

# Ecosystem Dynamics and Disturbance in Mountain Wildernesses: Assessing Vulnerability of Natural Resources to Change

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**Abstract**—An integrated program of ecosystem modeling and extensive field studies at Glacier and Olympic National Parks has quantified many of the ecological processes affected by climatic variability and disturbance. Models have successfully estimated snow distribution, annual watershed discharge, and stream temperature variation based on seven years of monitoring. Various climatic scenarios were applied with the models to examine potential future wilderness conditions. This modeling indicates that reduced net primary productivity and altered disturbance patterns can be expected in dry, east-side forest ecosystems in Montana and Washington under climatic warming. In addition, empirical studies show that climatic variability has strong teleconnections with tree growth and regeneration at annual to decadal scales, resulting in predictable, directional changes under different climatic scenarios. A transect of mountain bioregions from the Pacific Coast to the Rocky Mountains, which builds on past research, is determining how future climatic variability will affect wilderness in the context of regional ecosystem dynamics.

Mountains are a dominant feature of our planet, covering one-fifth of the terrestrial biosphere and being home to one-tenth of the earth's human inhabitants (Messerli and Ives 1997). Because of their steep environmental gradients and complex topography, mountains also have higher rates of endemism, greater ecological heterogeneity and more biodiversity than many lowland environments (Beniston and Fox 1996; Denniston 1995). Equally important, mountains are the 'water towers' of the world, providing 50% of the freshwater that humans consume (Liniger and others 1998). Mountains contain sacred sites for most of the world's major religions and are now part of robust tourism and recreation economies. Because mountains were typically last to be developed and are still relatively underdeveloped, they often are refugia for organisms extirpated elsewhere (such as grizzly bear [*Ursus arctos*]) and are disproportionately well-represented in the world's protected areas, such as national parks and designated wildernesses. Such wilderness areas

In: McCool, Stephen F.; Cole, David N.; Borrie, William T.; O'Loughlin, Jennifer, comps. 2000. Wilderness science in a time of change conference—Volume 3: Wilderness as a place for scientific inquiry; 1999 May 23–27; Missoula, MT. Proceedings RMRS-P-15-VOL-3. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

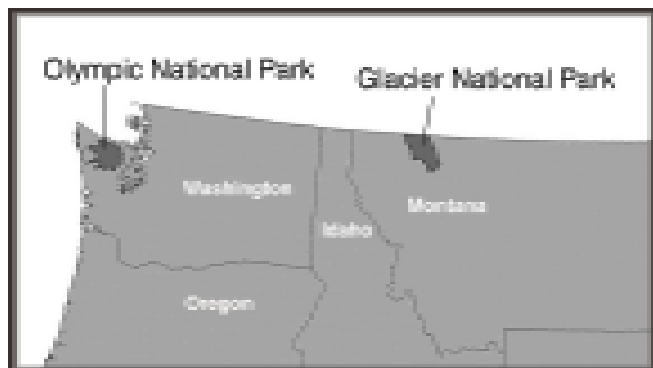
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also are the only places where we can learn how relatively unaltered natural systems work, and they serve as benchmarks against which the state of human-dominated systems can be compared. Thus, mountain wildernesses are globally important and affect people even great distances from mountains.

Mountain wildernesses worldwide are being affected by global-scale environmental stressors, such as increasing atmospheric pollution and climatic change. They also are being impacted by nearby landscape fragmentation, introductions of diseases, exotic plant invasions, increasing recreational pressures and, over the past century, alteration of natural fire regimes.

The potential for ecological change in mountainous national parks of the western United States was recognized and addressed by the National Park Service (NPS) when it initiated research programs in 1990 under the U.S. Global Change Research Program. The NPS program objectives were to (1) contribute to our understanding of ecosystem response to climatic change, (2) detect and document changes attributable to climatic change as part of a national monitoring network and (3) assess the future impacts of climatic change on the natural resources the NPS is charged with protecting in the parks.

Two of the national parks included in the NPS global change program were Olympic and Glacier National Parks (fig. 1). The global change program was transferred to the U.S. Geological Survey in 1996 but the overall goals remained the same. In this paper, we summarize some of the



**Figure 1**—Olympic and Glacier National Parks were two parks studied under the National Park Service's Global Change Research Program.

responses of Glacier and Olympic National Parks to global-scale environmental change and contrast differences in their responses due to regional sources of disturbance. We describe an approach for integrating the effects of differently scaled ecosystem stressors into assessments of the possible future conditions of mountain wildernesses.

## Study Areas

Glacier and Olympic National Parks are both large, wilderness-dominated parks near the United States-Canada border in the northern Rocky Mountains and on the Olympic Peninsula, respectively (fig. 1). Each Park encompasses mountains with similar topographic relief, numerous glaciers and expansive conifer forests; each is snow-dominated, acts as the headwaters for its region and contains relatively intact floral and faunal assemblages. Climate is controlled by dominant air masses, providing Olympic with a maritime climate and Glacier with a more continental climate. Thus, winter temperatures are moderate in the Olympics and cold in the northern Rockies. Summer precipitation as a proportion of annual precipitation is greater in the northern Rockies than in Olympics. Precipitation varies dramatically between westside and eastside locations within each park. For example, precipitation in the Olympic Mountains ranges from >600 cm/yr on Mt. Olympus to only 40 cm/year in the northeastern rainshadow. Precipitation in the northern Rockies varies from 350 cm/yr (westside, high elevation) to 30 cm/yr (eastside, low elevation). This contrast in precipitation over relatively small distances has a profound impact on microclimate, vegetation distribution and disturbance regimes (Peterson and others 1997).

Vegetation is dominated by coniferous forest, with species distribution and abundance varying along elevational gradients (extending to alpine vegetation) and from westside to eastside (including grassland). The western Olympics are dominated at low elevations by temperate rainforests with high biomass and abundant woody debris. Biomass and productivity generally are lower in the northern Rockies. The parks have 10 coniferous species and several plant communities in common, which allows for comparisons of biotic responses to climatic shifts.

## Responses to Climatic Change

The environments of both parks have experienced a warming trend since the end of the "Little Ice Age", a ca. 250-year cold period ending around 1850. Historic temperature records since 1880 from locales near current park boundaries show an increase of 1.7° C or more in annual average temperature (Finklin 1984). The natural resources of each Park have responded accordingly.

### Glaciers

Glaciers have generally receded for the past 150 years, with several periods of rapid retreat. At Glacier National Park, for instance, only 37 glaciers remain of the 150 estimated to have existed around 1850 (Carrara 1989). Furthermore, the remaining glaciers have been reduced to one-third their previous areas or less (Key and others in press). The

total ice and permanent snow coverage of the Park has been reduced 72%, and numerous valleys no longer have any glaciers in their upper reaches. The period of accelerated glacial retreat early this century was correlated with an upward shift in summer temperatures (fig. 2) and, despite considerable variability in summer temperatures and slight increases in precipitation, glaciers continued to shrink. Continued warming is forecast to eliminate all glaciers at Glacier National Park by 2030 (Hall 1994). Similar glacier retreats have been recorded for the Blue Glacier and others in the Olympic Mountains, although the loss of entire glaciers is not as prevalent due to a higher-snowfall climate.

Glaciers are excellent barometers of climatic change because, unlike biological organisms, they do not adapt to change but merely reflect them. Glaciers also tend to reflect decadal or longer climatic trends rather than year-to-year variation. Thus, the documented glacial recessions in these parks are indicators of directional climate change and suggest that other ecosystem changes are likely taking place. The loss of glaciers in mountain watersheds may have significant ecological effects because glacial meltwater can be important in providing minimum baseflow and cool water temperatures for streams during late summer. This, in turn, has implications for temperature-sensitive stream macroinvertebrates and the biota dependent on them.

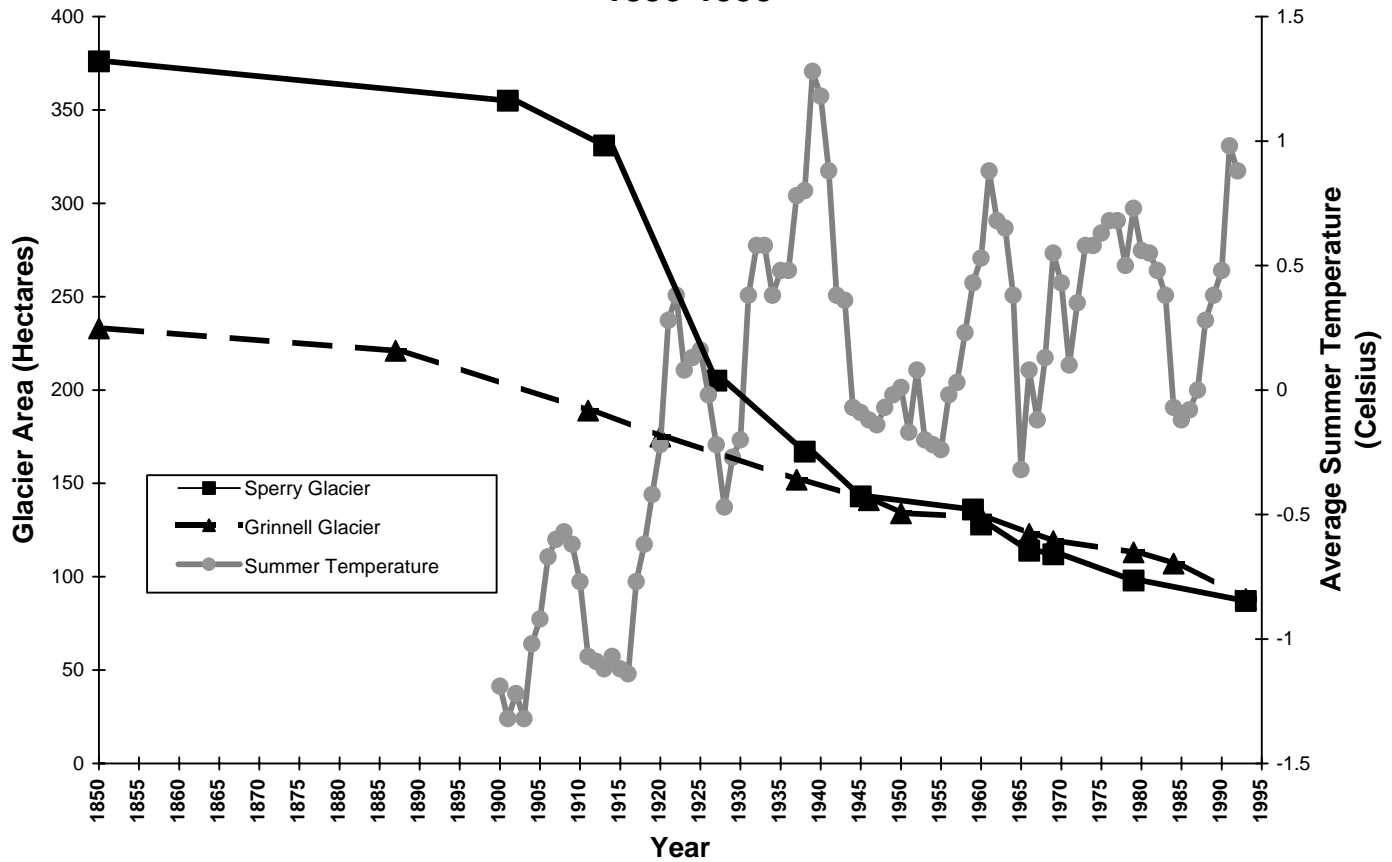
### High-Elevation Forest Responses

Many mountain environments have experienced greater increases in average temperature than have lowland areas (Oerlemans 1994). High-elevation tree species have responded where temperature and permanent snow coverage previously limited tree establishment and growth. In Pacific Northwest mountains, subalpine fir (*Abies lasiocarpa*) have been displacing subalpine meadows, particularly since the 1930s (Rochefort and Peterson 1996). This rapid regeneration of subalpine fir is most pronounced on the (wet) west side of the mountains during periods of warmer, drier climate and on the (dry) east side of the mountains during periods of cooler, wetter climate. Precipitation is more critical than temperature where duration of snowpack limits length of the growing season (west side) and summer soil moisture limits seedling survival (east side). Analysis of repeat photographs in Glacier National Park has documented similar invasions of meadows by subalpine fir. If climate becomes warmer and drier during the next century, continued regeneration of trees may displace much of the remaining meadows within wetter regions of the subalpine forest-meadow mosaic of both Parks.

More vigorous establishment and growth of high-elevation forests is also evident at treeline. At Logan Pass in Glacier National Park, krummholz patches have expanded to fill inter-patch spaces, and there has been a demonstrable trend of krummholz shifting to upright tree forms (Klasner 1998). Although treelines have not moved upslope, the treeline ecotone has become more abrupt as the density of krummholz increased (Butler and others 1994).

In addition to increased establishment of trees and expansion of krummholz at treeline, high-elevation forests at several locations in western North America have experienced increased growth rates, presumably related to increased temperature, increased atmospheric CO<sub>2</sub>, less

## Changes in Glacier Area and Summer Temperature 1850-1995



**Figure 2**—An upward shift in summer temperatures in Glacier National Park accelerated the melting of two park glaciers, Sperry and Grinnell. Glaciers respond slowly to temperature shifts and incorporate numerous year-to-year climatic variations into an integrated response.

extreme or variable conditions and other atmospheric factors (Peterson 1998). The response of tree growth to climatic variability is spatially and temporally variable with aspect, elevation, landform, soil and other site characteristics being important (Ettl and Peterson 1995). However, duration of snowpack dominates growth response to climate by affecting the length of growing season. Thus, predictions that snowpack will be two months shorter in duration at Glacier National Park (Running and Nemani 1991) or that snowlines may rise in Pacific Northwest mountains (Lettenmaier 1992) have profound implications for forest growth response in these wilderness areas.

### Responses to Other Stressors

Although both parks have been subjected to similar global-scale environmental change, there are differences in the other stressors to which they are exposed. These will shape ecosystem responses to climatic change in ways still unquantified.

The Olympic Mountains owe much of their unique species assemblage to their partial isolation on a peninsula, surrounded on three sides by seawater and to the south by a major river. This geographic situation altered the impacts of

past glaciations on this biota (Peterson 1998), accentuating the ecological traits of a biogeographic isolate. In addition, Olympic National Park is now a more distinct ecological island due to extensive landscape alteration on the peninsula. An abrupt change in vegetation that mirrors the border between national park lands and state and private land is due to extensive logging and other human activities. This loss of connectivity to an intact regional landscape inhibits the dynamic flow of species, energy and other resources necessary to maintain biodiversity and other ecosystem attributes. The increased boundary with altered landscapes increases rates of exotic plant establishment and the potential for introduced diseases. Indeed, Olympic National Park has 166 exotic plant species. In contrast, Glacier National Park is surrounded by mostly intact landscapes, with its sister park in Canada, Waterton Lakes National Park, to the north and the Bob Marshall Wilderness Complex to the south, providing regional connectivity along the Continental Divide. Such landscape connectivity allowed natural recolonization by gray wolves (*Canis lupus*) into Glacier National Park and allows Glacier to act as a source for grizzly bear dispersal.

Another important contrast is in the proximity to urban areas. Olympic National Park borders Puget Sound, where

major cities and millions of people are located. One measure of this potential impact is in the levels of tropospheric ozone in Puget Sound, which have exceeded U.S. national ambient air quality standards on numerous occasions and have reached 150 ppbv (a measure of average ozone concentration) (Brace and Peterson 1998, Cooper and Peterson 1999). Ozone concentrations frequently exceed 80 ppbv during the summer months, a level considered potentially injurious to sensitive vascular plant species (Reich and Amundson 1985). In contrast, Glacier National Park is located far from major cities and has near-background levels of ozone for most of the year and peak ozone concentrations of 60 ppbv.

Although Glacier potentially is subjected to fewer sources of disturbance than Olympic, it functionally has lost a keystone species, the whitebark pine (*Pinus albicaulus*), to an introduced pathogen (Kendall 1995). White pine blister rust (*Cronartium ribicola*) was introduced in the early 20th century on plant stock from Europe and has been progressively killing whitebark pine throughout its range. Glacier has lost 90% of this high-elevation tree species to blister rust, leaving tree “skeletons” in its wake. Whitebark pine nuts provided a critical food source for Clark’s nutcracker (*Nucifraga columbiana*), grizzly bear, and Native Americans prior to its loss from the subalpine areas of the Park. Whitebark pine appears to facilitate subalpine fir establishment near treeline, and may play an important role in snow retention in subalpine forests. In contrast, Olympic National Park has few whitebark pine, infection rates have been lower, and, consequently, this keystone species has not been lost.

In addition to climatic change and regional external impacts described above, both parks have undergone change within their boundaries from other disturbance sources. There has been heavy historic use of the parks from eras when large lodges and roads were built and the backcountry saw large groups of horses used to transport visitors to the alpine areas of the mountains. Later infrastructure development included campgrounds, visitor centers and restaurants. Perhaps the greatest human impact on park ecosystems stems from the exclusion of lightning-caused fires, which has led to increased fuel loads, promoted insect outbreaks and altered nutrient cycling in some forests with high-frequency fire regimes. Trying to account for the effects of park use and management in the context of a changing climate and regional landscape disturbance presents an almost unmanageable list of factors that can drive ecosystem change. Achieving a coherent understanding on which to base decisions presents scientists and managers alike with a formidable challenge and necessitates new approaches and new tools to address such complicated issues and their interactions.

## Implementing an Integrated Approach

Ecosystem modeling provides a partial solution to such problems because computers can store and organize large amounts of existing information and simulate quantified ecosystem responses for measuring management outcomes or different levels of disturbance. This “cyber-symbiosis” between ecologists, who provide the established ecological relationships reduced to computer code, and computers,

with vast memory and ability to process multiple relationships simultaneously, gives us unprecedented opportunities for understanding wilderness ecosystems and making natural resource decisions with a better foundation.

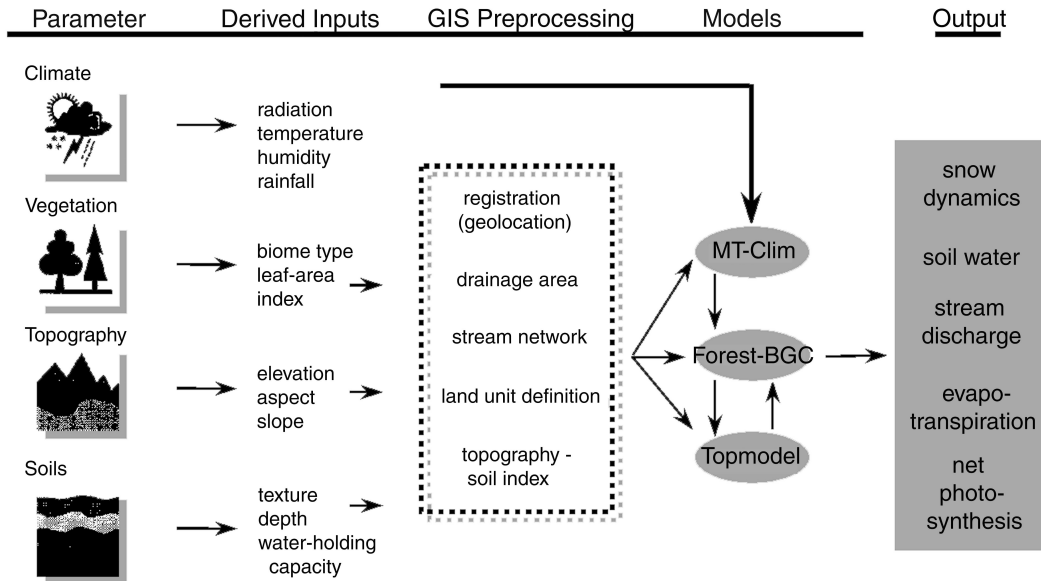
In order to better understand the impacts of climatic change and regional landscape disturbance on mountain wilderness integrity in Olympic and Glacier National Parks, we developed integrated programs of ecosystem modeling and extensive field studies with numerous university and federal agency collaborators whose work is cited below. Our goals were to (1) quantitatively estimate the major ecological processes of these areas, (2) compare simulated and observed wilderness responses to current climate and (3) use these capabilities to estimate responses to future stressors, such as increased climatic variability or changes in frequency and intensity of forest fires. This approach was initially developed and applied to Glacier National Park wilderness and is summarized below.

We further developed and used the Regional Hydro-Ecological Simulation System (RHESSys) to estimate ecosystem processes and changes in mountain environments (Band and others 1991, 1993). RHESSys combines remote sensing, ecological modeling and geographic information system technologies to produce and map spatially explicit estimates of various processes such as evapotranspiration and hydrologic outflows (fig. 3). Satellite-based sensors, such as those on the Landsat Thematic Mapper, provide estimates of leaf area index, a measure of plant photosynthetic capability for each spatial unit throughout the mountain topography. Using a daily mountain climate estimator, such as MTCLIM (Hungerford and others 1989) or DAYMET (Thornton and others 1997), and algorithms describing tree physiology (Running and Gower 1991), RHESSys estimates net primary productivity and other dynamic ecosystem properties for combinations of slope, aspect, and elevation. Given daily climatic data for a particular period, RHESSys also calculates daily water balance for a drainage and provides stream discharge. A topographically sensitive routing routine was incorporated to better distribute water dynamically through mountain watersheds (White and Running 1994). This improved estimates of stream discharge and provided insights into the sensitivity of the model to scaling issues.

Another model, FIRE-BGC, combines a gap-phase succession model and a forest biogeochemistry model to estimate stand-level dynamics, accumulated carbon and tree regeneration, growth, and mortality (Keane and others 1996). This allows FIRE-BGC to estimate large woody debris, duff depth and other characteristics important for assessing forest fire frequency and, with FARSITE (Finney 1998), to map the perimeter and intensity of those fires. By explicitly modeling the successional response of the landscape to simulated forest fires, FIRE-BGC forecast future landscape mosaics and their influence on future ecosystem processes (Keane and others 1999). Overall, RHESSys and FIRE-BGC reasonably predicted the structure and composition of mountain forest communities and the daily rates of ecosystem processes at various spatial scales (White and others 1998).

However, model performance needed to be determined by comparing simulated ecosystem processes with the real thing—measurements of key outputs. Our model validation used seven years of field data on mountain climatology,

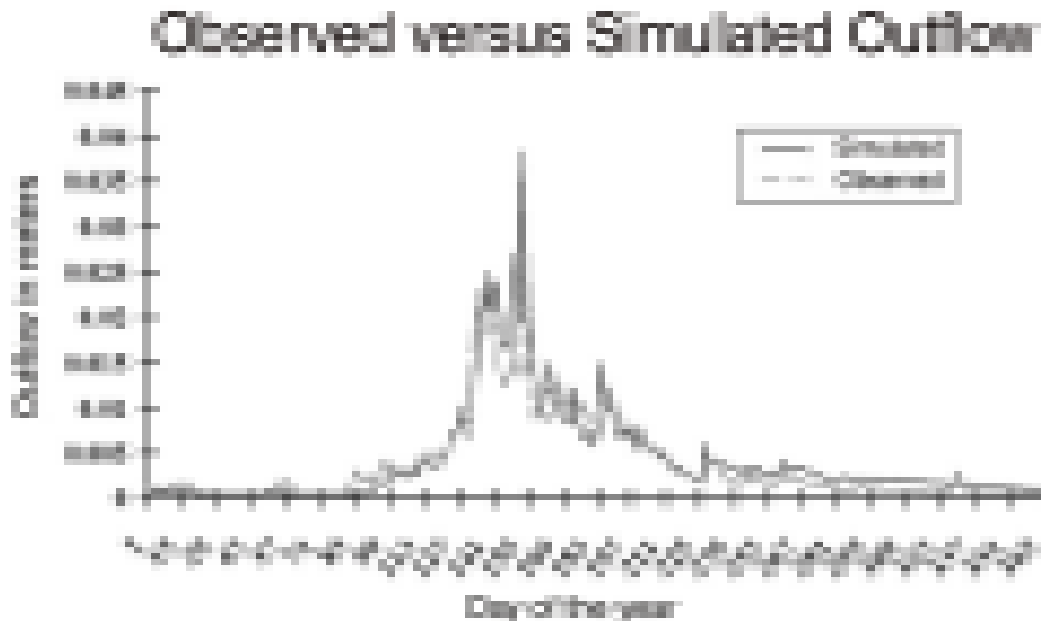
## Regional Hydro-Ecological Simulation System (RHESSys)



**Figure 3**—A depiction of inputs, outputs, and modeling steps used in one of the simulation systems for estimating ecosystem processes at Glacier National Park.

snow distribution, glacier activity, stream hydrology, aquatic biota, forest demographics and soil respiration. For instance, over 4,500 snow measurements, taken from a variety of slopes and aspects in two topographically diverse mountain watersheds (approximately 400 km<sup>2</sup> each), correlated well with model estimates (Fagre and others 1997). Similarly, hydrographs (daily discharges measured for a

year) from seven streams continuously monitored for seven years compared well with those simulated by the models for that period using climatic data (fig. 4). In watersheds with remnant glaciers, however, higher observed values during late summer underscored both the contributions of glacial meltwater to streamflow and the need to include this source in future models of mountain hydrology.



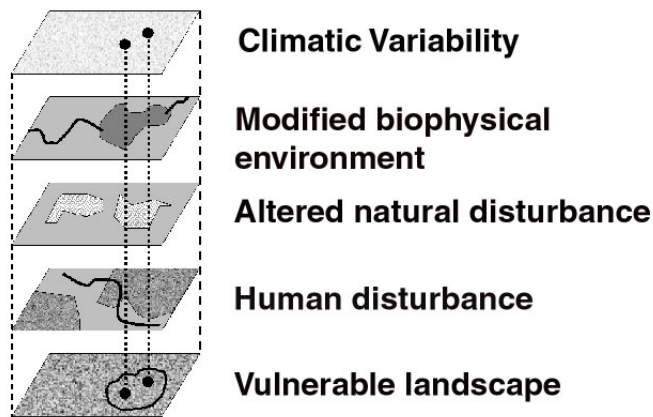
**Figure 4**—Comparison of observed daily stream outflow and computer-simulated outflow for McDonald Creek in Glacier National Park.

Modeled stream temperatures closely reflected observed values from electronic dataloggers placed in the streams at various elevations (Fagre and others 1997). Frequent monitoring of stream macroinvertebrates clearly showed that predictable species replacement along different sections of the streams was tied to water temperature rather than other variables such as substrate particle size (Hauer and others 1999). This suggests that general warming of stream water temperatures due to earlier snowmelt and loss of glaciers will cause an upslope migration of those macroinvertebrates with narrow thermal tolerances.

Numerous forest plots throughout both study watersheds were selected to represent various combinations of slope, aspect and elevation. Measurements of stand characteristics, such as stem density, were made at each plot and compared to FIREBGC estimates for the same area. Most forest attributes were accurately estimated, but net primary productivity and evapotranspiration in early seral forest stand were underpredicted, because undergrowth ecosystem processes are not simulated at the detail provided for tree species (Keane and others 1996).

One of the major strengths of an ecosystem model, if successfully validated for a specific mountain wilderness, is the ability to envision future conditions by applying different climatic and management scenarios. For instance, with a 30% increase in precipitation and 0.5° C increase in annual temperature for the next 200 years, many mesic tree species, such as western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*), are predicted to expand in the valley bottoms on the west side (White and others 1998). However, fuel loads and potential fire intensity, size and frequency also may increase, especially if fire suppression policies keep interim fire frequency low (Keane and others 1999). Net primary productivity and available nitrogen increase when fire exclusion is reduced. Subalpine tree communities, however, become increasingly nitrogen-stressed, especially when interannual variability is increased in the modeled future scenarios (White and others 1998). Upper and lower treelines shift upward, and increased smoke emissions (and lower air quality) may become future problems if prescribed natural fire management is used to counteract increased fuel loads (Keane and others 1997).

In addition to evaluating the impacts of management and future climate on wilderness resources, ecosystem modeling can be used to improve current management programs. For instance, monitoring will be more efficient if focused on resources or areas that models suggest are most vulnerable to change (fig. 5). Using the same climatic scenario described above, we found that one sub-drainage of the McDonald watershed would have water temperature increases four to five times greater than others. This area would be a candidate for detecting early and pronounced change and would indicate more pervasive changes to come. We also examined a climatic change scenario in which average temperatures did not increase, but the variability did. The eastern side of Glacier National Park responded more dramatically than did the western side of the Continental Divide. Significant reductions in net primary productivity occurred on the eastern side as trees underwent stress during more frequent droughts (White and others 1998). Some scenarios indicate an eventual conversion to grasslands. Thus, the



**Figure 5**—Ecosystem models can identify potentially more vulnerable landscapes within mountainous regions by accounting for multiple sources of disturbance and variability. These vulnerable landscapes can be the focus of monitoring programs for early detection of regional change.

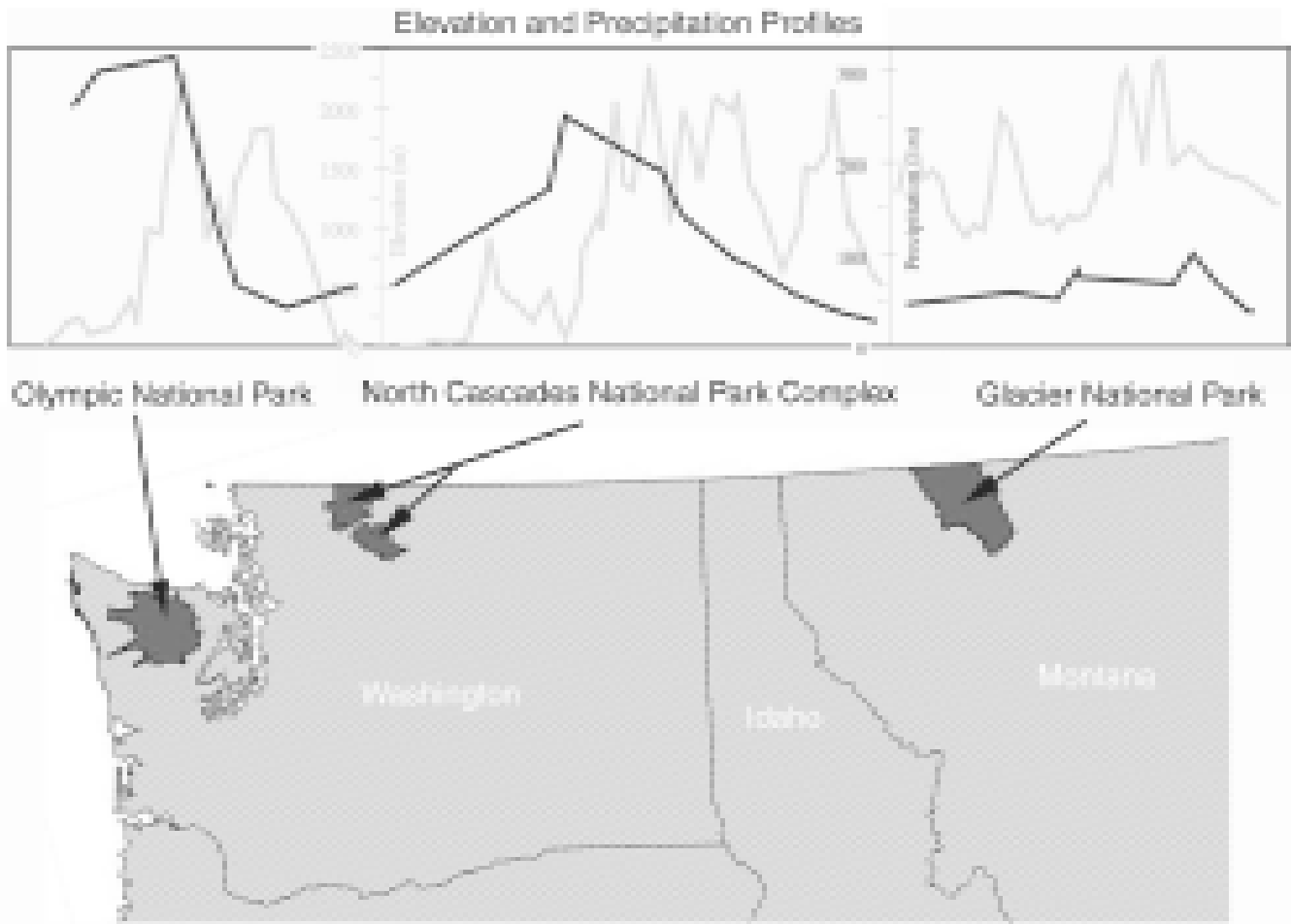
eastern vegetation represents a more vulnerable resource and may warrant additional monitoring and management attention.

## The Future

The approach described above has provided new insights into the present dynamics and possible future conditions of a mountain wilderness at Glacier National Park. However, the influence of surrounding land use/land cover change was explicitly not considered. The modeling tools developed to date urgently need to be refined and strengthened by application to Olympic National Park, where a history of mountain ecosystem studies can provide ample data for model parameterization and validation.

To address the issue of the regional context in which these mountain wildernesses function, we extended existing efforts and initiated a long-term research program on three bioregions that represent a gradient of disturbance intensity and climatic variability (fig. 6). All three bioregions are near the same latitude (47 to 49°N), have contrasting westside vs. eastside precipitation and similar topographic relief, and share numerous other characteristics; they vary primarily by overall climatic regime and degrees of landscape alteration. The Olympic bioregion, with Olympic National Park at its core, is a maritime-influenced climate and has the greatest degree of landscape fragmentation and external stressors. The north Cascades bioregion, with North Cascade National Park at its core, represents an intermediate climatic regime and disturbance level. The northern Rockies bioregion, with Glacier National Park at its core, has the driest, most continental climate and the least disturbed regional context.

Building on existing capabilities and data, we will quantitatively assess the relative roles of climatic change and landscape alteration in determining the future integrity of these mountain wilderness areas. The ecosystem modeling is scale-sensitive so that we can examine the



**Figure 6**—Three National Parks, at the core of larger bioregions surrounding them, represent a gradient of climate regimes, landscape fragmentation and disturbance along a transect from the West Coast to the edge of the Great Plains.

dynamics of change for resources at different spatial scales. For instance, the invasion of meadows by subalpine fir may be ecologically significant at the species scale but will not contribute much to regional-scale estimates of net primary productivity.

Ultimately, we can quantitatively assess the contribution of mountain wilderness areas to the ecological dynamics of the bioregions to underscore their value to our daily lives. Coupled with the ability to make forecasts using different climate and management scenarios, this enhanced perspective on the ecological services that wilderness can provide should lead to better management decisions and stronger public support for wilderness.

## Acknowledgments

We thank the extended team of scientists, students, and technicians with whom we have cooperated for the past nine years and whose work is reflected in this paper. Research has been supported by the Global Change Research Program of the National Park Service, National Biological Service, and U.S. Geological Survey.

## References

- Band, L. E.; Patterson, P.; Nemani, R. R.; Running, S. W. 1993. Forest ecosystem processes at the watershed scale: incorporating hillslope hydrology. *Agricultural and Forest Meteorology*. 63:93-126.
- Band, L. E.; Peterson, D. L.; Running, S. W.; Coughlan, J.; Lammers, R.; Dungan, J.; Nemani, R. 1991. Forest ecosystem processes at the watershed scale: basis for distributed simulation. *Ecological Modelling*. 56:171-196.
- Beniston, M.; Fox, D. G. 1996. Impacts of climate change on mountain regions. In: Watson, R. T.; Zinyowera, M.; Moss, R. H.; Dokken, D. J., eds. *Climate Change 1995—Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses*; Cambridge University Press; Cambridge, UK: 191-213.
- Brace, S.; Peterson, D. L. 1998. Spatial patterns of tropospheric ozone in the Mount Rainier region of the Cascade Mountains, U.S.A. *Atmospheric Environment*. 32:3629-3637.
- Butler, D. R.; Malanson, G. P.; Cairns, D. M. 1994. Stability of alpine treeline in northern Montana, USA. *Phytocoenologia*. 22:485-500.
- Carrara, P. E. 1989. Late Quaternary glacial and vegetative history of the Glacier National Park region, Montana. *U.S. Geological Survey Bulletin* 1902. 64 p.
- Cooper, S. M. and D. L. Peterson. 1999 (In Press). Tropospheric ozone distribution in western Washington. *Environmental Pollution*.

- Denniston, D. 1995. High Priorities: Conserving Mountain Ecosystems and Cultures. Worldwatch Paper 123; Worldwatch Institute, Washington, D. C.: 80 p.
- Ettl, G. J. and D. L. Peterson. 1995. Growth response of subalpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains, Washington, USA. *Global Change Biology*. 1: 213-230.
- Fagre, D. B.; Comanor, P. L.; White, J. D.; Hauer, F. R.; Running, S. W. 1997. Watershed responses to climate change at Glacier National Park. *Journal of the American Water Resources Association*. 33:755-765.
- Finklin, A. I. 1986. A Climatic Handbook for Glacier National Park—with Data for Waterton Lakes National Park. General Technical Report INT-204; USDA Forest Service Intermountain Research Station, Ogden, UT.
- Finney, M. 1998. FARSITE: Fire Area Simulator—model development and application. USDA. Forest Service Research Paper RMRS-RP-4; Rocky Mountain Research Station, Ogden, UT.
- Hall, M. H. P. 1994. Predicting the impact of climate change on glaciers and vegetation distribution in Glacier National Park to the year 2100. M.S. Thesis, State University of New York, Syracuse.
- Hauer, F. R.; Stanford, J. A.; Giersch, J. J.; Lowe, W. H. 1999 (In Press). Distribution and abundance patterns of macroinvertebrates in a mountain stream: an analysis along multiple environmental gradients. *Verh. Internat. Verein. Limnol.*
- Hungerford, R. D.; Nemani, R. R.; Running, S. W.; Coughlan, J. C. 1989. MT-CLIM: a mountain microclimate simulation model. USDA Forest Service Research Paper INT-414; Intermountain Research Station, Ogden, UT.
- Keane, R. E.; Morgan, P.; White, J. D. 1999. Temporal pattern of vegetation communities and ecosystem processes on simulated landscapes of Glacier National Park, USA. *Landscape Ecology*. 14:311-329 .
- Keane, R. E.; Hardy, C. C.; Ryan, K. C.; Finney, M. A. 1997. Simulating effects of fire on gaseous emissions and atmospheric carbon fluxes from coniferous forest landscapes. *World Resource Review*. 9:177-205.
- Keane, R. E.; Ryan, K. C.; Running, S. W. 1996. Simulating effects of fire on northern Rocky Mountain landscapes with the ecological process model FIRE-BGC. *Tree Physiology*. 16:319-331.
- Kendall, K. C. 1995. Whitebark pine: ecosystem in peril. In: LaRoe, E. T., ed. *Our Living Resources*, U.S. Dept. of Interior, National Biological Service, Washington, D.C.: 228-230.
- Key, C. H.; Fagre, D. B.; Menicke, R. K. In Press. Glacier recession in Glacier National Park, Montana. In: Williams, R. S.; Ferrigno, J., eds. *Satellite Image Atlas of Glaciers of the World*. Vol. U.S. Geological Survey Professional Paper 1386-J. United States Government Printing Office. Washington D.C.
- Klasner, F. L. 1998. Spatial changes in alpine treeline vegetation patterns along hiking trails in Glacier National Park, Montana. M.S. thesis, Oregon State University, Corvallis.
- Lettenmaier, D. P. 1992. Sensitivity of Pacific Northwest water resources to global warming. *Northwest Environmental Journal* 8:265-274.
- Liniger, H.; Weingartner, R.; Grosjean, M. 1998. *Mountains of the World: Water Towers for the 21<sup>st</sup> Century*. University of Bern, Switzerland.
- Messerli, B.; Ives, J. D. eds. 1997. *Mountains of the World: A Global Priority*. Parthenon Publishing, New York.
- Oerlemans, J. 1994. Quantifying global warming from the retreat of glaciers. *Science*. 264:243-245.
- Peterson, D. L. 1998. Climate, limiting factors and environmental change in high-altitude forests of Western North America. In: Beniston, M.; Innes, J. L., eds. *The Impacts of Climate Variability on Forests*. Springer, New York: 191-208.
- Peterson, D. L.; Schreiner, E. G.; Buckingham, N. M. 1997. Gradients, vegetation and climate: spatial and temporal dynamics in the Olympic Mountains, U.S.A. *Global Ecology and Biogeography Letters*. 6:7-17.
- Reich, P. B.; Amundson, R. G. 1985. Ambient levels of ozone reduce net photosynthesis in tree and crop species. *Science*. 230:566-570.
- Rocheftort, R. M.; Peterson, D. L. 1996. Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park, Washington, U.S.A. *Journal of Arctic and Alpine Research*. 28:52-59.
- Running, S. W.; Gower, S. T. 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology*. 9:147-160.
- Running, S. W.; Nemani, R. R. 1991. Regional hydrologic and carbon balance responses of forests resulting from potential climate change. *Climatic Change*. 19:349-368.
- Thornton, P. E.; Running, S. W.; White, M. A. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology*. 190:214-251.
- White, J. D.; Running, S. W. 1994. Testing scale dependent assumptions in regional ecosystem simulations. *Journal of Vegetation Science*. 5: 687-702.
- White, J. D.; Running, S. W.; Thornton, P. E.; Keane, R. E.; Ryan, K. C.; Fagre, D. B.; Key, C. H. 1998. Assessing regional ecosystem simulations of carbon and water budgets for climate change research at Glacier National Park, USA. *Ecological Applications*. 8:805-823.