

# 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).

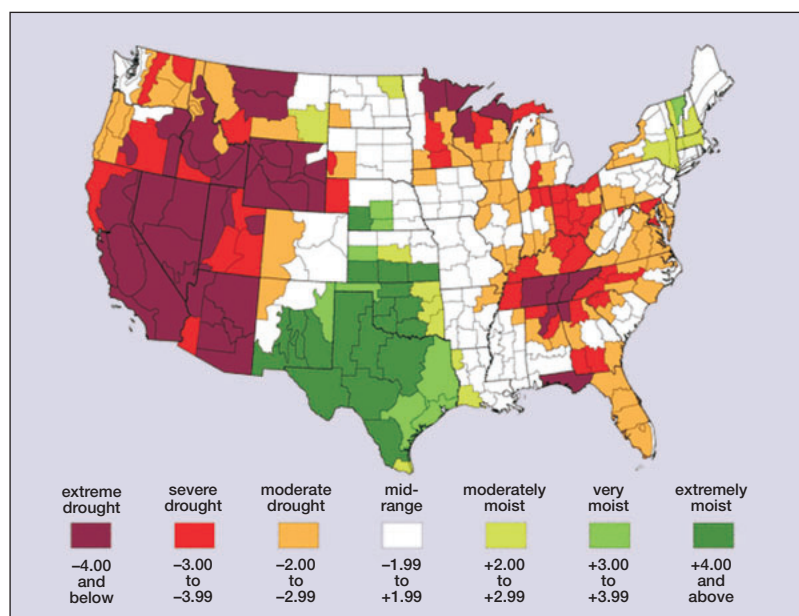
Climate also influences human population distribution and human land-use practices (Peters *et al.* 2006). For example, changes in land use, driven by government policies and technological change, interacted with long-term, extreme drought to result in one of the most serious regional- to continental-scale 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

## 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

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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](http://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.

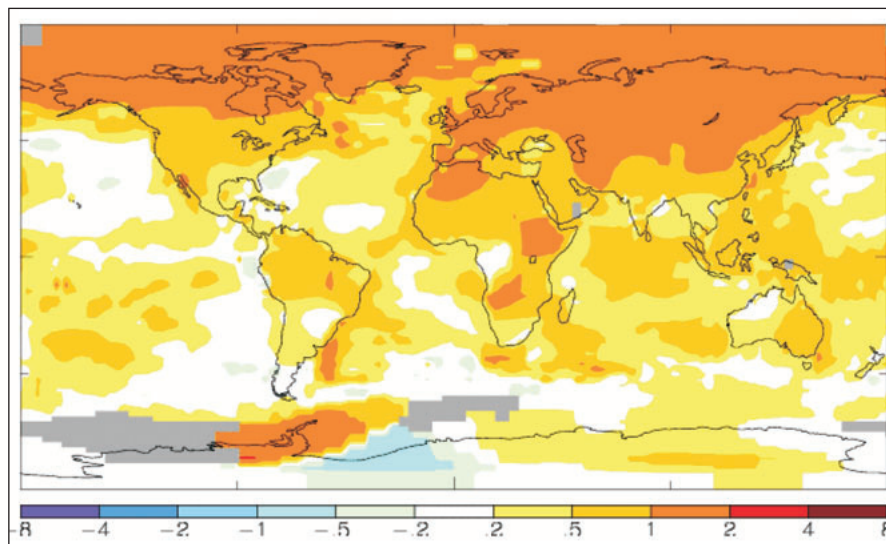
In 2007, severe droughts occurred across much of the western US, the upper Great Lakes, and parts of the Southeast (Figure 1). Predicting the ecological impacts of future droughts has been identified as a national research priority. Droughts restrict biological activity and therefore change ecosystem 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.

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<sub>2</sub> 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 pat-



**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>.

terns 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).

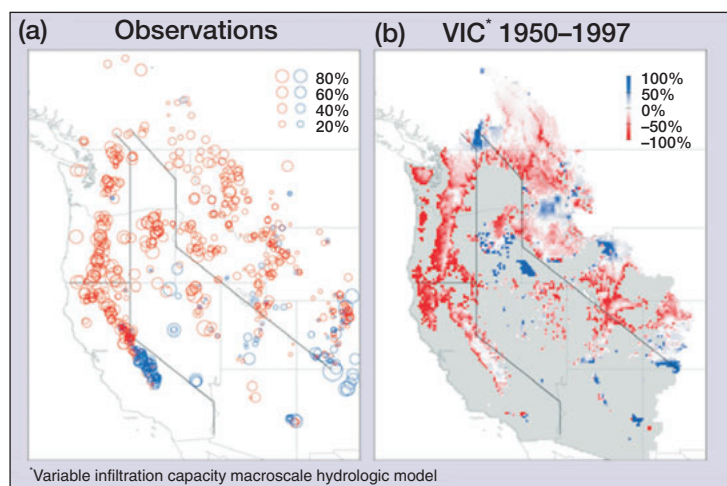
### ■ Increased mean annual temperatures

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](http://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 con-

tinental 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.

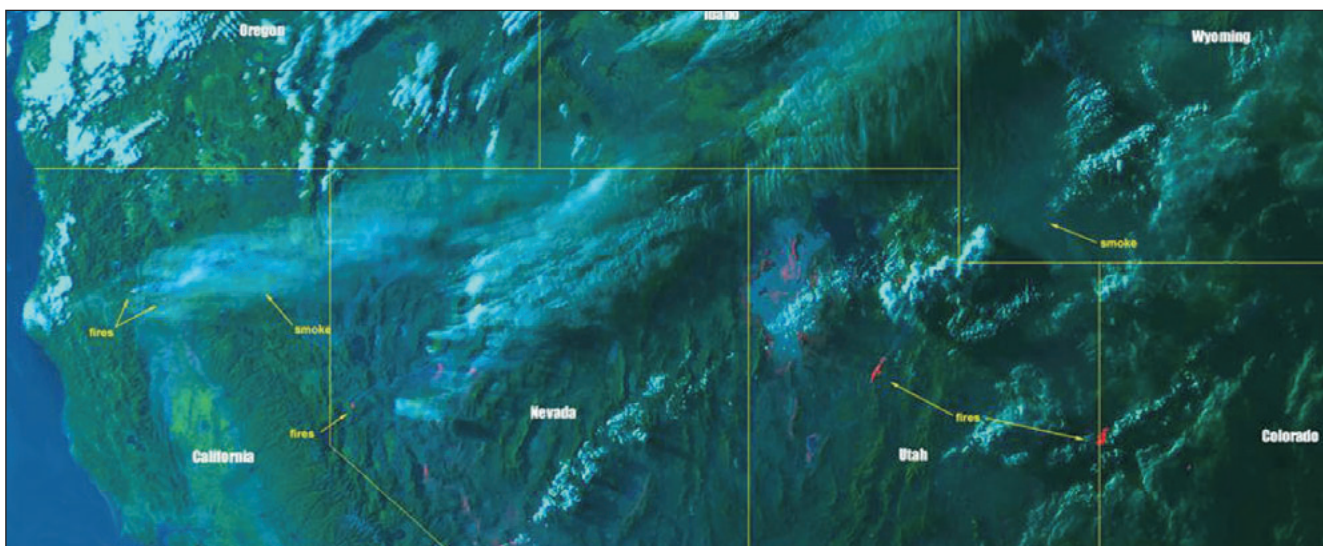
The earlier disappearance of the snowpack will result in earlier commencement of biological activity in the spring, which is often delayed until the disappearance of snow, when temperatures can rise above 0°C to become more suitable for rapid metabolism. This phenological effect will result in an earlier 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  $5.8 \pm 1.6$  days per century; meanwhile, ice breakup has occurred an average of  $6.5 \pm 1.2$  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.

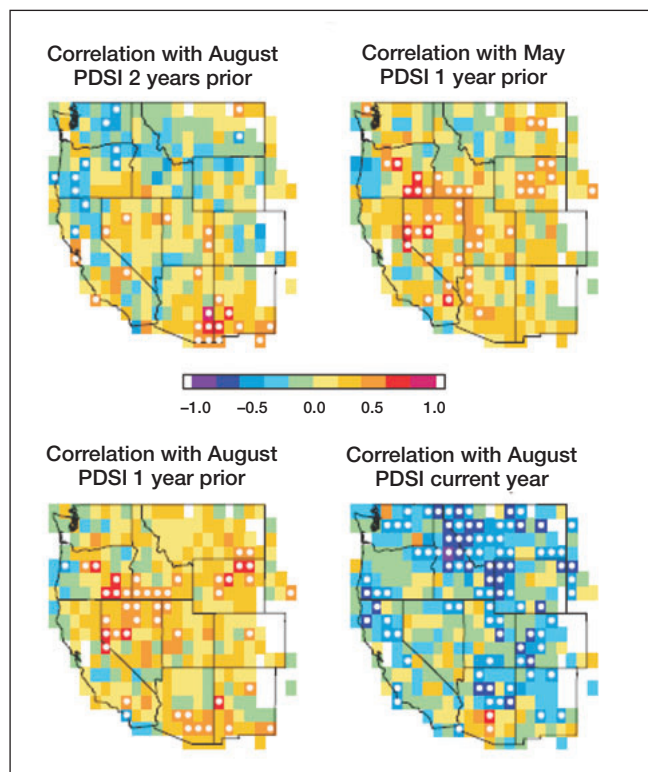
Wildfires often start with a single ignition point, yet can increase rapidly to affect large spatial extents. Fire behavior across scales (rate, direction, intensity) is difficult to predict because of positive feedbacks among local and regional weather (eg wind speed and direction, relative humidity), 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<sub>2</sub> 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](http://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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