Predicting and understanding ecosystem responses to climate change at continental scales

John D Marshall[1*], John M Blair[2], Debra PC Peters[3], Greg Okin[4], Albert Rango[3], and Mark Williams[5]

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.

Front Ecol Environ **2008; 6(5): 273–280, doi:10.1890/070165**

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

[1]*College of Natural Resources, University of Idaho, Moscow, ID* [*]*(jdm@uidaho.edu);* [2]*Division of Biology, Kansas State University, Manhattan, KS;* [3]*USDA-ARS, Jornada Experimental Range, Las Cruces, NM;* [4]*Department of Geography, University of California, Los Angeles, CA;* [5]*INSTAAR, University of Colorado, Boulder, CO*

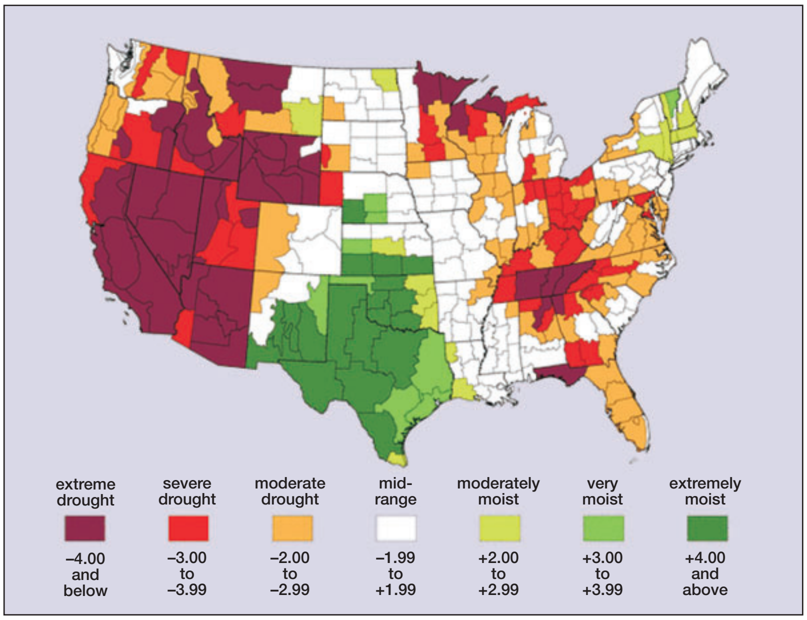


Figure 1. *The Palmer drought severity index (PDSI) for the period July 8–14, 2007, shows extreme drought (purple) and severe drought (red) for large portions of the West and parts of the Midwest and Southeast (www.ncdc.noaa.gov/oa/climate/research/drought/palmer-maps/index.php).*

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

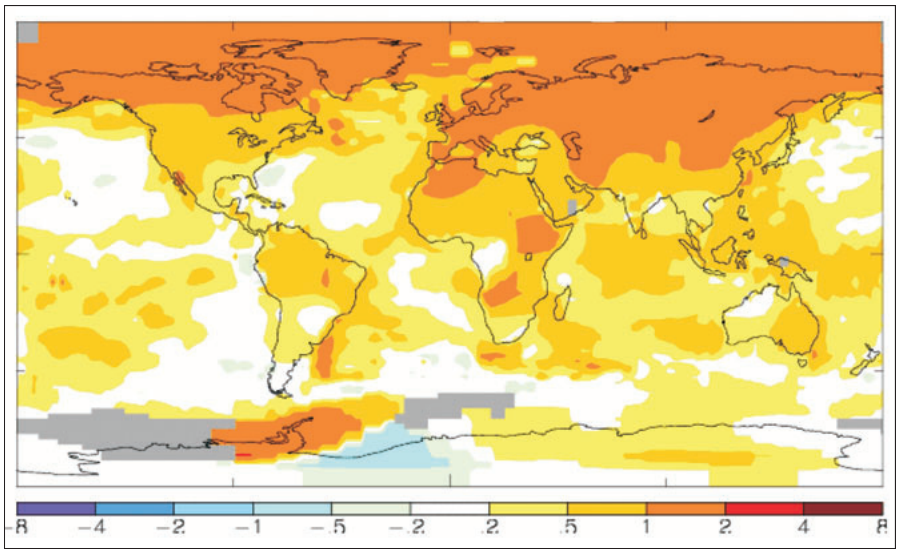


Figure 2. *Mean annual temperature anomaly, 2000–2006 versus 1951–1980. The orange regions, which are mostly at high northern latitudes, have increased by 1–2°C compared to the base period (1951–1980). Data from http://data.giss.nasa.gov/gistemp.*

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.

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-

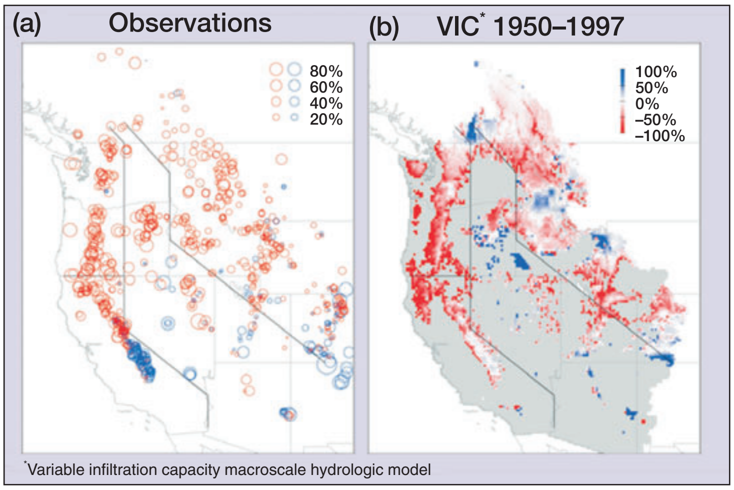


Figure 3. *(a) Measured and (b) modeled changes in the amount of water stored in the April 1 snowpack (snow water equivalent) in western North America. (a) Red circles show declines and blue circles show increases; size of the circle denotes the magnitude of the change during the period 1950–1997. (b) 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).

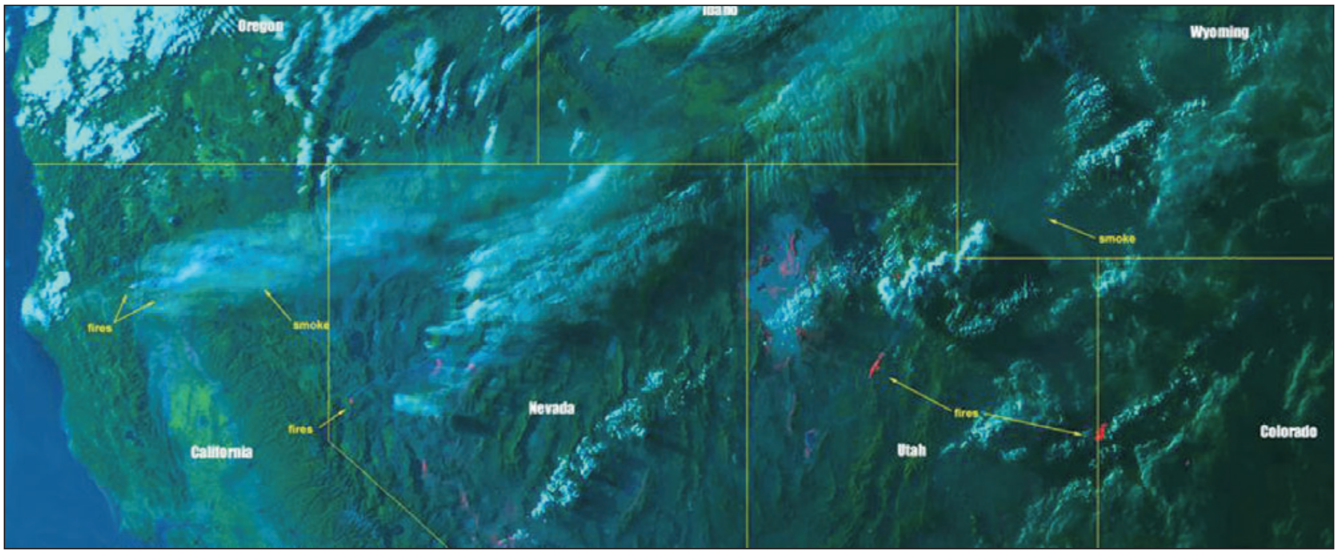


Figure 4. *Heat signatures and smoke plumes from fires burning in the western US in 1999. From NOAA-15 POES AVHRR HRPT.*

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

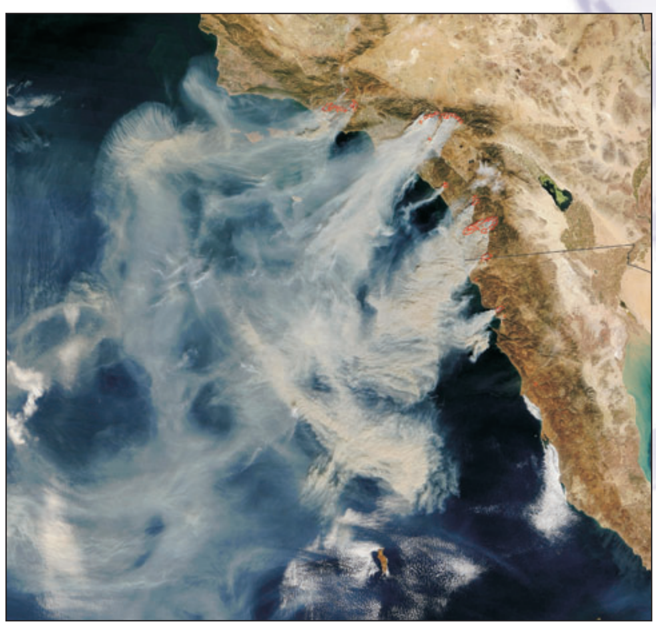


Figure 5. *Clusters of fires along the west coast of California on October 25, 2003, affect broad-scale air circulation patterns. From http://earthobservatory.nasa.gov/NaturalHazards.*

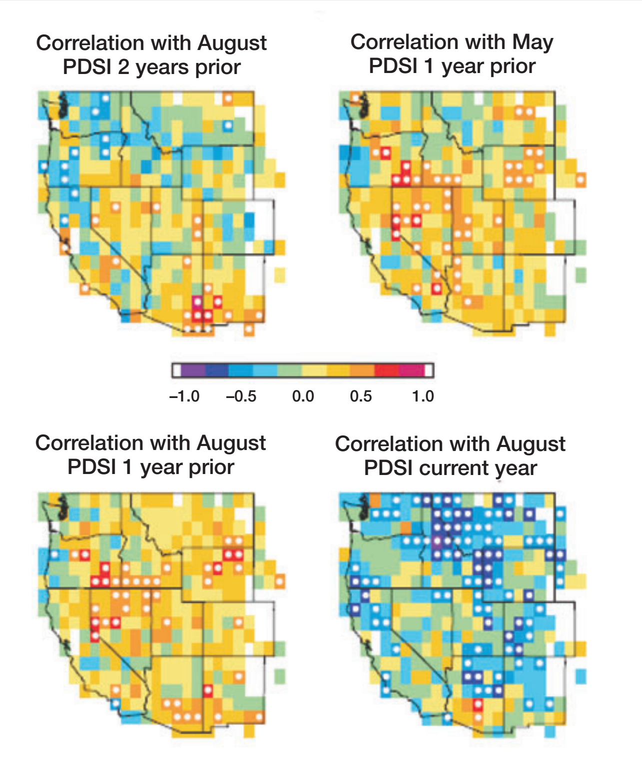


Figure 6. *Correlations of Palmer drought severity index (PDSI) with acres burned at varying time lags. White dots show correlations significant at 95% confidence level. Because the PDSI becomes more negative under dry conditions, negative correlations denote positive relationships with fire severity. 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.

Acknowledgements

We thank the participants in our fruitful discussions at the Las Cruces meeting, and the NSF LTER program for its support.

References

Albertson FW and Weaver JE. 1942. History of the native vegetation of western Kansas during seven years of continuous drought. *Ecol Monogr* **12**: 23–51.

Bachelet D, Neilson RP, Lenihan JM, and Drapek RJ. 2001. Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems* **4**: 164–85.

Bradley NL, Leopold AC, Ross J, and Huffaker W. 1999. Phenological changes reflect climate change in Wisconsin. *P Natl Acad Sci USA* **96**: 9701–04.

Breshears DD, Cobb NS, Rich PM, *et al.* 2005. Regional vegetation die-off in response to global-change type drought. *P Natl Acad Sci USA* **102**: 15144–48.

Briggs JM, Knapp AK, Blair JM, *et al.* 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* **55**: 243–54.

Brown JKM and Hovmøller MS. 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science* **297**: 537.

Carrasco JF, Casassa G, and Quimtana J. 2005. Changes of the 0°C isotherm and the equilibrium line altitude in central Chile during the last quarter of the twentieth century. *Hydrol Sci J* **50**: 933–48.

Chadwick OA, Derry LA, Vitousek PM, *et al.* 1999. Changing sources of nutrients during four million years of ecosystem development. *Nature* **397**: 491–97.

Chernov Y. 1985. The living tundra. Cambridge, UK: Cambridge University Press.

Connin SL, Virginia RA, and Chamberlain CP. 1997. Carbon isotopes reveal soil organic matter dynamics following arid land shrub expansion. *Oecologia* **110**: 374–86.

Dahlgren RA, Boettinger JL, Huntington GL, and Amundson RG. 1997. Soil development along an elevational transect in the western Sierra Nevada, California. *Geoderma* **78**: 207–36.

D'Antonio CM and Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* **23**: 63–87.

Dodds WK. 2006. Nutrients and the "dead zone": the link between nutrient ratios and dissolved oxygen in the northern Gulf of Mexico. *Front Ecol Environ* **4**: 211–17.

Duce RA and Tindale NW. 1991. Atmospheric transport of iron and its deposition in the ocean. *Limnol Oceanogr* **36**: 1715–26.

Easterling DR, Meehl GA, Parmesan C, *et al.* 2000. Climate extremes: observations, modeling, and impacts. *Science* **289**: 2068–74.

Eder B and Yu S. 2006. A performance evaluation of the 2004 release of models-3 CMAQ. *Atmos Environ* **40**: 4811–24.

Epstein PR. 1999. Climate and health. *Science* **285**: 347–48.

Fournier N, Pais VA, Sutton MA, *et al.* 2002. Parallelisation and application of a multi-layer atmospheric transport model to quantify dispersion and deposition of ammonia over the British Isles. *Environ Pollut* **116**: 95–107.

Gillette DA. 1999. A qualitative geophysical explanation for "hot spot" dust emission source regions. *Contrib Atmos Phys* **72**: 67–77.

Gillette DA and Hanson KJ. 1989. Spatial and temporal variability of dust production caused by wind erosion in the United States. *J Geophys Res* **94**: 2197–06.

Gonzalez P. 2001. Desertification and a shift of forest species in the West African Sahel. *Climate Res* **17**: 217–28.

Griffin DW, Garrison VH, Herman JR, and Shinn EA. 2001. African desert dust in the Caribbean atmosphere: microbiology and public health. *Aerobiologia* **17**: 203–13.

Gurney KR, Law RM, Denning AS, *et al.* 2002. Towards robust regional estimates of CO_2 sources and sinks using atmospheric transport models. *Nature* **415**: 626–30.

Helbing D and Nagel K. 2004. The physics of traffic and regional development. *Contemp Phys* **45**: 405–26.

Hicke J, Logan AJA, Powell J, and Ojima DS. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *J Geophys Res–Biogeosciences* **111**: G02019, doi:02010.01029/02005JG000101.

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: the physical science basis. Summary for policymakers. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: IPCC.

Johnson LE, Ricciardi A, and Carlton JT. 2001. Overland dispersal of aquatic invasive species: a risk assessment of transient recreational boating. *Ecol Appl* **11**: 1789–99.

Kaufman M. 2006. Research team seeking clues to a hurricane's birth. *Washington Post*. **Aug 7**: Sect A: 6.

Kerr RA 2004. A few good climate shifters. *Science* **306**: 591–601.

Kiesecker JM, Blaustein AR, and Belden LK. 2001. Complex causes of amphibian population declines. *Nature* **410**: 681–84.

Knapp AK, Fay PA, Blair JM, *et al.* 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* **298**: 2202–05.

Lipson DA, Schadt CW, and Schmidt SK. 2002. Changes in soil microbial community structure and function in alpine dry meadow following spring snow melt. *Microb Ecol* **43**: 307–14.

Magnuson JJ, Robertson DM, Benson BJ, *et al.* 2000. Historical trends in lake and river ice cover in the northern hemisphere. *Science* **289**: 1743–46.

Martinec J, Rango A, and Roberts R. 1998. Snowmelt runoff model (SRM) user's manual. Berne, Switzerland: University of Berne.

Miller C and Urban DL. 2000. Connectivity of forest fuels and surface fire regimes. *Landscape Ecol* **15**: 145–54.

Monson RK, Lipson DL, Burns SP, *et al.* 2006. Winter forest soil respiration controlled by climate and microbial community composition. *Nature* **439**: 711–14.

Mote PW, Hamlet AF, Clark MP, and Lettenmaier DP. 2005. Declining mountain snowpack in western North America. *B Am Meteorol Soc* **86**: 39–49.

Nolin AW and Daly C. 2006. Mapping "at risk" snow in the Pacific Northwest. *J Hydrometeorol* **7**: 1164–71.

Okin GS, Mahowald N, Chadwick OA, and Artaxo P. 2004. The impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. *Global Biogeochem Cy* **18**. doi:10.1029/2003GB002145.

Osterkamp TE. 2003. A thermal history of permafrost in Alaska. In: Phillips M, Springman SM, and Arenson LU (Eds). Proceedings of the 8th International Conference on Permafrost. 2003 Jul 21–25; Zurich, Switzerland. Lisse, Netherlands: AA Balkema.

Painter TH, Barrett AP, Landry CC, *et al.* 2007. Impact of disturbed desert soils on duration of mountain snow cover. *Geophys Res Lett* **34**: L12502. doi:10.1029/2007GL030284.

Pearson RG and Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol and Biogeogr* **12**: 361–71.

Peters DPC, Pielke Sr RA, Bestelmeyer BT, *et al.* 2004. Cross scale interactions, nonlinearities, and forecasting catastrophic events. *P Natl Acad Sci USA* **101**: 15130–35.

Peters DPC, Bestelmeyer BT, Herrick JE, *et al.* 2006. Disentangling complex landscapes: new insights to forecasting arid and semiarid system dynamics. *BioScience* **56**: 491–501.

Peters DPC, Sala OE, Allen CD, *et al.* 2007. Cascading events in linked ecological and socio-economic systems: predicting change in an uncertain world. *Front Ecol Environ* **5**: 221–24.

Peters DPC, Groffman PM, Nadelhoffer KJ, *et al.* 2008. Living in an increasingly connected world: a framework for continental-scale environmental science. *Front Ecol Environ* **6**: 229–37.

Pyne S. 1997. Fire in America: a cultural history of wildland and rural fire. Seattle, WA: University of Washington Press.

Rango A, Martinec J, and Roberts R. 2007. Relative importance of glacier contributions to streamflow in changing climate. In: Wilson J (Ed). Proceedings of the IASTED International Conference on Water Resources Management. 2007 Aug 20–22; Honolulu, Hawaii. Calgary, Canada: Acta Press.

Rango A and Martinec J. 2000. Hydrological effects of a changed climate in humid and arid mountain regions. *World Resour Rev* **12**: 493–508.

Reynolds JF, Virginia RA, Kemp PR, *et al.* 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecol Monogr* **69**: 69–106.

Rosenfeld D, Rudich Y, and Lahav R. 2001. Desert dust suppressing precipitation: a possible desertification feedback loop. *P Natl Acad Sci USA* **98**: 5975–80.

Schlesinger WH, Fonteyn PJ, and Reiners WA. 1989. Effects of overland flow on plant water relations, erosion, and soil water percolation on a Mojave Desert landscape. *J Soil Sci Soc Amer* **53**: 1567–72.

Schneider DW, Ellis CD, and Cummings KS. 1998. A transportation model assessment of the risk to native mussel communities from zebra mussel spread. *Conserv Biol* **12**: 788–800.

Vergara W, Deeb AM, Valencia AM, *et al.* 2007. Economic impacts of rapid glacier retreat in the Andes. *EOS* **88**: 261–64.

Vörösmarty CJ, Green P, Salisbury J, and Lammers RB. 2000. Global water resources: vulnerability from climate change and population growth. *Science* **289**: 284–88.

Wainwright J, Parsons AJ, Schlesinger WH, and Abrahams AD. 2002. Hydrology–vegetation interactions in areas of discontinuous flow on a semi-arid bajada, southern New Mexico. *J Arid Environ* **51**: 319–38.

Westerling AL, Gershunov A, Brown TJ, *et al.* 2003. Climate and wildfire in the western United States. *B Am Meteorol Soc* **84**: 595–604.

Westerling AL, Hidalgo HG, Cayan DR, and Swetnam TW. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* **313**: 940–43.

Woodhouse CA and Overpeck JT. 1998. 2000 years of drought variability in the central United States. *B Am Meteorol Soc* **79**: 2693–2714.

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.

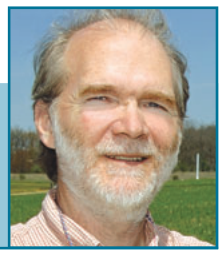
Equal in importance to collaborations across physical networks are collaborations across disciplinary networks. If there is one overarching lesson to be learned from the evolution of LTER, it is the crucial importance of engaging with other disciplines – and especially with the social and behavioral 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,

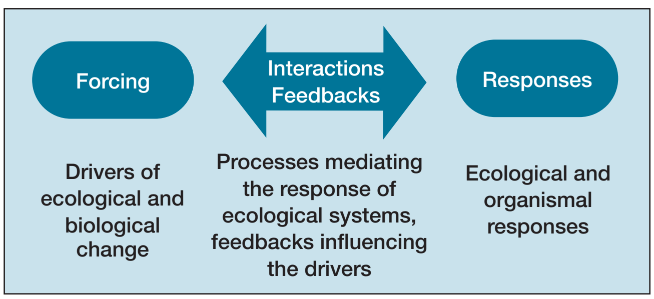


Figure 1. *NEON differs from other environmental monitoring networks because, by design, it integrates processes, interactions, and responses.*

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.

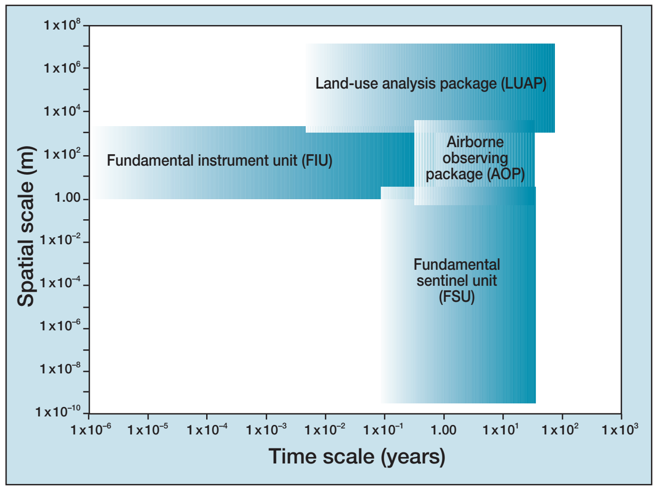


Figure 2. *A Stommel diagram of temporal and spatial scales for the components of the observational design of NEON.*

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

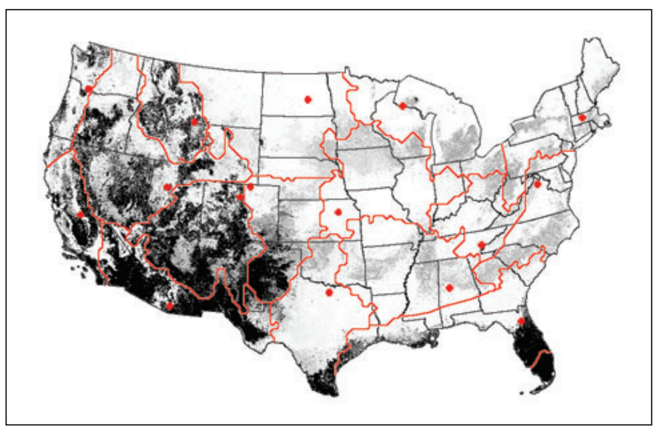


Figure 3. *NEON domain boundaries for the conterminous US (in red) determined using the procedure described in WebPanel 1. Locations of candidate core sites (Table 2) are represented by red symbols. The shading from white (well-represented) to black indicates the quality of representation for a given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

Acknowledgements

We thank the participants in the Sioux Falls workshop and J MacMahon, P Duffy, T Hobbs, B Wee, D Johnson, K Remington, D Greenlee, H Loescher, A Marshall, B Hayden, D Urban, and J Franklin for their contributions to the NEON design. We thank S Aulenbach for his assistance with graphics.

References

Bailey RG. 1983. Delineation of ecosystem regions. *J Environ Manage* **7**: 365–73. doi:10.1007/BF01866919.

Berkner LV and Marshall LC. 1964. The history of oxygenic concentration in the Earth's atmosphere. *Discuss Faraday Soc* **37**: 122–41. doi:10.1039/DF9643700122.

Crutzen PJ and Steffen W. 2003. How long have we been in the Anthropocene Era? *Climatic Change* **61**: 251–57.

Doney SC and Schimel DS. 2007. Carbon and climate system coupling on timescales from the Precambrian to the Anthropocene. *Annu Rev Environ Resour* **32**: 31–66.

Field C, DeFries R, Foster D, *et al.* 2006. Integrated science and education plan for the National Ecological Observatory Network. www.neoninc.org/documents/ISEP_2006Oct23.pdf. Viewed 8 Mar 2008.

Hargrove WW and Hoffman FM. 1999. Using multivariate clustering to characterize ecoregion borders. *Comput Syst Sci Eng* **1**: 18–25.

Hargrove WW and Hoffman FM. 2004. The potential of multivariate quantitative methods for delineation and visualization of ecoregions. *Environ Manage* **34**: S39–S60.

Hargrove WW and Pickering J. 1992. Pseudoreplication: a sine qua non for regional ecology. *Landscape Ecol* **6**: 251–58.

Omernik JM. 1987. Ecoregions of the conterminous United States. *Ann Assoc Am Geogr* **77**: 118–125. doi:10.1111/j.1467-8306.1987.tb00149.x.

Ruddiman WF. 2003. The Anthropogenic greenhouse era began thousands of years ago. *Climatic Change* **61**: 261–93. doi:10.1023/B:CLIM.0000004577.17928.fa.

Authors – left to right
Michael Keller
NEON Inc, Boulder, CO; USDA Forest Service, PR
David S Schimel
NEON Inc, Boulder, CO
William W Hargrove
USDA Forest Service, Asheville, NC
Forrest M Hoffman
Oak Ridge National Laboratory, Oak Ridge, TN