography, soil moisture, roads, other natural fire breaks; Figure 5). These constantly changing conditions can result in catastrophic events, such as the fires that raged across southern California in October 2007. Thus, there is a clear need for forecasting fire spread in real-time, using data streams on each variable. The forecasts make predictions at multiple scales simultaneously and should be combined with simulation models that dynamically update the forecast spatially. A coordinated network of sites with sensors and cyberinfrastructure spanning a range of spatial and temporal scales is needed to enable these forecasts.

Fire regimes are correlated with recent weather in complex ways. We describe these correlations using the Palmer drought severity index (PDSI), which takes on negative values under drought conditions. The correlation is as expected; current drought conditions are correlated with an increase in the number of acres burned (Westerling *et al.* 2003; Figure 6). Perhaps less expected is that burned acreage is correlated with wetter conditions in May and August of the previous year. These correlations reflect the accumulation of vegetative fuels during unusually wet periods. As climate change continues, we can expect increased precipitation variability (ie more frequent wet-and-then-dry periods). In addition, fuels are already being dried by earlier snowpack

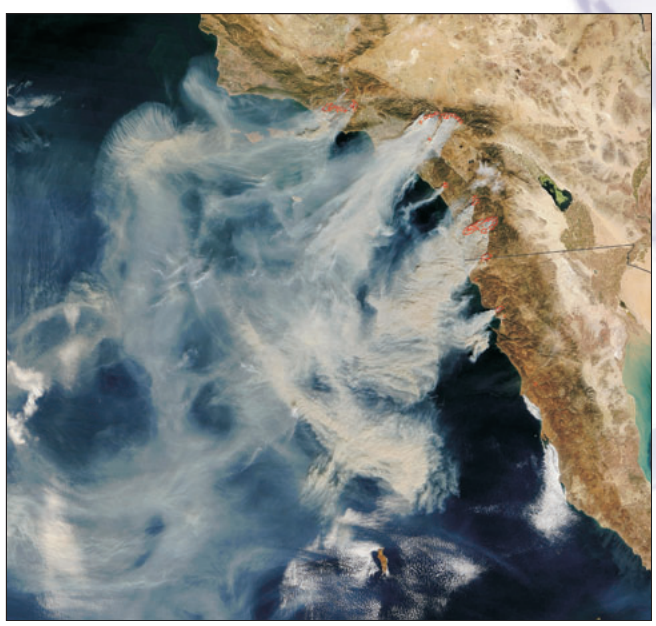

Figure 5. *Clusters of fires along the west coast of California on October 25, 2003, affect broad-scale air circulation patterns. From http://earthobservatory.nasa.gov/NaturalHazards.*

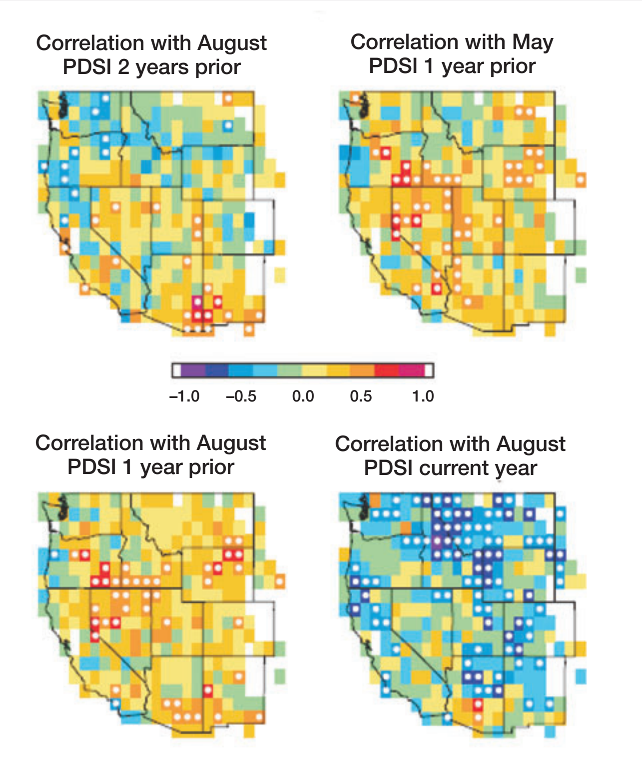

Figure 6. *Correlations of Palmer drought severity index (PDSI) with acres burned at varying time lags. White dots show correlations significant at 95% confidence level. Because the PDSI becomes more negative under dry conditions, negative correlations denote positive relationships with fire severity. Dry Augusts are associated with ready combustion, especially in the Rockies and Sierras. Dry conditions in either spring or summer of the preceding year reduce fire severity, presumably due to reductions in fuel accumulation (Westerling* et al. *2003).*

disappearance, earlier commencement of transpiration, and higher temperatures (Westerling *et al.* 2006). Such changes in fire frequency or intensity are almost certain to influence ecosystem structure and function. Fire suppression can result in invasions by exotic (D'Antonio and Vitousek 1992) and native fire-intolerant species (Briggs *et al.* 2005). These invasions may include expansion of woody species in the central US (juniper and oak species) and the arid west (sagebrush, mesquite, salt-cedar, and juniper). Conversely, where fire frequency and intensity are allowed to increase, they may lead to reductions in woody vegetation.

■ Approach to predicting multi-scale responses to changing climate

A network of sites spatially distributed across the continental US is necessary to adequately capture the effects of climate change and their connectivity from local to regional and continental scales. In designing such a network, the connections between nodes in the network are as important as the nodes themselves. The internodal connections will provide information on sources of input (eg dust and smoke) and transport vectors that move the materials and energy among nodes (eg wind, water, animal migrations, human transport). The dataset from a connected network of sites will provide unique and critical information for the parameterization and testing of models describing the transport vectors. These models will, in turn, improve our ability to integrate local-scale data to the regional and continental scales, to test whether continental-scale behavior can be modeled as averaged behavior integrated over a vast area, or whether it displays "emergent" properties (ie whether the behavior of the whole differs from the summed behaviors of its parts).

This network of sites should be linked to biogeochemical and population models parameterized to run at a variety of scales. The completeness and quality of the driver and response datasets will provide an excellent model testbed. The provision of soil moisture, snowpack, atmospheric microclimate, stable isotope, and biotic data would be particularly valuable in this respect, but there will also be value in standardizing methods for measuring ecological responses. For example, models of mountain hydrology (such as the snowmelt runoff model [SRM]) can be run with combinations of real-time ground observations and daily remote sensing of snowpack areas from the moderate-resolution imaging spectroradiometer (MODIS) and other satellite sensors. SRM and similar models are accurate in both short-term and seasonal forecasts, provided that modelers have access to high-quality input data. By building a long-term dataset, including extreme years, the models will be capable of forecasting into the future, when climate change will progress to a point at which minimal or no snow cover will be found in current source areas. Similarly, biogeochemical models can be run with combinations of real-time climate data, ground data, and remotely sensed data. Such models will be useful for predicting the timing and location of thresholds in ecological responses.

The network should also be linked to simulation models of the transport vectors that control connectivity. The influence of climate change on transport vectors could be assessed by extending existing models of atmospheric transport, river flows, human population trends, and patterns of human movement (eg vehicular traffic). The atmospheric models begin with surface fluxes, and disperse the transported materials into the churning layer of air at the bottom of the troposphere. They describe, for example, the transport, dispersion, and deposition of ammonia (Fournier *et al.* 2002). Other models begin with atmospheric data and infer upwind sources and sinks, of CO_2 for example (Gurney *et al.* 2002). Some account for processes that consume materials, such as chemical reactions, biological processes, and gravitational settling. Applications of such models include the BlueSky framework for predicting smoke transport from forest fires (www.airfire.org/bluesky) and community multiscale air quality (CMAQ), which describes the continental distributions of ozone, nitrogen and sulfur species, and elemental and organic carbon (Eder and Yu 2006). Although the parameterization of such models continues to be refined, it seems reasonable to expect that, in the near future, they could be coupled to networked environmental sensors to backcast source information and forecast downwind consequences. We have already discussed the likely effects of climate change on hydrologic vectors relating to snowmelt using the SRM model (Martinec *et al.* 1998). Such models could likewise be used to backcast climate-change effects in upstream source areas and to forecast their downstream consequences, including oceanic effects (Dodds 2006). The monitoring and modeling of the spread of invasive species facilitated by human transport is also under development (Schneider *et al.* 1998; Johnson *et al.* 2001). Linkage to regional-scale predictions of human transportation systems (eg Helbing and Nagel 2004) will increase the feasibility of studying the transport and dissemination of propagules under climate-change scenarios. Coupling these models to estimates of connectivity will provide important insights into continental-scale ecological responses to climate change.

Regionally intensive gradients of sites may be necessary, in some cases, to provide connectivity from fine to continental scales. For example, mountain ranges modify surface climate as a result of elevation, orographic precipitation, and cold-air drainage. These effects are superimposed on regional climate trends. Similarly, major river basins could be instrumented to examine the ecological impacts of snowmelt and other hydrologic processes from the mountains to the sea. Finally, in areas with high water tables, small changes in water-table depth or water throughflow may induce large changes in ecological variables. Because cities tend to occur at low elevations and near watercourses, many urban areas could also serve as sites for land-use, pollution, and climate gradients. These elevation and drainage transects would therefore fill in gaps in datasets from the broader network.

Conclusions

We have focused here on four key broad-scale drivers that will be profoundly affected by climate change, and that will have their own downstream, downwind, or down-corridor effects. Changes in drought, temperature, snowpack, and fire regime have already been detected in recent decades, and are predicted to continue. Each of these four drivers has clear downwind or downstream impacts (eg dust, reduced runoff, smoke, reactive nitrogen compounds in air and water). A connected network of research sites will allow us to sample the range of conditions at nodes distributed across North America. As importantly, the network will improve our understanding of the transport processes that connect the nodes. A critical need for the future will be knowledge of the effects of climate on these transport vectors: downwind, downstream, and down migration corridors. These transport processes provide the linkages from points to regions to continents.

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Long-term ecological research: re-inventing network science

Few of those involved in the birth of the National Science Foundation's (NSF) Long Term Ecological Research (LTER) network almost 30 years ago could have envisioned its leading role in defining continental-scale ecological science, as outlined in this issue of *Frontiers*. In these pages, 26 authors share their views on continental-scale ecological connectivity; 24 are LTER-affiliated. In his editorial (p 228), Steve Carpenter notes the importance of self-organizing networks of environmental scientists for identifying and addressing the non-linear and cross-scale phenomena that underlie and, in some cases, define global environmental change today. The LTER network is one of the best examples of such groupings: from early comparisons of populations and processes among two or three sites in the same biome have come groundbreaking, cross-network analyses of ecological change across multiple biomes exposed to varying degrees of human influence. And now, with the emergence of new, complementary networks, such as the National Ecological Observatory Network (NEON), the Global Lake Ecological Observatory Network (GLEON), the Water and Environmental Systems Network (WATERS), and the Oceans Observatory Initiative (OOI), comes the potential for research synergies hardly imaginable even 15 years ago.

Equal in importance to collaborations across physical networks are collaborations across disciplinary networks. If there is one overarching lesson to be learned from the evolution of LTER, it is the crucial importance of engaging with other disciplines – and especially with the social and behavioral sciences – to address today's big ecological questions. The greenlash discussed by Carpenter is often created, and usually abetted, by social interactions and institutions; we ignore this at our peril. LTER came of age alongside the Ecological Society of America's Sustainable Biosphere Initiative (SBI), and SBI's imprint is unmistakable in LTER science. LTER research increasingly embraces questions with human dimensions, as the ecological research community in general, and the LTER community in particular, have come to recognize the heavy, sometimes hidden hand of human influence in even the most remote locations. That recognition is abundantly clear in the articles in this issue of *Frontiers*: connectivity occurs within and across landscapes experiencing varying levels of human influence, sometimes direct and intentional, sometimes indirect and inadvertent – but rarely, if ever, absent.

The LTER network has embraced this challenge with a new, forward-looking initiative that is highly relevant to an emerging era of networked networks: Integrated Science for Society and the Environment (ISSE; www.lternet.edu/isse) recognizes and seeks to understand socioecological connections among organisms, processes, and ecosystems across varying geographic scales. Society receives services from ecosystems; in some cases, services are actively extracted, while in others they are underappreciated or even unrecognized. How these services are perceived, how perceptions affect behavior, and how behavioral change, in turn, affects ecosystem form and function are central to understanding the sustainability of the ecosystems on which we all depend. It is impossible to understand these linkages in the absence of interconnected, coordinated research sites, at which environmental scientists of all stripes – ecological, geophysical, social, and others – collaborate to address interdependent questions.

One major challenge facing connectivity science is nodal: how many sites are needed to test theories about the types, strengths, and interdependencies of connections among network nodes? For this reason, LTER is actively seeking partner networks with which to interact and, where possible, to share cyberinfrastructure and other resources common to environmental data collection and access. Continental-scale connectivity science requires continental-scale coverage by sites that are well-grounded in place-based science; how, otherwise, can socioecological hypo-theses related to connectivity be rigorously tested?

Early examples of socioecological research abound – many are described in this issue – and as new networks join the emerging constellation of environmental observatories, connectivity science will grow to more fully illustrate and define key linkages among globally dispersed ecosystems. Most LTER authors in this issue have also been heavily involved in the creation and development of more recent networks – NEON, GLEON, and WATERS among them – because the expertise and historical perspective afforded by LTER reinforce the value of new information from emerging networks, and provide a context for understanding and predicting future dynamics. All these networks recognize the importance of the coordinated sampling that allows information from multiple sites in disparate environments to address what is arguably the most pressing ecological question of our time: how to meet the needs of a sustainable future in an increasingly connected world.

This Special Issue of *Frontiers* is one of the strongest statements yet for the need to forge new networks, new collaborations, and new science to meet this increasingly global challenge. The LTER network stands ready to fully participate.

G Philip Robertson
Chair, US LTER Network Science Council, Michigan State University, East Lansing, MI

A continental strategy for the National Ecological Observatory Network

One of the great realizations of the past half-century in both biological and Earth sciences is that, throughout geologic time, life has been shaping the Earth's surface and regulating the chemistry of its oceans and atmosphere (eg Berkner and Marshall 1964). In the present Anthropocene Era (Crutzen and Steffen 2003; Ruddiman 2003), humanity is directly shaping the biosphere and physical environment, triggering potentially devastating and currently unpredictable consequences (Doney and Schimel 2007). While subtle interactions between the Earth's orbit, ocean circulation, and the biosphere have dominated climate feedbacks for eons, now human perturbations to the cycles of CO_2, other trace gases, and aerosols regulate the pace of climate change. Accompanying the biogeochemical perturbations are the vast changes resulting from biodiversity loss and a profound rearrangement of the biosphere due to species movements and invasions. Scientists and managers of biological resources require a stronger basis for forecasting the consequences of such changes.

In this Special Issue of *Frontiers*, the scientific community confronts the challenge of research and environmental management in a human-dominated, increasingly connected world (Peters *et al.* p 229). Carbon dioxide, a key driver of climate change produced by a host of local and small-scale processes (eg clearing of forests, extraction and use of fossil fuels), affects the global energy balance (Marshall *et al.* p 273). Invasive species, though small from a large-scale perspective, nonetheless modify the continental biosphere (Crowl *et al.* p 238). Aquatic systems are tightly coupled to both terrestrial systems and the marine environment (Hopkinson *et al.* p 255). Flowing water not only intrinsically creates a highly connected system, but acts a transducer of climate, land-use, and invasive species effects, spreading their impacts from terrestrial and upstream centers of action downstream and into distant systems (Williamson *et al.* p 247). Human activities such as urbanization create new connections; materials, organisms, and energy flow into cities from globally distributed sources and waste products are exported back into the environment (Grimm *et al.* p 264).

All of the papers in this issue of *Frontiers* conclude that a new approach to studying the biosphere is required in the present era. In response to this challenge, with the support of the National Science Foundation (NSF), ecologists in the US are planning a National Ecological Observatory Network (NEON). The conceptual design of this network (Field *et al.* 2006) gives rise to several general questions:

(1) How will the ecosystems (of the US) and their components respond to changes in natural- and human-induced forcings, such as climate, land use, and invasive species, across a range of spatial and temporal scales? What is the pace and pattern of the responses?
(2) How do the internal responses and feedbacks of biogeochemistry, biodiversity, hydroecology, and biotic structure and function interact with changes in climate, land use, and invasive species? How do these feedbacks vary with ecological context and spatial and temporal scales?

NEON will enable us to answer these questions by providing data and other facilities to support the development of ecological forecasting at continental scales. Required data range spatially from the genome to the continental scale, and temporally from seconds to decades. Control of transport in, and the chemistry of, the atmosphere, modulation of the physics of land surfaces, and influence over water supply and quality emerge from the aggregated behavior of almost innumerable organisms (Hopkinson *et al.* p 255). The disparity between the scale of organisms and the scales of their effects on the global environment represents an important problem for large-scale ecological research (Hargrove and Pickering 1992). While the consequences of life for the environment occur on the largest spatial and longest temporal scales, biological processes must be understood by documenting the responses of organisms, communities, populations, and other small-scale phenomena.

To bridge this diversity of scales, NEON will approach such questions through an analysis of processes, interactions, and responses, including those mediated by transport and connectivity (Figure 1). Most environmental monitoring networks focus either on processes or responses and do not link these with key interactions and feedbacks. NEON addresses the multi-scaled nature of the biosphere. The fundamental NEON observations (the Fundamental Sentinel Unit, focused on sentinel organisms, and the Fundamental Instrument Unit,

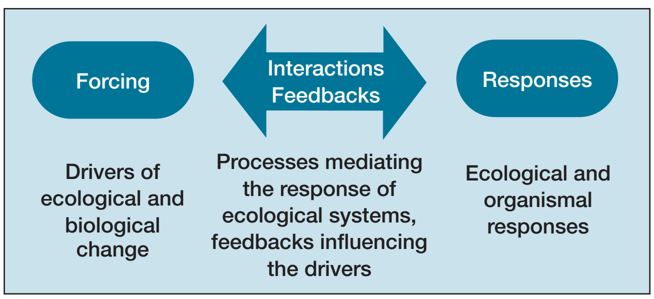

Figure 1. *NEON differs from other environmental monitoring networks because, by design, it integrates processes, interactions, and responses.*

focused on airsheds and watersheds) start at the scales of organisms, populations, and communities of organisms and directly observe biological processes (Figure 2).

A finite budget limits the number and the spatial extent of the fundamental observations; therefore, NEON uses a parsimonious continental strategy for placement of the observational units. The observations must systematically sample the US in a system design that objectively represents environmental variability. Existing maps spatially divide the US into ecological regions (Bailey 1983; Omernik 1987). In contrast to these earlier maps, NEON domains are based on a new, statistically rigorous analysis using national datasets for ecoclimatic variables. The statistical design is based upon algorithms for multivariate geographic clustering (MGC; Hargrove and Hoffman 1999, 2004; WebPanel 1). The optimized outcome of the geographical analysis results in 20 domains (Figure 3).

Relocatable sites will be moved on a 3- to 5-year rotation. Candidate core wildland sites have been specifically selected to be as representative as possible of the ecoclimatic variability in each domain (Table 1; WebTable 1). Nonetheless, one may question whether 20 sites can adequately address the ecoclimatic variability in a large, diverse continental area. The shading in Figure 3 represents the degree to which the ecoclimatic characteristics of the candidate core wildland sites represents environments in the conterminous US. Inspection of the figure shows that the Eastern portion of the country is generally well-represented, although southern Florida and the Gulf Coast are somewhat less well covered than the majority of the East. Representation in these areas would probably increase if the NEON Core site for the Atlantic Neotropical domain had been included in the analysis. In the West, representation is more heterogeneous, particularly in the desert Southwest and in the Rocky mountains. This is because of the high degree of linked climatic and biological variation related to complex mountainous terrain.

The observatory design, including both permanent core sites and relocatable sites, allows for planned contrasts within domains (eg mature versus young forest, urban versus wildland) and comparisons across domains (eg urban–rural in the Northeast and Southwest, nitrogen deposition effects in forests from the Southeast to the Northeast), using a core-and-constellation strategy. Mobile systems for short deployments (weeks to months) supplement the core and relocatable sites to explore details within these sites and to study discrete events and variability in the domains. Currently, there is approximately one planned mobile system per domain. These systems may be assigned to network tasks or to calls from individuals or groups of investigators. The design is based on rigorous scientific priorities and scaled to maintain budget discipline. Present scientific questions guide the first cycle of deployment; additional questions will be implemented as the network matures.

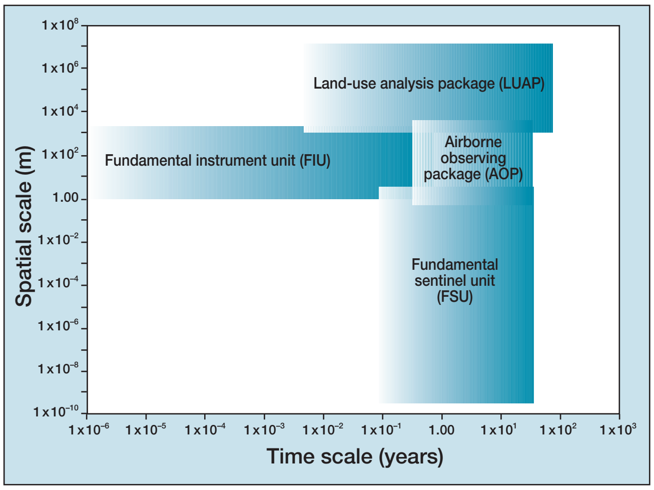

Figure 2. *A Stommel diagram of temporal and spatial scales for the components of the observational design of NEON.*

While the set of candidate core sites provides a reasonable, static representation of the ecoclimatic variability for the continental region, scaling from point observations to the continent remains challenging. Each NEON domain observatory physically occupies a relatively small area and trades breadth of coverage for depth of insight. Modern, high-resolution, airborne remote sensing allows us to add a second strategy; the combination of imaging spectrometry (which can retrieve the chemical composition and, often, species composition of vegetation) with imaging lidar (light detection and ranging, which retrieves three-dimensional structural properties of vegetation) will provide regional coverage of key ecosystem properties. Imaging each NEON site regularly with 1.5-m resolution coverage, but expanding the scale to hundreds of square kilometers, provides a context for each site that allows the local observations of processes and responses to climate to be extended in space and generalized.

NEON data products will integrate the local and

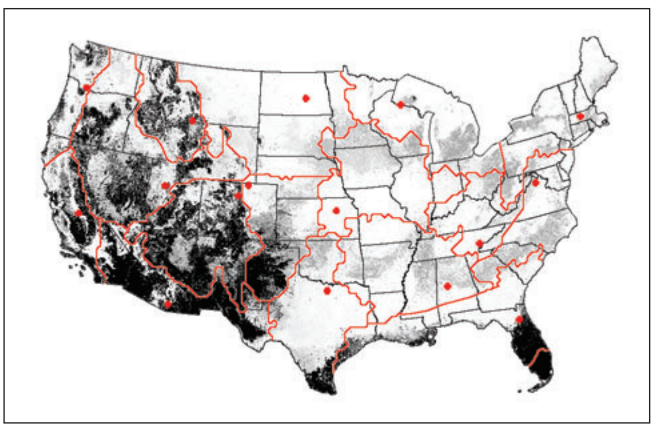

Figure 3. *NEON domain boundaries for the conterminous US (in red) determined using the procedure described in WebPanel 1. Locations of candidate core sites (Table 2) are represented by red symbols. The shading from white (well-represented) to black indicates the quality of representation for a given area, based on the set of candidate core sites.*

Table 1. Criteria for NEON candidate core sites

(1) A wildland[1] site representative of the domain (vegetation, soils/landforms, climate, ecosystem performance)

(2) Provides access to relocatable sites that respond to regional- and continental-scale science questions[2,3], including connectivity[4] within the domain

(3) Year-round access, permitting available land tenure secure for 30 years, air space unimpeded for regular air survey, potential for an experimental set-aside

Notes: [1]Wildland is defined as "a predominantly unmanaged ecosystem that has vegetation characteristics representative of its domain" (Field *et al.* 2006). [2]Science questions posed at the continental and domain scale:
- Land-use theme: what are the within-domain contrasts that can be studied with this site?
- Biodiversity–invasives–disease theme: what are the within-domain contrasts?
- Climate change–ecohydrology–biogeochemistry theme: what are the within-domain contrasts?
- Climate change–ecohydrology–biogeochemistry theme: what are the across-domain contrasts?

[3]Relocatable sites should generally be located within three hours' travel time of the core site. [4]Connectivity is defined by NEON as "the linkage of ecological processes across space" (see www.neoninc.org/documents/NEONDESIGN-0001vA.pdf).

regional measurements to quantify how processes are responding to climate, land use, and species changes across each NEON domain. The combined site data and airborne remote sensing data extend NEON observations of ecological processes and responses to scales large enough to correspond to space-borne remote sensing and other geographic data collected operationally (Figure 2). The NEON information system is structured with time–space coordinates that allow a natural merger between NEON's local and regional observations and national-scale satellite observations, to systematically link detailed ecological observations with global surveillance.

The NEON observing strategy provides strategic, critical biological and physical observations, distributed over the landscape via a statistical observing design, so that, together, the observatories constitute a single, virtual instrument sampling the entire US. This virtual instrument can not only determine average changes over the whole country (through its sampling, scaling, and observing design) but, like a telescope, can observe the critical texture within the country and distinguish among regions with different drivers of change, or different responses to change, as well as sampling vectors for transport of materials, organisms, and energy. NEON strategically addresses gaps in the scales of our current observing systems by recognizing that biology is both a global and a highly local phenomenon, and reconciling the scale-observing requirements of these two aspects of life. While the NEON design cannot address all of the questions raised in this Special Issue (Peters *et al.* p 229), as a research platform, it will be the backbone of evolving efforts to observe, understand, and forecast environmental change in the Anthropocene Era.

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