

# Directional Changes in Ecological Communities and Social-Ecological Systems: A Framework for Prediction Based on Alaskan Examples

F. Stuart Chapin III,<sup>1</sup> Martin D. Robards,<sup>1</sup> Henry P. Huntington,<sup>2</sup> Jill F. Johnstone,<sup>1</sup> Sarah F. Trainor,<sup>1</sup> Gary P. Kofinas,<sup>1</sup> Roger W. Ruess,<sup>1</sup> Nancy Fresco,<sup>1</sup> David C. Natcher,<sup>3</sup> and Rosamond L. Naylor<sup>4</sup>

1. Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775;

2. Huntington Consulting, Eagle River, Alaska 99577;

3. Memorial University of Newfoundland, St. John's, Newfoundland A1C FS7, Canada;

4. Stanford Institute for the Environment, Stanford University, Stanford, California 94305

---

**ABSTRACT:** In this article we extend the theory of community prediction by presenting seven hypotheses for predicting community structure in a directionally changing world. The first three address well-studied community responses to environmental and ecological change: ecological communities are most likely to exhibit threshold changes in structure when perturbations cause large changes in limiting soil or sediment resources, dominant or keystone species, or attributes of disturbance regime that influence community recruitment. Four additional hypotheses address social-ecological interactions and apply to both ecological communities and social-ecological systems. Human responsiveness to short-term and local costs and benefits often leads to human actions with unintended long-term impacts, particularly those that are far from the site of decision making or are geographically dispersed. Policies are usually based on past conditions of ecosystem services rather than expected future trends. Finally, institutions that strengthen negative feedbacks between human actions and social-ecological consequences can reduce human impacts through more responsive (and thus more effective) management of public ecosystem services. Because of the large role that humans play in modifying ecosystems and ecosystem services, it is particularly important to test and improve social-ecological hypotheses as a basis for shaping appropriate policies for long-term ecosystem resilience.

*Keywords:* common-pool resources, community, human impacts, resilience, social-ecological system, threshold.

---

Hypotheses that seek to predict the structure (i.e., the number, types, and relative abundances of species) of eco-

logical communities have had a profound impact on the development of ecological theory. These hypotheses (table 1) provide testable predictions about the relationship between the structure or dynamics of ecological communities and their presumed controls. They are also a framework for predicting the consequences of environmental and biotic change (Huston 1994; Chapin et al. 1996a). However, many of these hypotheses assume that community patterns emerge from the steady state relationship between community structure and its physical and biotic controls.

Human activities are altering, at unprecedented rates, many of the variables that are assumed to structure ecological communities (Vitousek et al. 1997; Langston 1998; Steffen et al. 2004; Foley et al. 2005). These changes include climate, disturbance frequency, nitrogen availability, landscape fragmentation and modification, species migration and extinction rates, and the abundances of top predators. Although people have always affected ecosystems, the increasing magnitude and extent of these impacts now require their explicit incorporation into conservation management strategies (Berkes 2004; Elmqvist et al. 2004; Wallington et al. 2005). Hypotheses that seek to predict the future composition of ecological communities must therefore be extended to incorporate non-steady state dynamics in a directionally changing world. These dynamics of change are complex because ecological communities are often initially resilient (maintaining their structure and function) to changes in driving variables and then change abruptly when some threshold is exceeded (Scheffer and Carpenter 2003; Walker and Meyers 2004). Community prediction hypotheses that address these nonlinear responses of community structure would contribute significantly to policies designed to manage and mitigate current global changes (Wallington et al. 2005). Given the anthropogenic nature of many of the drivers of ecological change, community predictions could also be substantially improved by identifying circumstances where human impacts are most likely to be pronounced. We therefore ex-

**Table 1:** Examples of community prediction hypotheses based on steady state assumptions

Hypothesis	Predictor	Response variable	Reference
Species packing	Latitude	Species richness	MacArthur 1965
Island biogeography	Distance, area	Species richness	MacArthur and Wilson 1967
Intermediate disturbance	Disturbance, production	Species richness	Connell 1978
Gradient analysis	Environmental gradient	Species composition	Whittaker 1967
Plant strategies	Disturbance, stress	Species composition	Grime 1977
Resource ratio hypothesis	Resource ratio	Competitive outcome	Tilman 1982
Plant functional types	Resource supply	Functional type composition	Chapin et al. 1996a
Food web structure	Productivity	Food web structure	Pimm 1982
Trophic cascades	No. of trophic links	Primary production	Power 1990
State factor analysis	State factors	Ecosystem structure	Jenny 1980

tend our predictive framework to include social drivers of community change.

### Definitions

The structure and dynamics of ecological communities are sensitive to variables ranging from those that are relatively constant (usually regarded as fixed parameters) to those that are slowly changing (slow variables) to those that are rapidly changing (fast variables) over the timescale of interest. Although variables often interact, fixed parameters constrain slow variables, which constrain the behavior of fast variables. For example, geological substrate, climate, and topography, which are relatively constant over ecological timescales, constrain the water-holding and cation exchange capacities of soils (slow variables), which constrain short-term water and nutrient supplies to vegetation (fast variables). These variables can range from having very strong effects (critical controls) to having effects that are difficult to detect against background variability in other factors. A critical control can be inferred from strong correlation, or it can be demonstrated by controlled experiments in which community structure responds strongly to a change in a single manipulated factor. For example, nitrogen supply or some more slowly changing variable such as abundance of nitrogen fixers would be considered a critical variable in a forest whose structure responded strongly to nitrogen addition or to the invasion of exotic nitrogen-fixing species (Vitousek et al. 1987). Similarly, reindeer would be considered a critical variable in a culture that was disrupted by loss of reindeer-herding opportunities. In this article, we are particularly interested in critical slow variables and parameters, factors that change so slowly (or events that occur so infrequently; e.g., wildfire) that they are frequently overlooked by managers but that have profound effects on community structure. In most ecosystems, there are a few (perhaps three to five) critical slow variables that strongly influence community structure and ecosystem functioning (Carpenter et al. 2002). Many critical slow variables are changing directionally—that is,

there is a trend in their mean value over time—as a result of increasing human modification of the global environment.

We must integrate social and ecological processes in a common conceptual framework if we want to predict changes in ecological communities in an increasingly human-dominated world. We approach this problem by first presenting hypotheses that predict community responses to those critical slow ecological variables that are most strongly affected by human activities. We then consider the circumstances under which society is most likely to address and modify these ecological impacts. None of our individual hypotheses are new. However, collectively they define a new framework for predicting the response of ecological communities or social-ecological systems to recent environmental, biotic, and social changes.

### Conceptual Framework

Hypotheses based on steady state assumptions (table 1) provide a fundamental starting point for predicting the structure and dynamics of ecological communities, especially where direct human impacts have been modest (Pickett et al. 1992). Each of the hypotheses in table 1 predicts patterns of community structure or dynamics over commonly observed ranges of predictor variables when other potential influences (e.g., human impacts) are held relatively constant. Spatial variation in ecosystem structure, for example, has been predicted from a suite of independent control variables (state factors) that are treated as constant parameters over ecologically important timescales. These state factors include climate, the regional species pool, topography, and geological substrate (Jenny 1980; Chapin et al. 2002). Recently, however, human activities have substantially altered climate (Prentice et al. 2001), species pool (Sala et al. 2000), and geological impacts on ecosystems (Driscoll et al. 2001) over decadal timescales, so a steady state relationship between state factors and ecosystem structure may no longer apply. Human activities have also altered many of the other predictor and

response variables listed in table 1, so the steady state assumptions underlying many community prediction hypotheses are no longer sufficient to predict future community structure and dynamics. Consequently, maps of potential vegetation based on simple prediction rules diverge increasingly from vegetation patterns detected by satellites.

We view ecological and human communities as subsystems of a social-ecological system (Berkes and Folke 1998). The subsystems are linked by human impacts on ecosystems and ecosystem services that benefit society. The nature of a social-ecological system is shaped by external state factors that are relatively independent of processes occurring within the system. The structure and dynamics of the ecological community are determined by a few critical slow variables, such as soil resources, disturbance regime, and functional types of organisms. These critical slow variables are constrained by state factors, change relatively slowly, and strongly influence and respond to the structure and dynamics of the ecological community (Chapin et al. 2002). Although there are reciprocal interactions and feedbacks between state factors, slow variables, and fast variables, differences in temporal and spatial scale cause the chain of cause and effect to be most pronounced from larger to smaller scales, that is, from state factors to slow variables to fast variables. For example, regional climate (e.g., the climate of interior Alaska over the past several centuries) exerts a strong effect on the presence or absence of permafrost in a forest stand, which influences instantaneous water availability to individual trees. Evapotranspiration by individual trees also influences soil water content and the recycling of water to the atmosphere, but these effects are temporally and spatially variable, so fast variables in a single location and time are less useful in predicting slow variables, which are less useful in predicting state factors.

The structure and dynamics of the social community are also determined by a few critical slow variables, including some political, cultural, and economic institutions that are constrained by state factors, change relatively slowly, and strongly influence and respond to the structure and dynamics of the social community (Chapin et al. 2006). Changes in ecological or social communities depend on the magnitude of change in critical slow variables, the sensitivity of communities to these changes, and internal feedbacks that modify these sensitivities (Turner et al. 2003). The identity of critical slow variables can often be determined a priori through observations and analysis of their controlled or unplanned alteration.

Community structure and dynamics often exhibit nonlinear or threshold responses to changes in critical slow variables. Resilience theory provides a framework for interpreting these changes (Holling and Gunderson 2002),

and feedback theory from systems ecology provides a set of general mechanisms to explain these patterns (Chapin et al. 1996*b*). The structure of communities is strongly influenced by interactions among positive and negative feedbacks. Environmental changes, disturbance, or management actions that generate new positive feedbacks or weaken negative feedbacks often precipitate community change. A strengthening of positive feedbacks (e.g., the unconstrained population growth of an exotic species that has escaped its natural predators), for example, tends to amplify changes that occur and push the community toward a new state. In contrast, strong negative feedbacks (e.g., limits to population growth conferred by predation, harvest, or disease) confer resilience and maintain a community in its current state (Chapin et al. 1996*b*), although these negative feedbacks may also induce variability at the population level. Ecological communities that have relatively stable feedback patterns reflect steady state predictions more clearly than do communities undergoing rapid change. Communities that lack strong internal feedbacks are particularly vulnerable to perturbations, and their structure is less predictable than communities with strong internal feedbacks.

The resilience associated with strong negative feedbacks also creates a path dependence of community change. Legacies of previous events such as the occurrence of a hurricane, soil tillage, or invasion of an exotic species can significantly affect community structure (Shea and Chesson 2002; Foster et al. 2003), which influences its response to changes in critical slow variables. This path dependence and associated time lags generate idiosyncratic patterns that may be understandable on a case-by-case basis but are difficult to predict a priori.

As a result of resilience and path dependence, more than one stable state is possible in a given environment, and the resilience of a system determines its probability of remaining in its original state or switching to an alternative state (Holling and Gunderson 2002; Walker et al. 2004). The relationship among alternative states is dynamic, so alternative domains of attraction may appear or disappear, and the ease of moving from one state to another changes over time (Beisner et al. 2003; Walker et al. 2004). We therefore suggest that in a directionally changing world, a new set of hypotheses is required that addresses community resilience and thresholds leading to transformative change (table 2).

In the remainder of this article, we develop hypotheses that address non-steady state dynamics in a directionally changing world and illustrate these with Alaskan examples. We first propose a set of hypotheses that predict threshold changes in ecological communities in response to environmental and anthropogenic change. These hypotheses are limited in scope because they ignore the feedbacks from

**Table 2:** Hypotheses for community predictions in a directionally changing world

Hypothesis	
1.	Directional changes in processes that alter critical soil or sediment resources will trigger threshold changes in community structure and dynamics
2.	Directional changes in the abundance of species that alter soil resource supply or disturbance regime often trigger threshold changes in communities and ecosystems
3.	Disturbance events, especially those that are extreme in size, frequency, or severity, often catalyze community change in a directionally changing environment
4.	Responsiveness to short-term costs and benefits often leads to human actions with unintended long-term human impacts on social-ecological systems
5.	Human impacts that occur far from the site of decision making or that are geographically dispersed are often overlooked in policies that affect social-ecological systems
6.	Societal expectations of ecosystem services based on past conditions constrain the capacity of people to adjust their ecological impacts in a directionally changing world
7.	Institutions that strengthen negative feedbacks between human actions and social-ecological consequences can reduce human impacts through more responsive (and thus more effective) management of common-pool resources

ecological change to human actions. We therefore expand our framework to consider hypotheses governing changes in the structure of social-ecological systems, including both the structure of ecological communities and the interactions between ecological and social processes. These hypotheses are blatantly speculative and intended to stimulate discussion between ecologists and social scientists about how to improve predictions of future ecological and social change in an increasingly human-dominated world (Benda et al. 2002).

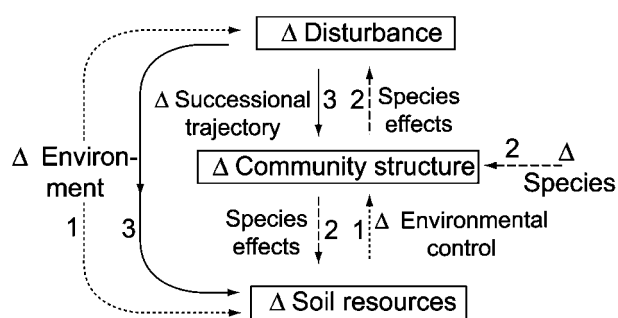
### Thresholds to Resilience: Regime Shifts

*Hypothesis 1. Directional changes in processes that regulate critical soil or sediment resources will trigger threshold changes in community structure and dynamics.* Within any climatic zone, factors such as parent material, topsoil depth, and soil organic content govern the supply of soil resources (water or a nutrient) that determine much of the spatial variation in community structure and dynamics. Changes in nutrient inputs (e.g., nitrogen deposition to forests or phosphorus inputs to lakes) may initially have only a modest effect on community structure because negative feedbacks such as mineral fixation, microbial immobilization, or uptake and storage by perennial plants sequester nutrients in pools that cycle slowly (Driscoll et al. 2001; Chapin et al. 2002; Carpenter 2003). If the limits to these negative feedbacks are exceeded, however, large, rapid changes in community structure are likely to occur (fig. 1). A new set of negative feedbacks often stabilizes the new system, reducing the likelihood that it will revert to the original state (Carpenter 2003).

In the Alaskan boreal forest, the temperature of permafrost (permanently frozen ground) is the slow variable that most strongly influences the supply of soil resources

to vegetation. Permafrost governs soil temperature, hydrology, and the supply rate of soil nitrogen, the nutrient that most frequently limits plant production (Van Cleve et al. 1991). Over the past 6,000 years, permafrost and community structure have remained relatively stable despite considerable climatic fluctuation (Lloyd et al. 2006). In response to recent high-latitude amplification of global warming, however, shallow permafrost in interior Alaska has warmed to within 0.2°–2°C of thawing (Osterkamp and Romanovsky 1999) and is projected to disappear by the end of this century (Lawrence and Slater 2005). Thawing of permafrost creates a physical threshold that converts the ecosystem from a poorly drained state with cold, nutrient-poor soils to either a well-drained ecosystem in uplands (due to free vertical drainage) or a flooded ecosystem in lowlands (due to subsidence of the ground surface when ice-rich permafrost thaws). These hydrologic changes alter several important controls over community composition and lead to new community-environment interactions. Improved drainage and faster nutrient turnover caused by thawing of permafrost in uplands, for example, allows growth of more productive broadleaf trees that support a higher transpiration rate, which maintains the drier soils (a positive feedback). In lowlands, subsidence of the ground surface creates open water that conducts heat more readily and increases the rate of permafrost thaw (another positive feedback). Ecologists and resource managers in most regions know the soil resources that control community composition as well as regional environmental changes that might plausibly alter these controls and can therefore anticipate many of the types of environmental changes that are likely to precipitate threshold changes in community composition.

*Hypothesis 2. Directional changes in the abundance of species that alter soil resource supply or disturbance regime often*



**Figure 1:** Relationships among hypotheses 1–3. Numbers show the mechanisms underlying each hypothesis. Hypothesis 1 describes the effects of environmental changes on soil resources, which in turn affect community structure. Hypothesis 2 describes the effect of species changes on community structure, which, in turn, affects both soil resources and disturbance regime. Hypothesis 3 describes the effects of disturbance in triggering changes in community structure. This figure shows that all of these processes interact in a complex fashion.

*trigger threshold changes in communities and ecosystems.* The biotic community often plays a central role in feedback loops that stabilize critical slow variables such as the supply of soil resources or disturbance frequency. Changes in the abundance of a species that maintains this feedback loop can therefore lead to disproportionately large (threshold) changes in control variables and therefore community composition (fig. 1). Dominant species (those that account for the most biomass) and keystone species (those that have ecological impacts disproportionate to their biomass; Power et al. 1996) are, by definition, the species most likely to exert these effects. Introduction of new keystone species such as nitrogen fixers in strongly nitrogen-limited ecosystems, for example, frequently changes nitrogen supply and community composition (Bradshaw 1983; Vitousek 2004). In Alaska, the arrival of nitrogen-fixing alder 7,000 years ago coincided with  $^{15}\text{N}$  enrichment (indicating greater nitrogen inputs), increased carbon and nitrogen concentrations of lake sediments (indicating greater terrestrial productivity), and increased concentrations of biogenic silicates and diatom diversity (suggesting an increase in aquatic productivity and trophic complexity; Hu et al. 2001).

Currently, nitrogen deposition rates are low in interior Alaska (Jones et al. 2005), and exotic nitrogen fixers are largely restricted to anthropogenic disturbances. In non-anthropogenic landscapes, most nitrogen input comes from alder and its nitrogen-fixing symbionts, particularly in early succession (Van Cleve et al. 1971; Uliassi and Ruess 2002). The abundance of this keystone species is sensitive to disease, herbivory, and shading by other plants, all of which are sensitive to recent climatic changes.

Another biotically driven threshold in interior Alaska is the successional shift from deciduous to conifer domi-

nance (Van Cleve et al. 1991). The leaf litter of early successional broadleaf trees smothers mosses, whereas the thin needles of conifers fall between moss fronds, allowing the development of a moss layer 10–30 cm thick that insulates the soil in summer and contributes to permafrost integrity and the development of a mat of undecomposed organic matter that sequesters nutrients. The cold, nutrient-poor soils associated with permafrost favor slow-growing conifers, contributing to the negative feedbacks that stabilize the conditions supporting this community type. Thus, the sensitivity of permafrost to climate warming depends on the relative dominance by broadleaf or conifer trees (a climate-vegetation interaction).

Trophic cascades frequently influence the abundance of plant species with strong ecosystem effects. In the boreal forest, for example, moose and snowshoe hares cause two important vegetation shifts: (1) they enhance the dominance of nitrogen-fixing alder in early succession by browsing on competing willow shrubs (Kielland and Bryant 1998), and (2) later in succession, browsers reduce the abundance of deciduous species and speed succession toward conifer- and permafrost-dominated community types (Pastor et al. 1988; Kielland and Bryant 1998). Climatically driven changes in the outbreak dynamics of herbivorous insects can also cause threshold changes in community dynamics. Spruce bark beetles, for example, caused extensive spruce mortality in south-central Alaska, triggering logging operations to reduce fire risk (Berg 1998).

Although ecologists recognize many of the species changes that are likely to precipitate threshold changes in community composition, biotic interactions are key sources of surprise, and observed responses often depend on local conditions and cannot be broadly generalized. Consequently, the effect of species interactions on the abundance of dominant and keystone plant species is an important research area that is likely to improve predictions of threshold changes in community structure and composition (Eviner and Chapin 2003; Scheffer and Carpenter 2003).

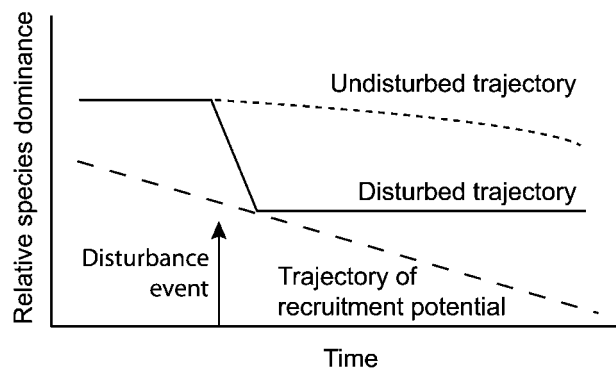
*Hypothesis 3. Disturbance events, especially those that are extreme in size, frequency, or severity, often catalyze community change in a directionally changing environment.* Although changes in soil resources or the abundance of species that modulate soil resource supply may be the ultimate causes of threshold changes in community composition, managers can seldom predict when these thresholds will be exceeded. We suggest that disturbance events frequently trigger threshold changes by acting on both soil resources and community composition (fig. 1).

Ecological communities are often surprisingly resilient to directional changes in critical slow variables for long periods of time because biotic interactions or legacies constrain the community response to these changes. In these situations, a disturbance that is sufficient to interrupt bi-

otic interactions (e.g., through biomass removal) can trigger rapid community change (fig. 2). In addition, changes in disturbance regime can initiate threshold changes in community organization by altering the regeneration environment to allow new combinations of species to colonize (Holling 1986; Frelich and Reich 1999; Petraitis and Latham 1999). Once colonization has occurred, the successional convergence toward a mature community type (Kashian et al. 2005) may be less sensitive to environmental variation or biotic invasion. Interactions between community composition and subsequent disturbance regime then tend to stabilize the new community type. Thus, the interval immediately after disturbance is often a key time period when the community either returns to its original state or shifts to a new state (Carpenter et al. 2001; Holling and Gunderson 2002).

Fire-related changes in Alaskan forests illustrate the key role of disturbance in community change. The species composition of Alaskan white and black spruce forests has changed relatively little in response to multidecadal increases in summer drought that have reduced the growth rate of the dominant trees (Barber et al. 2000). This buffering of species composition in mature forests, despite large regional environmental changes, reflects biogeochemical feedbacks that maintain slow rates of nitrogen flux from soil to trees (the feathermoss–soil temperature–nitrogen mineralization feedback loop) and low rates of evapotranspiration (slow growth–low evapotranspiration–moist soils feedback loop), particularly in black spruce forests (Van Cleve et al. 1991).

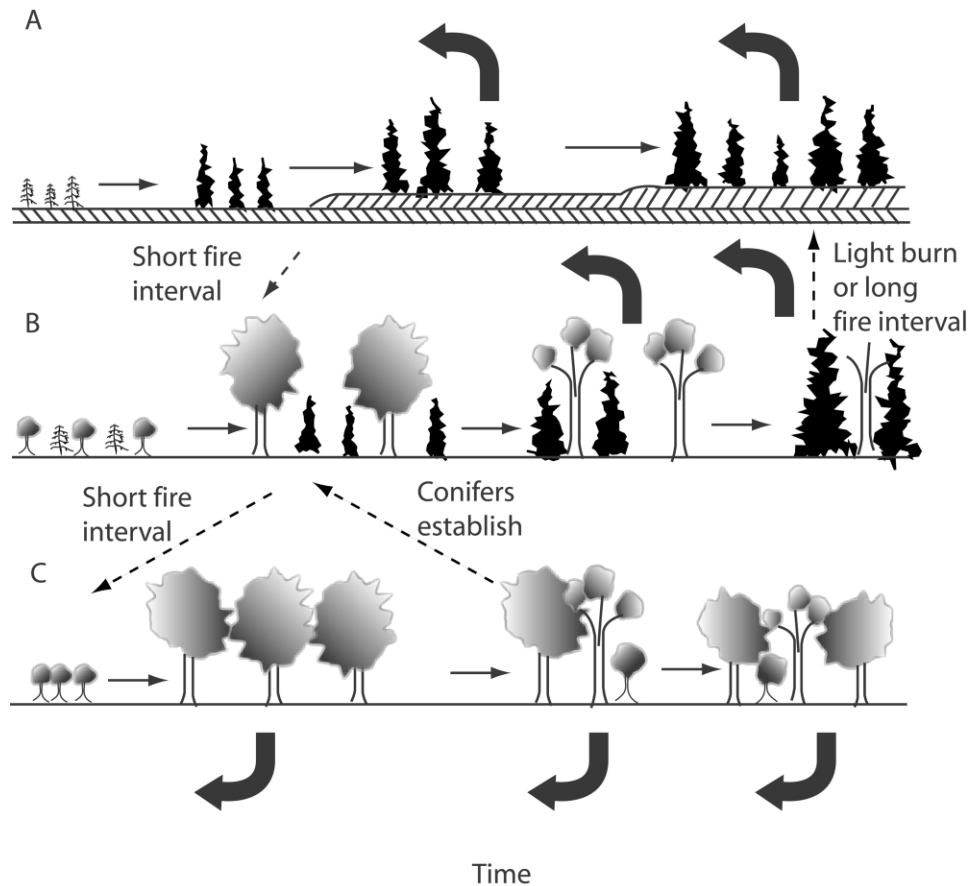
Once the processes that buffer community composition are interrupted by fire, however, various successional trajectories are possible (fig. 3). A common postfire successional sequence in interior Alaska is initial dominance by deciduous species, followed by conifer dominance (Van Cleve et al. 1991). After a light burn or long fire interval, however, deciduous species may not resprout or establish on highly organic seedbeds, leading to conifer dominance. Conversely, after an extremely severe burn or short fire interval, deciduous species may dominate the seedbed during the 5- to 20-year window for postfire establishment, leading to deciduous dominance (Johnstone and Kasischke 2005; Johnstone and Chapin 2006). Once either conifers or deciduous trees preempt a site, their persistence is promoted by a set of reproductive and life-history traits and species effects on biogeochemistry (Johnstone 2003). About 6,000 years ago, for example, black spruce became widespread in interior Alaska in response to a gradual cooling and moistening of climate (Lynch et al. 2002). This species supports the growth of an understory of evergreen shrubs and mosses, which together with black spruce are highly flammable (Van Cleve et al. 1991). The arrival of black spruce therefore coincided with a dramatic



**Figure 2:** Temporal changes in species dominance in a directionally changing world. In the absence of disturbance, community composition may change slowly (*dotted line*), despite substantial changes in factors governing recruitment potential (*dashed line*). After disturbance, the community may change rapidly to a new state (*solid line*), the nature of which depends on the environment and recruitment potential at the time of disturbance.

increase in fire frequency, which persists today (Lynch et al. 2002). A continuation of recent high-latitude warming (Hinzman et al. 2005) could cause further increases in fire frequency and severity (Flannigan et al. 1998), perhaps increasing the proportion of deciduous forests on the landscape (Chapin et al. 2003, 2004). Arrival of new species could also initiate a change in fire regime and community composition. Lodgepole pine is actively migrating northward from western Canada to Alaska and grows well in experimental plantations in Alaska. The serotinous cones of lodgepole provide an abundant seed source after fire (Johnstone and Chapin 2003). Once established, lodgepole pine promotes fire through development of a flammable decay-resistant litter layer and a flammable forest structure. From a management perspective, a key outcome of this pattern is that systems may experience hidden changes in resilience that become apparent only when a disturbance occurs (fig. 2). Restoration ecologists often have a good understanding of the impact of different types of disturbance on subsequent community development, providing the expertise necessary to influence this source of uncertainty in community change.

In summary, we frequently have a strong basis for qualitative predictions about vulnerability of ecological communities to directional anthropogenic and environmental change but are only beginning to develop the hypotheses that describe their threshold behavior and resilience (Walker et al. 2004). In general, we suggest that knowledge of steady state dynamics and limiting factors provides a strong basis for identifying the slow variables to which a system is most sensitive. Critical slow variables that are altered by human activities often include soil resource sup-



**Figure 3:** Three alternative successional trajectories that occur after fire in interior Alaska. Each row shows the temporal change in community composition (from left to right) after postfire recruitment. Thin arrows show the normal successional transitions. Thick arrows show the most likely postfire transition (to an early successional stage of the same successional trajectory). Dashed arrows show events that lead to new successional trajectories. Successional trajectories shown are (A) conifer succession, (B) relay floristics in which conifers replace deciduous trees, and (C) deciduous succession. The hatched ground cover represents an organic mat that prevents establishment of deciduous tree seedlings. Modified from Johnstone (2003) with permission.

ply, relative abundance of plant functional types, and disturbance regime. Studies of these critical slow variables help to identify which thresholds are most likely to be exceeded and the circumstances under which this might occur. We are optimistic that ecologists can develop improved predictions, both specific and general, that link thresholds to changes in community structure (fig. 1) (Gunderson and Holling 2002; Walker et al. 2004).

The hypotheses described above for predicting changes in ecological communities have logical implications for social-ecological systems when these ecological changes have strong societal consequences. Like ecological communities, social-ecological systems are vulnerable to threshold changes when perturbations or disturbances alter critical slow variables (Gunderson and Holling 2002). Critical slow variables in social components of social-

ecological systems include cultural beliefs and practices, stakeholder groups, and political and economic institutions. These slow variables are sensitive to events such as the creation of new transportation and trade corridors, a shift to an economy based on resource extraction, or changes in national or international policies that are insensitive to local repercussions. The next section of this article addresses changes in ecological communities as components of social-ecological systems.

#### Community and Ecosystem Predictions in a Human-Dominated World

The role of people as components of integrated social-ecological systems warrants additional attention because (1) the impacts of human actions on ecological commu-

nities are increasing in magnitude and extent (Foley et al. 2005), and (2) there are often temporal, spatial, and institutional disconnects between these ecological consequences and further human actions. These disconnects result in systems with weak negative feedbacks, which reduce resilience and increase the likelihood of a state change in the system. Local harvests, for example, may have local impacts and thus relatively strong negative feedbacks. Distant harvests, by contrast, may have negligible local impacts and thus few or no short-term feedbacks. Actions with indirect or incidental impacts, such as pollution or habitat degradation, are also likely to be disconnected in time and/or space from their consequences. Such disconnects can be exacerbated by institutional arrangements that separate the management of human action (e.g., incentives for development) from the management of ecological consequences (e.g., habitat restoration). In this section we suggest four social-ecological hypotheses, with emphasis on Alaskan examples, to predict when human activities are most likely to induce, amplify, or dampen directional changes in social-ecological systems. For each hypothesis we suggest policy strategies that could enhance social-ecological resilience.

*Hypothesis 4. Responsiveness to short-term costs and benefits often leads to human actions with unintended long-term human impacts on social-ecological systems.* Human actions have both long- and short-term effects on ecological systems that, in turn, influence human well-being. Although some of these impacts and feedbacks are obvious, others are subtle, resulting in a range of responding human action, reaction, and inaction. In general, people respond most strongly to short-term effects and discount those effects that occur more slowly or are less certain. In other words, people and institutions tend to manage resources based on changes in fast variables rather than the slow variables that ultimately control long-term changes in social-ecological systems (hypotheses 1–3).

We illustrate this hypothesis with respect to human-fire interactions in interior Alaska. Most Alaskans live in communities or along road networks surrounded by forests, where naturally occurring wildfires are a threat to life and property. Fire suppression reduces short-term fire risk but over the long term converts an increasing proportion of the landscape to a late-successional flammable forest type that is a greater threat to life and property and is less productive of ecosystem resources that people harvest, such as blueberries and moose (Chapin et al. 2003). Although some fire managers recognize the long-term benefits of allowing fires to burn, public perceptions tend to focus on the short-term costs of fire (risk to life, property, and health via smoke). After a record wildfire season in 2004, there was strong public outcry to increase fire suppression efforts to further reduce the short-term costs of

wildfire (Todd and Jewkes 2005). These observations lead to a simple set of social-ecological predictions in which focus on short-term fire effects leads to fire suppression, which reduces long-term social benefit by reducing subsistence resources associated with early successional habitats and increasing the probability of large catastrophic fires.

The use of marginal cost-benefit analysis in decision making can reinforce the focus on short-term costs and benefits if the cumulative effects over time are ignored or highly discounted. Sale of remote parcels of public land for recreational cabin sites in Alaska, for example, is evaluated based on economic gains to the state and its immediate impacts on recreational benefits without considering its incremental effect on number of human ignitions and fire regime. Similarly, rezoning a small area of forest for suburban development may have immediate social and economic benefits to local communities, but the cumulative effect of this policy is the creation of a wildland-urban interface where fire and wildlife management are major challenges. When analyses focus on fast variables that immediately affect people and ignore the slow variables, conditions arise that foster threshold ecological changes (hypotheses 1–3). Marginal analyses that place a higher value on long-term costs and benefits are less likely to exacerbate this risk (NRC 2005).

Astute policy makers, scientists, and some activist groups focused on local sustainability are usually aware of many of the long-term effects of human actions on their local region. These effects include logging impacts on species requiring late-successional habitat, tillage effects on soil organic content and soil fertility, over-harvest of desirable fish and game species, pollution effects on ecosystem nitrogen retention and species diversity, effects of predator removal on prey abundance, and effects of pesticides on the evolution of resistance (Foley et al. 2005). Temporal disconnects can be minimized by identifying, quantifying, and assessing the long-term social costs of human impacts and developing policies that internalize these costs.

*Hypothesis 5. Human impacts that occur far from the site of decision making or that are geographically dispersed are often overlooked in policies that affect social-ecological systems.* When people cause ecological impacts that do not directly affect them because the effects occur elsewhere or are geographically dispersed, overexploitation can become an attractive opportunity (Hardin 1968). Under these circumstances, larger-scale institutions, such as international conventions, have been used to prevent overexploitation (Dietz et al. 2003). For example, international institutions such as the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR 2000) are intended to reduce the spatial disconnect between economic pres-

tures for overfishing and their ecological consequences. The effectiveness of these international conventions is often compromised, however, by self-interest and power politics among participating countries (Young 1989, 1994).

High-latitude climate change is a prime example of spatial disconnects. Global warming is driven primarily by activities that are concentrated in nonarctic regions, including fossil fuel emissions of CO<sub>2</sub>, CH<sub>4</sub> emissions from rice paddies and cattle, and N<sub>2</sub>O derived from nitrogen fertilizers in intensive agriculture. Feedbacks in the climate system (e.g., melting of sea ice) amplify this warming and its societal consequences at high latitudes. In Alaska, for example, warming causes hunting fatalities associated with travel on thin river or sea ice, a decline in availability of ice-dependent marine mammals (particularly pinnipeds) for harvest, and property damage and disruption of infrastructure from thawing permafrost (ACIA 2005). These impacts, however, have relatively little effect on the trace-gas-producing activities of low-latitude residents. Because of this spatial disconnect, global-scale institutions (e.g., the Kyoto Protocol) have had only modest success in reducing the causes of warming (Chapin et al. 2005).

Spatial disconnects can also occur within a relatively fine-scaled mosaic, when there is a heterogeneous group of stakeholders, some of whom reap most of the benefits and others of whom bear most of the costs. In Alaska, for example, commercial fishing near the mouth of the Yukon and Kuskokwim Rivers reduces the availability of fish upstream, and elaborate but controversial rules have been developed to manage this allocation (NRC 2004). Similarly, in southeast Alaska, cruise ships reap most of the economic benefits from large-scale tourism, and local communities suffer the pollution costs. A thorough cost accounting of social and ecological costs and benefits of resource use across the spatial mosaic can inform policies that reduce social inequities and their ecological impacts.

Scientists and managers often recognize the spatial patterns of human impacts sufficiently to identify spatial disconnects between human actions and their consequences. Well-recognized spatial disconnects include climate change, air and water pollution, marine overfishing, and tropical deforestation. One mechanism to reduce excessive human impacts is to assess the geographic patterns of costs and benefits from development projects and develop institutions that internalize these costs. These institutions are most effective when developed at scales that incorporate the major causes and consequences. Because of cross-scale interactions, this often requires multiple institutions functioning at different scales (Holling and Gunderson 2002; Berkes et al. 2005). Addressing the consequences of climate change, for example, may require international conventions that oblige nations to address their contribution to climate change, national regulations

of emissions, and local policies that encourage specific regions to mitigate local impacts.

*Hypothesis 6. Societal expectations of ecosystem services based on past conditions constrain the capacity of people to adjust their ecological impacts in a directionally changing world.* There is increasing recognition among policy makers, managers, and the general public that directional changes in slow variables are inevitably changing the world in which we live. Nonetheless, expectations based on past conditions frequently inhibit policy shifts that allow adaptation to new conditions. This institutional inertia (Smith 2000) can generate temporal or spatial disconnects (hypotheses 4 and 5) that degrade social-ecological feedbacks.

The U.S. Forest Service, for example, instituted a policy of suppressing all wildfires in the wake of extensive wildfires in 1910 (Pyne 2001; Busenberg 2004). In some forests, this led to a directional pattern of fuel accumulation that increased the risk of large fires (Schoennagel et al. 2004). Despite widespread recognition of this increasing fire risk among fire managers, national fire policy remained largely unchanged, and public education continued to emphasize the “Smokey the Bear” philosophy that wildfires are detrimental. Only recently (e.g., 2000 and 2001), when wildfires caused extensive property damage, has this policy been closely scrutinized (Busenberg 2004). Public policies often remain relatively constant until times of crisis, when they can change rapidly. These moments of crisis provide windows of opportunity to formulate new policies that alter social-ecological feedbacks in ways that can either augment or reduce human impacts on communities (Walker et al. 2004).

Similarly, protected areas based on historic ranges of key wildlife species are often established with the expectation that the current location is the ideal site for their future conservation. Directional changes of climate may, however, make today’s critical habitat areas (e.g., caribou calving grounds or terrestrial walrus haulouts) unsuitable in the future, leading to a spatial disconnect that results in ecological loss. Conservation planning increasingly recognizes the need to consider both the current habitat requirements of organisms and the necessity for shifts in critical habitats and corridors that allow future migration to new locations where future environmental conditions make that habitat more suitable (Elmqvist et al. 2004).

Temporal and spatial disconnects (hypotheses 4 and 5) can also contribute to institutional rigidity (hypothesis 6) that restricts adaptive change. A frequent response to a decline in fisheries, for example, is to restrict the number of fishing vessels, which creates incentives for a capital-intensive fishing fleet that is more efficient in catching fish and increases the likelihood of fishery collapse. These policies often favor nonlocal fishing ventures and have not

supported the social health of local communities that rely on the fishery, as has occurred, for example, in Bristol Bay, Alaska (NRC 2004).

Managers and the public are not easily convinced that the future will be substantially different than the past, especially when there is high variability or uncertainty, so it is usually difficult to implement policies that respond in an appropriate and timely manner to directional environmental changes. This indicates a key role for public education in policy change.

*Hypothesis 7. Institutions that strengthen negative feedbacks between human actions and social-ecological consequences can reduce human impacts through more responsive (and thus more effective) management of common-pool resources.* Hypothesis 7 shifts our discussion squarely into the human dimension by focusing on the performance of social institutions (formal and informal rules of decision making). This hypothesis provides one potential solution to problems that arise from the conditions described in hypotheses 4–6.

Many natural resources harvested by society are “common-pool,” or shared, resources (Ostrom 1990). In the absence of effective rules for managing common-pool resources, there can be strong pressures to harvest more resources than the ecosystem can sustain, leading to significant ecological degradation (Hardin 1968). Economic and political forces can foster the maximization of short-term profit, often overlooking the long-term ecological consequences (hypothesis 4). Institutions that are well defined and responsive to change can function as negative feedbacks to avoid such tragedies.

Historical changes in common-pool institutions in the James Bay region of Canada exemplify the role of institutions in social-ecological feedbacks. Beaver were a traditional source of food and furs for Cree Indians, and traditional customs restricted harvest at times of low abundance (Berkes 1998). In the 1920s, however, the fur trade became a source of cash income for both local Cree residents and outsider trappers who moved into the area when new railways improved transportation between trapping areas and markets. Traditional constraints on beaver harvest dissolved, and beaver were severely depleted within a decade and began to recover only when the Cree, with the cooperation of the Quebec government, developed new institutions (beaver reserves) that were managed locally (Berkes 1998). Similar comanagement arrangements between state or federal agencies and local indigenous residents in Alaska and parts of Canada have been an important mechanism for strengthening the negative feedbacks between local subsistence hunters and the population dynamics of the animals that they harvest (Berkes et al. 1991; Kofinas 1998; Olsson et al. 2004). Although there are many examples of overexploitation (positive

feedbacks) by rural societies, the most sustainable management of common-pool resources occurs with the development of local institutions that link changes in resource harvest to variations in supply (Berkes et al. 1991; Huntington 1992).

The concept of maximum sustainable yield (MSY) was developed to provide an objective institutional basis for sustainably managing the harvest of natural resources on public lands and waters. The ecological assumptions underlying MSY are, however, often optimistic and frequently ignore the possibility of pest outbreaks, climatically driven fluctuations, and other surprises (Gunderson et al. 1995). The more we push the biological limits in harvesting ecosystem resources toward MSY, the more difficult it is to reduce harvest limits or land-use change, because people develop a vested interest in high levels of harvest. In marine fisheries, for example, the social response to the depletion of a fishery is to increase pressure on the remaining stock because of the large capitalization required for fishing and the public pressure to subsidize the industry at times of economic hardship. Subsidies can encourage continued participation in an unprofitable and ecologically unsustainable fishery because of the incentives to demonstrate participation, which may be required to qualify for subsidies (Munro and Sumaila 2002). As the larger fish are depleted, fishing pressure shifts to progressively lower trophic levels to provide food for both humans and farmed fish (Pauly and Christensen 1995; Naylor et al. 2000; NRC 2004).

Institutions that monitor and assess changes in common-pool resources, based on observations of resource users and research scientists, can provide the information needed for management under conditions of change (Berkes 2002; Kofinas et al. 2002). Although implementation of adaptive management is never simple (Walters 1997; Lee 1999), effective monitoring can serve as a critical negative feedback by providing the basis for experimentation and social learning that leads to human adaptation in the form of appropriate resource-use policies. This could be particularly important where human activities have weakened natural constraints and feedbacks. Institutions that reduce the likelihood of overharvest of common-pool resources are most likely to evolve when (1) the resources and their use by people can be monitored and verified at relatively low cost, (2) the rates of change in resources and the factors that influence their use are not too great, (3) there are social networks that communicate effectively about resource use, (4) outsiders can be excluded at relatively low cost from using the resources, and (5) local users support effective monitoring and rule enforcement (Ostrom 1990; Dietz et al. 2003). These conditions are rarely met fully. However, the social-ecological hypotheses described above provide a basis for predicting when institutional feedbacks will be

effective in constraining human impacts on ecological communities.

We are only beginning to develop a predictive understanding of the feedbacks between social and ecological processes and therefore human impacts on the structure of ecological communities. The hypotheses that we present suggest a clear role for science in identifying and quantifying the temporal, spatial, and institutional disconnects between human actions and ecological consequences. These hypotheses also suggest a role for scientifically informed public education, particularly in moments of crisis, to develop policies that reduce the magnitude of these disconnects (Pitcher and Pauly 1998), in part through development of alternative policy scenarios (Millennium Ecosystem Assessment 2003).

### Conclusion

In conclusion, we argue that the ecological community predictions that have guided the development of theoretical ecology continue to provide a fruitful framework for predicting the structure and composition of ecological communities, particularly under circumstances where strong negative feedbacks constrain changes in the slow variables that modulate long-term patterns of community structure. These community predictions are necessary but insufficient to predict the changes likely to occur in a directionally changing world. Our growing understanding of ecological thresholds and of social-ecological systems provides hope that a framework that incorporates some of these dynamics can improve our ability to predict future changes in ecological communities and social-ecological systems. Because of the large role that people play in modifying ecosystems and ecosystem services, it is particularly important to test and improve the social-ecological hypotheses as a basis for shaping appropriate policies for long-term ecosystem resilience.

### Acknowledgments

We thank M. Power and two anonymous reviewers for insightful comments and suggestions. This research was part of the Integrative Graduate Education and Research Training program in resilience and adaptation (National Science Foundation [NSF] grant DGE-0114423) and the Bonanza Creek Long-Term Ecological Research program (funded jointly by NSF grant DEB-0423442 and USDA Forest Service, Pacific Northwest Research Station grant PNW01-JV11261952-231), with additional funding from NSF grant OPP-0328282 for study of human-fire interactions.

### Literature Cited

- ACIA. 2005. Arctic climate impact assessment. Cambridge University Press, Cambridge.
- Barber, V. A., G. P. Juday, and B. P. Finney. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405:668–673.
- Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1:376–382.
- Benda, L. E., N. L. Poff, C. Tague, M. A. Palmer, J. Pizzuto, S. Cooper, E. Stanley, and G. Moglen. 2002. How to avoid train wrecks when using science in environmental problem solving. *BioScience* 52: 1127–1136.
- Berg, E. E. 1998. Spruce bark beetle history studies, Kenai Peninsula. Pages 1–66. Kenai National Wildlife Refuge, Soldotna, AK.
- Berkes, F. 1998. Indigenous knowledge and resource management systems in the Canadian subarctic. Pages 98–128 *in* F. Berkes and C. Folke, eds. *Linking social and ecological systems: management practices and social mechanisms for building resilience*. Cambridge University Press, Cambridge.
- . 2002. Cross-scale institutional linkages: perspectives from the bottom up. Pages 293–321 *in* E. Ostrom, T. Dietz, N. Dolsak, P. C. Stern, S. Stonich, and E. U. Weber, eds. *The drama of the commons*. National Academies Press, Washington, DC.
- . 2004. Rethinking community-based conservation. *Conservation Biology* 18:621–630.
- Berkes, F., and C. Folke. 1998. Linking social and ecological systems for resilience and sustainability. Pages 1–25 *in* F. Berkes and C. Folke, eds. *Linking social and ecological systems: management practices and social mechanisms for building resilience*. Cambridge University Press, Cambridge.
- Berkes, F., P. George, and R. Preston. 1991. Co-management: the evolution of the theory and practice of joint administration of living resources. Research Program for Technology Assessment in the Subarctic, Hamilton, Canada.
- Berkes, F., N. Bankes, M. Marschke, D. Armitage, and D. Clark. 2005. Cross-scale institutions: building resilience in the Canadian North. Pages 225–247 *in* F. Berkes, R. Huebert, H. Fast, M. Manseau, and A. Diduck, eds. *Breaking ice: renewable resource and ocean management in the Canadian North*. University of Calgary Press, Calgary.
- Bradshaw, A. D. 1983. The reconstruction of ecosystems. *Journal of Ecology* 20:1–17.
- Busenberg, G. J. 2004. Wildfire management in the United States: the evolution of a policy failure. *Review of Policy Research* 21: 145–156.
- Carpenter, S. R. 2003. Regime shifts in lake ecosystems: pattern and variation. International Ecology Institute, Oldendorf/Luhe, Germany.
- Carpenter, S. R., B. H. Walker, J. M. Andries, and N. Abel. 2001. From metaphor to measurement: resilience of what to what? *Ecosystems* 4:765–781.
- Carpenter, S. R., W. A. Brock, and D. Ludwig. 2002. Collapse, learning, and renewal. Pages 173–193 *in* L. H. Gunderson and C. S. Holling, eds. *Panarchy: understanding transformations in human and natural systems*. Island, Washington, DC.
- CCAMLR. 2000. Convention on the conservation of Antarctic marine living resources. <http://www.ccamlr.org>.
- Chapin, F. S., III, M. S. Bret-Harte, S. E. Hobbie, and H. Zhong.

- 1996a. Plant functional types as predictors of the transient response of arctic vegetation to global change. *Journal of Vegetation Science* 7:347–358.
- Chapin, F. S., III, M. S. Torn, and M. Tateno. 1996b. Principles of ecosystem sustainability. *American Naturalist* 148:1016–1037.
- Chapin, F. S., III, P. A. Matson, and H. A. Mooney. 2002. Principles of terrestrial ecosystem ecology. Springer, New York.
- Chapin, F. S., III, T. S. Rupp, A. M. Starfield, L. DeWilde, E. S. Zavaleta, N. Fresco, and A. D. McGuire. 2003. Planning for resilience: modeling change in human-fire interactions in the Alaskan boreal forest. *Frontiers in Ecology and the Environment* 1: 255–261.
- Chapin, F. S., III, T. V. Callaghan, Y. Bergeron, M. Fukuda, J. F. Johnstone, G. Juday, and S. Zimov. 2004. Global change and the boreal forest: thresholds, shifting states, or gradual change? *Ambio* 33:361–365.
- Chapin, F. S., III, M. Berman, T. V. Callaghan, P. Convey, A.-S. Crépin, K. Danell, H. W. Ducklow, et al. 2005. Polar systems. Pages 717–743 in *Millennium Ecosystem Assessment*, eds. Ecosystems and human well-being: current state and trends. Island, Washington, DC.
- Chapin, F. S., III, A. L. Lovcraft, E. S. Zavaleta, J. Nelson, M. D. Robards, G. P. Kofinas, S. F. Trainor, G. D. Peterson, H. P. Huntington, and R. L. Naylor. 2006. Plant strategies to address sustainability of Alaskan boreal forests in response to a directionally changing climate. *Proceedings of the National Academy of Sciences of the USA* (forthcoming).
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Dietz, T., E. Ostrom, and P. C. Stern. 2003. The struggle to govern the commons. *Science* 302:1907–1912.
- Driscoll, C. T., G. B. Lawrence, A. J. Bulger, T. J. Butler, C. S. Cronan, C. Eagar, K. F. Lambert, G. E. Likens, J. L. Stoddard, and K. C. Weathers. 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects and management strategies. *BioScience* 51:180–198.
- Elmqvist, T., F. Berkes, C. Folke, P. Angelstam, A.-S. Crépin, and J. Niemelä. 2004. The dynamics of ecosystems, biodiversity management and social institutions at high northern latitudes. *Ambio* 33:350–355.
- Eviner, V. T., and F. S. Chapin III. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology and Systematics* 34: 455–485.
- Flannigan, M. D., Y. Bergeron, O. Engelmark, and B. M. Wotton. 1998. Future wildfire in circumboreal forests in relation to global warming. *Journal of Vegetation Science* 9:469–476.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin III, et al. 2005. Global consequences of land use. *Science* 309:570–574.
- Foster, D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. *BioScience* 53:77–88.
- Frelch, L. E., and P. B. Reich. 1999. Neighborhood effects, disturbance severity, and community stability in forests. *Ecosystems* 2: 151–166.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Gunderson, L. H., and C. S. Holling, eds. 2002. *Panarchy: understanding transformations in human and natural systems*. Island, Washington, DC.
- Gunderson, L. H., C. S. Holling, and S. S. Light. 1995. *Barriers and bridges to the renewal of ecosystems and institutions*. Columbia University Press, New York.
- Hardin, G. 1968. The tragedy of the commons. *Science* 162:1243–1248.
- Hinzman, L. D., N. D. Bettez, W. R. Bolton, F. S. Chapin III, M. B. Dyurgerov, C. L. Fastie, B. Griffith, et al. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* 72:251–298.
- Holling, C. S. 1986. Resilience of ecosystems: local surprise and global change. Pages 292–317 in W. C. Clark and R. E. Munn, eds. *Sustainable development and the biosphere*. Cambridge University Press, Cambridge.
- Holling, C. S., and L. H. Gunderson. 2002. Resilience and adaptive cycles. Pages 25–62 in L. H. Gunderson and C. S. Holling, eds. *Panarchy: understanding transformations in human and natural systems*. Island, Washington, DC.
- Hu, F.-S., B. P. Finney, and L. B. Brubaker. 2001. Effects of Holocene *Alnus* expansion on aquatic productivity, nitrogen cycling and soil development in southwestern Alaska. *Ecosystems* 4:358–368.
- Huntington, H. P. 1992. *Wildlife management and subsistence hunting in Alaska*. University of Washington Press, Seattle.
- Huston, M. A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.
- Jenny, H. 1980. *The soil resources: origin and behavior*. Springer, New York.
- Johnstone, J. F. 2003. *Fire and successional trajectories in boreal forest: implications for response to a changing climate*. PhD diss. University of Alaska, Fairbanks.
- Johnstone, J. F., and F. S. Chapin III. 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology* 9:1401–1409.
- . 2006. Fire interval effects on successional trajectory in boreal forests of northwest Canada. *Ecosystems* 9:268–277.
- Johnstone, J. F., and E. S. Kasischke. 2005. Stand-level effects of soil burn severity on post-fire regeneration in a recently-burned black spruce forest. *Canadian Journal of Forest Research* 35:2151–2163.
- Jones, J. B., Jr., K. C. Petrone, J. C. Finlay, L. D. Hinzman, and W. R. Bolton. 2005. Nitrogen loss from watersheds of interior Alaska underlain with discontinuous permafrost. *Geophysical Research Letters* 32:LO2401, doi:2410.1029/2004GL021734.
- Kashian, D. M., M. G. Turner, W. H. Romme, and C. G. Lorimer. 2005. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. *Ecology* 86:643–654.
- Kielland, K., and J. Bryant. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos* 82:377–383.
- Kofinas, G. P. 1998. *The cost of power sharing: community involvement in Canadian porcupine caribou co-management*. PhD diss. University of British Columbia, Vancouver.
- Kofinas, G. P., and communities of Aklavik, Arctic Village, Old Crow, and Fort McPherson. 2002. Community contributions to ecological monitoring: knowledge co-production in the U.S.-Canada arctic borderlands. Pages 54–91 in I. Krupnik and D. Jolly, eds. *The earth is faster now: indigenous observations of arctic environmental change*. Arctic Research Consortium of the United States, Fairbanks, AK.
- Langston, N. E. 1998. *People and nature: understanding the changing*

- interactions between people and ecological systems, Pages 25–76 in S. I. Dodson, T. F. H. Allen, S. R. Carpenter, A. R. Ives, R. L. Jeanne, J. F. Kitchell, N. E. Langston, et al., eds. *Ecology*. Oxford University Press, New York.
- Lawrence, D. M., and A. G. Slater. 2005. A projection of severe near-surface permafrost degradation during the 21st century. *Geophysical Research Letters* 32:L24401, doi:24410.21029/22005GL025080.
- Lee, K. N. 1999. Appraising adaptive management. *Conservation Ecology*, vol. 3, issue 2. <http://www.ecologyandsociety.org/vol3/iss2/art3/>.
- Lloyd, A. H., M. E. Edwards, B. P. Finney, J. A. Lynch, V. Barber, and N. H. Bigelow. 2006. Holocene development of the Alaskan boreal forest. Pages 62–78 in F. S. Chapin III, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla, eds. *Alaska's changing boreal forest*. Oxford University Press, New York.
- Lynch, J. A., J. S. Clark, N. H. Bigelow, M. E. Edwards, and B. P. Finney. 2002. Geographical and temporal variations in fire history in boreal ecosystems of Alaska. *Journal of Geophysical Research* 108:8152, doi:1029/2001JD000332.
- MacArthur, R. H. 1965. Patterns of species diversity. *Biological Reviews* 40:510–533.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Millennium Ecosystem Assessment. 2003. *Ecosystems and human well-being*. Island, Washington, DC.
- Munro, G., and U. R. Sumaila. 2002. The impact of subsidies upon fisheries management and sustainability: the case of the North Atlantic. *Fish and Fisheries* 3:233–250.
- Naylor, R., R. Goldburg, J. Primavera, N. Kautsky, M. Beveridge, J. Clay, C. Folke, J. Lubchenco, H. Mooney, and M. Troell. 2000. Effect of aquaculture on world fish supplies. *Nature* 405:1017–1024.
- NRC (National Research Council). 2004. *Developing a research and restoration plan for Arctic-Yukon-Kuskokwim (western Alaska) salmon*. National Academies Press, Washington, DC.
- . 2005. *Valuing ecosystem services: toward better environmental decision-making*. National Academies Press, Washington, DC.
- Olsson, P., C. Folke, and F. Berkes. 2004. Adaptive co-management for building resilience in social-ecological systems. *Environmental Management* 34:75–90.
- Osterkamp, T. E., and V. E. Romanovsky. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes* 10:17–37.
- Ostrom, E. 1990. *Governing the commons: the evolution of institutions for collective action*. Cambridge University Press, Cambridge.
- Pastor, J., R. J. Naiman, B. Dewey, and P. McInnes. 1988. Moose, microbes, and the boreal forest. *BioScience* 38:770–777.
- Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature* 374:255–257.
- Petraitis, P. S., and R. E. Latham. 1999. The importance of scale in testing the origins of alternative community states. *Ecology* 80:429–442.
- Pickett, S. T. A., V. T. Parker, and P. Fielder. 1992. The new paradigm in ecology: implications for conservation biology above the species level. Pages 65–88 in P. Fielder and S. Jain, eds. *Conservation biology: the theory and practice of nature conservation*. Chapman & Hall, New York.
- Pimm, S. L. 1982. *Food webs*. Chapman & Hall, New York.
- Pitcher, T. J., and D. Pauly. 1998. Rebuilding ecosystems, not sustainability, as the proper goal of fishery management. Pages 311–325 in T. Pitcher, D. Pauly, and P. Hart, eds. *Reinventing fisheries management*. Chapman & Hall, New York.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* 250:411–415.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46:609–620.
- Prentice, I. C., G. D. Farquhar, M. J. R. Fasham, M. L. Goulden, M. Heimann, V. J. Jaramillo, H. S. Khesghi, C. Le Quéré, R. J. Scholes, and D. W. R. Wallace. 2001. The carbon cycle and atmospheric carbon dioxide. Pages 183–237 in J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson, eds. *Climate change 2001: the scientific basis*. Cambridge University Press, Cambridge.
- Pyne, S. J. 2001. *Year of the fires: the story of the great fires of 1910*. Viking, New York.
- Sala, O. E., F. S. Chapin III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, et al. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1776.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* 18:648–656.
- Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience* 54:661–676.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17:170–176.
- Smith, Z. A. 2000. *The environmental policy paradox*. Prentice Hall, Upper Saddle River, NJ.
- Steffen, W. L., A. Sanderson, P. D. Tyson, J. Jäger, P. A. Matson, B. Moore III, F. Oldfield, et al. 2004. *Global change and the earth system: a planet under pressure*. Springer, New York.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- Todd, S. K., and H. A. Jewkes. 2005. *Fire in Alaska: a history of organized fire suppression and management in the last frontier*. University of Alaska, Fairbanks.
- Turner, B. L., II, R. E. Kasperson, P. A. Matson, J. J. McCarthy, R. W. Corell, L. Christensen, N. Eckley, et al. 2003. A framework for vulnerability analysis in sustainability science. *Proceedings of the National Academy of Sciences of the USA* 100:8074–8079.
- Uliassi, D. D., and R. W. Ruess. 2002. Limitations to symbiotic nitrogen fixation in primary succession on the Tanana River floodplain, Alaska. *Ecology* 83:88–103.
- Van Cleve, K., L. A. Viereck, and R. L. Schlentner. 1971. Accumulation of nitrogen in alder (*Alnus*) ecosystems near Fairbanks, Alaska. *Arctic and Alpine Research* 3:101–114.
- Van Cleve, K., F. S. Chapin III, C. T. Dyrness, and L. A. Viereck. 1991. Element cycling in taiga forest: state-factor control. *BioScience* 41:78–88.
- Vitousek, P. M. 2004. *Nutrient cycling and limitation: Hawai'i as a model system*. Princeton University Press, Princeton, NJ.
- Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238:802–804.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson,

- D. W. Schindler, W. H. Schlesinger, et al. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* 7:737–750.
- Walker, B., and J. A. Meyers. 2004. Thresholds in ecological and social-ecological systems: a developing database. *Ecology and Society*, vol. 9, issue 2. <http://www.ecologyandsociety.org/vol9/iss2/art3>.
- Walker, B., C. S. Holling, S. R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability, and transformability in social-ecological systems. *Ecology and Society*, vol. 9, issue 2. <http://www.ecologyandsociety.org/vol9/iss2/art5>.
- Wallington, T. J., R. J. Hobbs, and S. A. Moore. 2005. Implications of current ecological thinking for biodiversity conservation: a review of the salient issues. *Ecology and Society*, vol. 10, issue 11. <http://www.ecologyandsociety.org/vol10/iss11/art15/>.
- Walters, C. 1997. Challenges in adaptive management of riparian and coastal ecosystems. *Conservation Ecology*, vol. 1, issue 2.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biological Reviews* 42:207–264.
- Young, O. R. 1989. *International Cooperation: building regimes for natural resources and the environment*. Cornell University Press, Ithaca, NY.
- . 1994. *International governance: protecting the environment in a stateless society*. Cornell University Press, Ithaca, NY.

Symposium Editor: Mark A. McPeck