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The great challenge now facing forest ecosystem scientists and managers is to address the need for multiple ecosystem services over relatively large spatial and temporal scales (e.g., whole national forests over 50- to 100-year time frames). Here we present a new conceptual model for the study of forest ecosystems that aids in the analysis of factors that influence ecosystem structure, function, and services. We then go on to show how this model has been applied to the long-term Hubbard Brook Ecosystem Study. Our new model has three main components: (1) controllers, (2) ecosystem pattern and process, and (3) ecosystem functions and services. The controllers are the factors that drive ecosystem pattern and process; we split them into two groups, state factors and variable–stochastic factors. This new model will help to ensure a comprehensive approach to forest ecosystem analysis and will facilitate interactions of research with policy and management at many locations.

Keywords: ecosystem services, state factors, ecosystem function, forests, conceptual models

Humans have diverse needs for forests, and many factors influence the ability of forests to provide these needs or services. The great challenge facing forest ecosystem scientists and managers is to address the need for multiple ecosystem services over relatively large spatial and temporal scales—whole national forests, for example, over 50- to 100-year time frames. This challenge is becoming ever more acute as the human population swells, increasing the number and intensity of influences on forest ecosystems (e.g., climate change, air pollution).

Conceptual models are critically important for addressing complex challenges in ecosystem science. A strong conceptual model must explicitly depict various spatial and temporal scales, multiple levels of ecological organization (e.g., ecosystem, community, species, and population), the primary components of biological diversity (structure, function, and composition), and the ways in which these components are connected by flows and direct biotic interactions. Such a model can help to establish linkages between human goals and the factors that influence the ability of ecosystems to provide specific services. Conceptual models are especially important in the long-term, multidisciplinary research studies that are common in ecosystem ecology, and they are essential to fundamental advancement in this discipline (Bormann and Likens 1979, Golley 1993, Carpenter 1998).

In this article, we present a new conceptual model for forest ecosystem research, using the Hubbard Brook Ecosystem Study (HBES) as an example and test case. Our objectives are to present a model that allows for (a) a systematic classification of the factors that control ecosystem structure and function, with a basis for evaluation and prediction of what factors are important at different times in specific places; (b) a flexible definition of ecosystem structure and function that fosters analysis of linkages between specific controlling factors and specific ecosystem services; and (c) a focus on ecosystem services that helps to articulate the key research questions needed to meet specific management objectives.

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Based at the Hubbard Brook Experimental Forest (HBEF), a 3160-hectare (ha) US Department of Agriculture Forest Service reserve located in the White Mountain National Forest in New Hampshire, HBES has been dedicated to the long-term study of forest and associated aquatic ecosystems since the early 1960s (see *www.hubbardbrook.org*). Much of the research program has focused on the mass-balance approach, analyzing inputs, outputs, and internal fluxes of water and elements in small (10 to 80 ha) forested watersheds (Bormann and Likens 1967, 1979, Likens and Bormann 1995). HBES has long been guided by a strong conceptual model (figure 1) that focuses on element fluxes among atmosphere, vegetation, soil, and stream. This model, first presented in 1967 (Bormann and Likens 1967), has been used to develop, guide, and summarize the many aspects of the HBES research program. It has also been used extensively to address difficult questions at the ecosystem scale (e.g., weathering; Likens and Bormann 1995).

Several factors have motivated us to search for a new conceptual model for HBES. Although the current model is an excellent integrative tool for biogeochemical, mass-balance–based studies, this framework is less explicit and comprehensive for other aspects of ecosystem structure, function, and development, such as biodiversity and trophic dynamics. As societal and scientific interest in the full range of ecosystem functions, processes, and services has grown, we have felt a need to develop a conceptual model that can be applied to a broader scope of ecosystem analysis.

Changes within the field of biogeochemistry also motivated us to develop a new conceptual model. Long-term observations of input–output budgets of water and chemical elements in the Hubbard Brook watersheds have stimulated greater interest in understanding the dynamics of biogeochemistry and energy flow within the watershed ecosystem (Likens 1992). Although the current model is excellent for conceptualizing inputs, dominant internal fluxes, and outputs, it is less effective for conceptualizing more complex relationships among ecosystem components, such as the effects of birds on net primary production through their predation on insects (Holmes 1990, Strong et al. 2000).

In addition to growing interest in internal ecoystem dynamics, the scope of biogeochemically oriented mass-balance studies has increased greatly over the last 30 years. Although our initial studies focused on clear-cutting and interactions between the atmosphere and ecosystems, we now address a much wider range of ecosystem perturbations—for example, canopy change caused by ice storms, changes in snowpack induced by global warming, calcium depletion caused by acid deposition, and fluctuations of large (moose) and small (canopy arthropods, zebra mussels) herbivores. We need a conceptual model that can be applied to this broad range of perturbations in a common context. To borrow a phrase from the historic Farley Post Office building in New York City (and Herodotus), we need a model that is deterred by "neither snow nor rain nor heat nor gloom of night."

Our new conceptual model for HBES (figure 2) has three main components: (1) controllers, (2) ecosystem pattern and process, and (3) ecosystem functions and services. "Controllers" are the factors that drive ecosystem pattern and process; they are split into two groups, state factors and variable–stochastic factors. "Ecosystem pattern and process" encompasses "all the organisms that function together in a

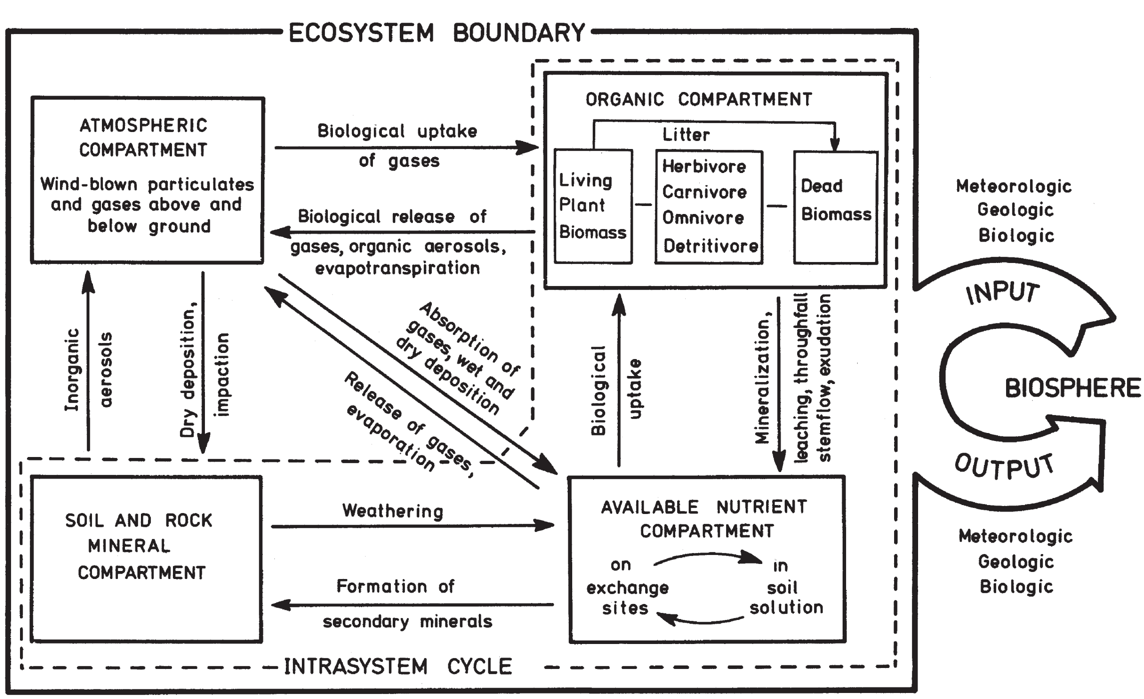

Figure 1. The traditional Hubbard Brook conceptual model, depicting nutrient relationships in a terrestrial ecosystem. From Likens and Bormann (1995).

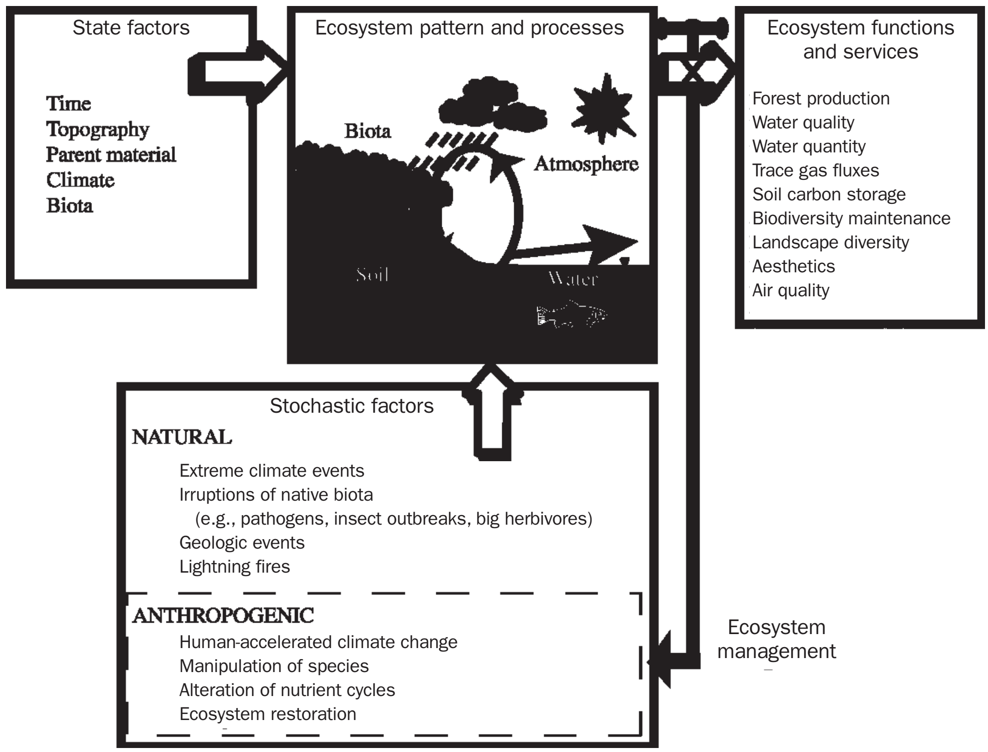

Figure 2. A new conceptual diagram for the Hubbard Brook Ecosystem Study, showing how state factors and variable–stochastic factors influence ecosystem pattern and process and, ultimately, ecosystem functions and services. Management actions can be directed to mitigate stochastic factors that are caused by human activities and, therefore, to improve ecosystem functions and services.

given area interacting with the physical environment so that a flow of energy leads to clearly defined biotic structures and cycling of materials between living and nonliving parts" (Odum 1983). The traditional HBES conceptual model was one way of envisioning this component of the new model. The concept of ecosystem functions and services refers to aspects of ecosystems that are valued by humans. These functions and services range from the supply of clean water to the support of aesthetically pleasing plants and animals, from the production of gases that influence the chemistry and physics of the atmosphere to the sequestration of carbon and nitrogen. In the sections below, we describe the components of our new model in detail. While we recognize that there is some inevitable overlap between the ecological features that constitute each of these major components, we hope to demonstrate the usefulness of our model by showing how it can be applied to some current research questions in HBES. Finally, we present an approach to using the new model quantitatively by linking it to the existing PnET family of simulation models (Aber and Driscoll 1997).

Controllers of ecosystem pattern and process

The idea that state factors control ecosystem patterns and processes is taken from the field of soil science, which has long been guided by the "five factors of soil formation" conceptual model of spatial patterns in soil development (Jenny [1941] 1994, Amundson and Jenny 1997). These five factors (table 1) effectively explain and predict spatial patterns of soil properties (e.g., the occurrence of Mollisols in grasslands and steppes in North America, South America, and Eurasia) and can be adapted easily as a conceptual guide to the analysis of terrestrial ecosystems (Jenny 1961, Matson et al. 1989, Amundson and Jenny 1997). Huggett (1995) proposed a similar framework using the biosphere, troposphere, atmosphere, pedosphere, and hydrosphere as state factors that make up a geoecosystem, which can be viewed as a hierarchy of spatial systems.

Consideration of the five state factors allows us to predict an expected state for an ecosystem. Put another way, state factors can be defined as the variables that determine the state of the ecosystem at a given time. More generally, given information on climate, parent material, topography, time (since parent material formation, i.e., primary ecosystem development), and biota (the comprehensive set of organisms that could occur in a given location), it is possible to make predictions about the structure and function of terrestrial ecosystems at a given location. Numerous studies have evaluated the influence of these state factors in controlling soil and ecosystem properties, although the state factor model is rarely invoked in these studies (Amundson and Jenny 1997, Schuur et al. 2001). It is rarely possible to experimentally evaluate the role of state factors by varying one factor while keeping all the

Table 1. State factors and variable–stochastic factors that control ecosystem pattern and process.

State factors	Variable–stochastic factors: Natural	Variable–stochastic factors: Anthropogenic
Time (since parent material deposition/primary succession)	Extreme climate events (e.g., hurricanes, ice storms)	Human-accelerated climate change
Topography	Irruptions of native biota (e.g., pathogens, insect outbreaks, large herbivores)	Manipulation of species (introduction of alien and invasive species)
Parent material	Geologic events (e.g., earthquakes)	Alteration of nutrient cycles (e.g., forest cutting, agriculture, atmospheric deposition)
Climate	Lightning fires	Ecosystem restoration
Biota (the set of organisms capable of living in a place)[a]		

a. This set of organisms should be distinguished from the set of organisms that are actually observed in a place, which is a state variable within the ecosystem box, not a state factor (controller).

others constant. The state factor approach is most useful as a tool for understanding broad variation among soils and ecosystems.

The need to articulate a set of variable–stochastic factors that control ecosystem pattern and process arises because researchers frequently do not observe the expected state of ecosystems. The mechanism or mechanisms for this deviation from the expected state of ecosystems have long been a source of debate in ecology, ranging from the "Clements versus Gleason" debate about self-organizing versus individualistic concepts of ecosystem development in the 1920s to the current debate about "balance of nature" versus "flux of nature" views of ecosystems (Pickett et al. 1992, O'Neill 2001). These debates, which arise from the great observed variation in ecosystem structure and function, address the utility of predicting an expected climax condition or equilibrium state for ecosystems. To resolve these debates, we suggest that it is useful to predict an expected state for an ecosystem, to consider and define the specific factors that cause an ecosystem to deviate from this expected state, and to use this process of definition to guide research and management programs.

The set of variable–stochastic factors is large (see table 1). Some of these factors are inherently "natural" (e.g., hurricanes, herbivore oscillations), while others are inherently human-induced or accelerated by humans (e.g., air pollution, clear-cutting). In many cases, these factors could be considered to be an inherent part of the ecosystem (e.g., fire in grasslands, drought, ice storms). However, we define any factor that does not fall into the set of state factors as "variable–stochastic." This approach allows us to identify factors that can influence specific aspects of ecosystem structure and function and then pose hypotheses about how this influence is expressed, a clear benefit to guiding a research program. Identifying separate factors in this way also fosters integration and comparison: For example, how important is fire, compared with herbivore dynamics, as a regulator of nitrogen loss? Time since disturbance (e.g., clear-cutting or fire) is a component of many of the variable–stochastic factors and must be distinguished from time as a state factor, which refers to time since deposition of parent material (i.e., the initiation of primary ecosystem development).

The distinction between state and variable–stochastic factors allows researchers to ask questions about the ability to predict when or where certain factors will be important. It would be much easier to manage forests for multiple services over large temporal and spatial scales if managers could predict when specific systems would be more or less vulnerable to specific factors. For example, in the northern hardwood forests at HBEF, we are asking whether we should really pay attention to increases in the populations of large herbivores (moose, deer) after forest cutting, because their preferential grazing can completely alter the trajectory of plant succession in the recovering ecosystem. A major goal of our long-term research is to develop theory, empirical data, and models about where and when certain kinds of factors are likely to be important. Distinguishing between state and variable–stochastic factors will be a great aid to this research.

Ecosystem pattern and process

It is difficult to define an ecosystem. Since Tansley (1935) first coined the term, there has been much debate about the components, size, and functions of an ecosystem (Likens 1998, O'Neill 2001, Pickett and Cadenasso 2002). The definition provided by Odum (1983) is the most comprehensive: An ecosystem is "any unit that includes all the organisms that function together (the biotic community) in a given area interacting with the physical environment so that a flow of energy leads to clearly defined biotic structures and cycling of materials between living and nonliving parts." While this definition is suitably comprehensive, it is very general; it provides little guidance for defining the essential nature of an ecosystem. This lack of guidance leads to disciplinary chauvinism. For example, physically oriented scientists might describe an ecosystem primarily in terms of water—the balance between precipitation and evapotranspiration or the partitioning of precipitation into surface runoff versus groundwater flow paths. In contrast, a biologist might describe an ecosystem in terms of the dominant vegetation or wildlife habitat.

It would be difficult, and not particularly useful, to produce one comprehensive "ecosystem box" for our model. Rather, the box can be reconstituted with a particular set of quantitative or conceptual patterns and processes that are suitable for addressing the specific question being posed about the relationships between controllers and functions or services. The traditional Hubbard Brook biogeochemistry (figure 1) and population dynamics (Holmes 1990) models are examples of different ways that the box could be filled. The contents of the box can vary in time, as changes in controlling factors can move the ecosystem into an alternate state (stable or not) (Holling 1973). This variable approach to defining the key components of an ecosystem is consistent with the wide range of spatial scales used in ecosystem analysis

(Likens 1992), and indeed, the spatial scale of our ecosystem box will vary on a question-by-question basis (see examples below). Thus, we see our conceptual model as dynamic—changing with time, need, and new information.

Ecosystem functions and services

The concept of ecosystem services has developed rapidly over the last several years (Daily et al. 1997). The idea that scientists and managers can quantify the aspects of ecosystems that benefit humans has broad appeal to those who are interested in merging the social and ecological sciences, providing a monetary basis for conservation, and reconciling conflicts in ecosystem management to achieve diverse goals (Carpenter and Turner 2000). This concept is based on a frank recognition that Earth is affected by humans (e.g., Noble and Dirzo 1997, Wilson and Carpenter 1999) and that humans have only a limited capacity for objective assessment of ecosystem function; there is no way that we can observe ecosystems without considering the attributes that benefit us.

The set of ecosystem services under consideration should be broad, ranging from biogeochemical functions to biodiversity (box 1). Ecosystem ecology, including the work of HBES, has traditionally focused on biogeochemistry and energy flux, including the flow of energy though food chains, water yield, water quality, carbon storage, and trace gas fluxes. A major challenge is to expand the scope of our analysis to include ecosystem functions that are perhaps less readily quantified but are of great interest to the public, such as aesthetic appreciation of biodiversity and landscape characteristics.

Including ecosystem services in our conceptual model can help connect research with environmental management and policy—an undertaking that may be the greatest challenge now facing environmental scientists (Walters 1998). A focus on ecosystem services allows researchers and managers to lay out the full range of ecosystem processes of interest to humans, thereby helping to identify and include stakeholders with different interests. They can then identify key research questions that are necessary to develop management and policy to achieve specific objectives. The model can also be useful for articulating the value of research and providing a mechanism for linking specific topics identified by scientists (invasive species of earthworms) with specific ecosystem services of interest to managers (water quality). Finally, the model allows researchers and managers to evaluate multiple factors in a comprehensive context: For example, how important to water quality are invasive earthworms compared with acid rain?

Box 1. Ecosystem functions and services for a northern hardwood forest

- Wood for paper, construction, and other uses
- Water quality
- Water quantity
- Air quality
- Production and consumption of gases that influence the chemistry and physics of the atmosphere
- Storage of elements (carbon, nitrogen, sulfur, trace metals)
- Biodiversity maintenance
- Landscape diversity
- Recreational opportunities
- Aesthetics

Examples from current research of the Hubbard Brook Ecosystem Study

In this section, we show how different research activities of the Hubbard Brook Ecosystem Study fit into our new conceptual model. Our objective is to show how the model helps to identify diverse drivers of ecosystem pattern and process that influence a full set of ecosystem functions and services.

Depletion of available calcium from soil by acidic deposition. Concern about long-term depletion of calcium in soil and vegetation by acidic deposition (Likens et al. 1996, 1998) led to the initiation of a watershed-scale calcium addition experiment at HBEF in 1999. We treated an 11.8-ha watershed (Watershed 1) with a calcium silicate mineral (wollastonite) to restore the calcium that we estimate was leached from the ecosystem by 50 years of acidic deposition. Our objective in using wollastonite was to add a calcium source that mimics the natural weathering process as closely as possible, but at a faster rate. The 1999 addition was designed to increase the base saturation of the watershed soils from approximately 10 percent to 19 percent (the condition before acid rain), altering a variable–stochastic factor that we suggest has caused the northern hardwood forest and aquatic ecosystems at HBEF to deviate from their expected state in many ways. In 10 years, we may make a second addition to raise the base saturation to 25 percent, altering an inherent state factor (parent material).

Concern about soil calcium depletion at HBEF arose from our long-term studies that have shown marked changes in the acid–base status of soil and drainage waters over the last 30 years, resulting from changes in atmospheric deposition (Likens et al. 1996, 1998). Decreases in atmospheric deposition of sulfate (SO_4^{2-}), coinciding with decreases in sulfur dioxide emissions in the eastern United States, have resulted in marked decreases in stream water concentrations of SO_4^{2-} (Likens et al. 2001). Despite these reductions, there have been only very limited increases in stream pH. Rather, we have observed near-equivalent decreases in the sum of base cation concentrations in stream water. Budget calculations suggest that atmospheric inputs of strong acids to HBEF have resulted in marked depletion of labile pools of calcium from the forest ecosystem (Likens et al. 1996, 1998). This process has delayed the recovery of drainage waters from decreases in atmospheric deposition. At the same time, we have observed a number of long-term changes in the abundance of biotic populations, including sugar maple *(Acer saccharum)*, acidophilic and calciphilic herbs, gastropods, and stream invertebrates and amphibians; the inorganic nutrition of others has been altered as well (Likens et al. 1998, Driscoll et al. 2001).

From a more fundamental, state factor perspective, pH and base saturation are important components of the parent material state factor, components that have a strong influence on the structure and function of ecosystems through their effects on microbial processes, on abiotic reactions in soil and water, on the bioavailability of nutrients and toxic substances, and on the distribution and abundance of biological species (Reuss and Johnson 1986, Driscoll et al. 2001). In turn, biogeochemical processes influence pH through the transfer of major ionic solutes (Reuss and Johnson 1986). In forest ecosystems, these element transfers include atmospheric deposition, mineral weathering, soil chemical processes (e.g., cation exchange, secondary mineral formation, anion adsorption), mineralization of soil organic matter, microbial transformations involving ionic solutes, uptake of ionic nutrients by vegetation, and gaseous and drainage losses of major elements.

Our calcium addition study is designed to address both inherent state factor and variable–stochastic factor controls over the pattern and process of the northern hardwood forest and aquatic ecosystems at HBEF (table 1). Our evaluation of these controls will be comprehensive, including a key set of ecosystem elements and a full suite of ecosystem services, from water quality to trace gas fluxes to biodiversity (box 1). Our new conceptual model is useful as a guide for this extremely long-term (50-year) research. First, it provides perspective for the treatments that we apply, fostering recognition that we are evaluating a human-driven variable–stochastic factor (acid rain) in the context of an inherent state factor (base saturation). Second, it encourages us to define a specific, yet diverse, set of ecosystem elements that are affected by these controllers, ranging from obvious changes in soil chemistry to more subtle possible changes, such as changes in water yield and quality that may emerge if ecosystem productivity changes in response to the calcium addition. We can define our ecosystem box at several scales, from the whole watershed ecosystem to specific elevation and vegetation zones that might respond differently within the watershed (Johnson et al. 2000). Finally, it allows for a complete accounting and comparison of what may be complex and contradictory effects on ecosystem services—for example, the calcium addition may restore or increase the diversity of spring ephemeral communities but decrease water quality. Ultimately, our conceptual model, and the comprehensive synthesis and integration that it fosters, may be extremely useful as managers and policymakers consider possible ways to address acid rain and its effects on forest ecosystems.

Soil freezing events. Analysis of the indirect effects of climate change on ecosystem processes is a critical challenge in environmental biogeochemistry. Snow depth is an important regulator of nitrogen cycling in ecosystems (Mitchell et al. 1996, Williams et al. 1996) and is highly responsive to changes in climate (Cooley 1990). A lack of snow during winter leads to increases in soil freezing, which have a marked influence on patterns of nitrogen cycling and loss through their effects on root and microbial processes (Groffman et al. 2001).

Soil freezing has been relatively rare throughout the period of long-term research at HBEF, because a deep snowpack normally develops and insulates the soil from frigid winter temperatures. Observations of periodic freezing, and ideas about the effects of freezing on nitrogen cycling (Likens and Bormann 1995, Mitchell et al. 1996), led to the initiation of a snow manipulation experiment in 1997. In this ongoing experiment, snow is removed by shoveling from a series of 10-meter x 10-meter plots through January to simulate the late development of snowpack, which may occur in a warmer climate. The plots are instrumented to allow for quantification of treatment responses in soil solution chemistry, fine root production and mortality, soil-to-atmosphere trace gas fluxes, and nitrogen mineralization and nitrification.

In the mild winters of 1997–1998 and 1998–1999, our snow manipulation induced mild soil freezing. This change had significant effects on nutrient outputs from the northern hardwood forest, but it did not modify nutrient inputs or dramatically affect system hydrology or vegetation. Rather, its effects were manifested through subtle changes in fine root dynamics and root–microbial interactions (Groffman et al. 2001). In addition to water quality, ecosystem services related to atmospheric chemistry, water quantity, and soil carbon storage were affected by changes in snow depth and soil freezing. The links between freezing effects and these services are being analyzed quantitatively with mechanistic simulation models that function as tools for synthesis, integration, and extrapolation of results from the field manipulation experiment (see the discussion of PnET models below). For these analyses, instead of filling the ecosystem box with the pools and fluxes of the traditional HBES conceptual model, we are using a more detailed model that focuses on the subtle changes affected by freezing, such as root mortality and root–microbial interactions.

Our new conceptual model, as applied in the snow manipulation project, is useful for linking research with management and policy in two ways. From the management and policy side, if we ask, "What are the factors likely to influence water quality over the long term?" we can look at our list of variable–stochastic factors and suggest that the effects of climate change on soil freezing are likely to be important. From the research side, investigators interested in exploring the importance of soil freezing events can recognize the potential utility of their research by considering the full list of ecosystem services that are of interest to the management and policy communities.

The snow manipulation study raises interesting questions about the distinction between state factors and variable–stochastic factors in our conceptual model. Certainly, climate is a state factor, and freezing frequency is a feature of climate. We maintain, however, that the climate state factor represents the long-term mean climate for an ecosystem. Long-term change in temperature and precipitation patterns should be viewed as a state factor change, similar to the change created by raising the base saturation of HBEF soils above their level before the advent of acidic deposition. However, extreme climate events (e.g., hurricanes, soil freezing) that cause the ecosystem to deviate from its mean or expected state should be viewed as variable–stochastic factors. This distinction is consistent with that made between endogenous and exogenous drivers by Bormann and Likens (1979), according to which a tree falling down as part of autogenic ecosystem development processes is an endogenous driver, whereas trees knocked over by windthrow or destroyed by fire (forces external to the autogenic development process) are exogenous drivers. The distinction between state factors and variable–stochastic factors prompts researchers to ask questions and test hypotheses about specific, often subtle factors and to evaluate their importance relative to more obvious factors.

Diversity and abundance of insectivorous bird species. Long-term investigations have shown that the species composition of the bird community and the abundances of individual bird species have changed markedly within the unfragmented and relatively undisturbed forest ecosystem at Hubbard Brook. For instance, in the 30-year period between 1969 and 1998, 12 of the 24 regularly occurring species decreased significantly in abundance (4 to local extinction), 3 increased significantly, and 9 remained relatively constant in abundance (Holmes and Sherry 2001). The most important factor affecting these patterns has been temporal change in forest vegetation structure, resulting from natural forest succession and from local disturbances (e.g., pathogens such as *Nectria coccinea,* which causes beech bark disease, and storm damage caused by high winds or heavy icing during winter). Both succession and disturbance have resulted in changes in canopy structure, which affects the suitability of the site for different bird species (Holmes and Sherry 2001).

Another important factor affecting bird abundances at Hubbard Brook is food availability, which varies from year to year and is particularly influenced by outbreaks of the defoliating Lepidoptera larvae (Holmes et al. 1986, 1991, Holmes and Sherry 2001), which serve as prey for birds. Food abundance affects bird reproductive success and recruitment (Holmes et al. 1992, 1996, Sillett et al. 2000), a finding that has been confirmed by experimental food manipulations (Rodenhouse and Holmes 1992). Recent evidence suggests that climatic variation may be an important factor influencing food (Lepidoptera) availability at Hubbard Brook, which in turn affects the annual productivity and survival of bird populations (Sillett et al. 2000).

These results illustrate how changes in forest composition via succession (a state factor), along with disturbance, insect outbreaks, and global climate events (variable–stochastic factors), affect bird species abundance and diversity within a forest ecosystem and hence influence the temporal and spatial impacts of these organisms on ecosystem processes (e.g., as consumers of herbivorous insects; Holmes et al. 1979, Holmes 1990, Strong et al. 2000). The new conceptual model thus provides a framework for evaluating the causes and consequences of the structure and dynamics of heterotroph populations and of the role of those populations in ecosystem processes.

Conceptual and quantitative models

There is a great need for quantitative approaches in environmental science (Canham et al. 2003). The ultimate test of the value of our new conceptual model may well be its ability to foster quantitative integration and synthesis of our results into mechanistic simulation models. Development of these models is critically important for prediction and for the interaction of science with policy and management.

Modeling has long been important in HBES. Hydrologic modeling was a fundamental component of the early work at HBEF, which focused on the effects of forest management on water yield (Federer 1979, Hornbeck et al. 1997). Later, hydrologic modeling served as a critical integrator in the mass-balance studies that were guided by the traditional HBES conceptual model. The JABOWA family of forest gap–development models originated at Hubbard Brook (Botkin et al. 1972). There is now a strong focus on using modeling to integrate across disciplines, both in HBES and in ecology in general (Canham et al. 2003).

The PnET model (PnET-CN; Aber and Driscoll 1997), a simple, generalized, and well-validated model of monthly carbon, water, and nutrient balances, provides estimates of forest net primary productivity, nutrient uptake by vegetation, and water balances. We have recently coupled PnET with a soil column model that simulates abiotic soil processes such as cation exchange, weathering, adsorption, and solution speciation. The result is a comprehensive forest–soil–water model, PnET-BGC, designed to simulate element cycling in forest and interconnected aquatic ecosystems (figure 3; Gbondo-Tugbawa et al. 2001). The PnET models have been used extensively at Hubbard Brook to investigate the effects of disturbance (e.g., cutting, climatic disturbance, air pollution) on forest and aquatic resources (Aber and Driscoll 1997, Gbondo-Tugbawa et al. 2001) and the effects of climatic variation, atmospheric pollution, and physical and biotic disturbances on nitrate losses (Aber et al. 2002) and to predict the past and current effects of carbon dioxide, nitrogen deposition, ozone, and land use on net primary production and net ecosystem production (Ollinger et al. 2002).

The PnET models can readily serve as a platform for integration and quantification of our new conceptual model for HBES. Different components of the model can be amplified

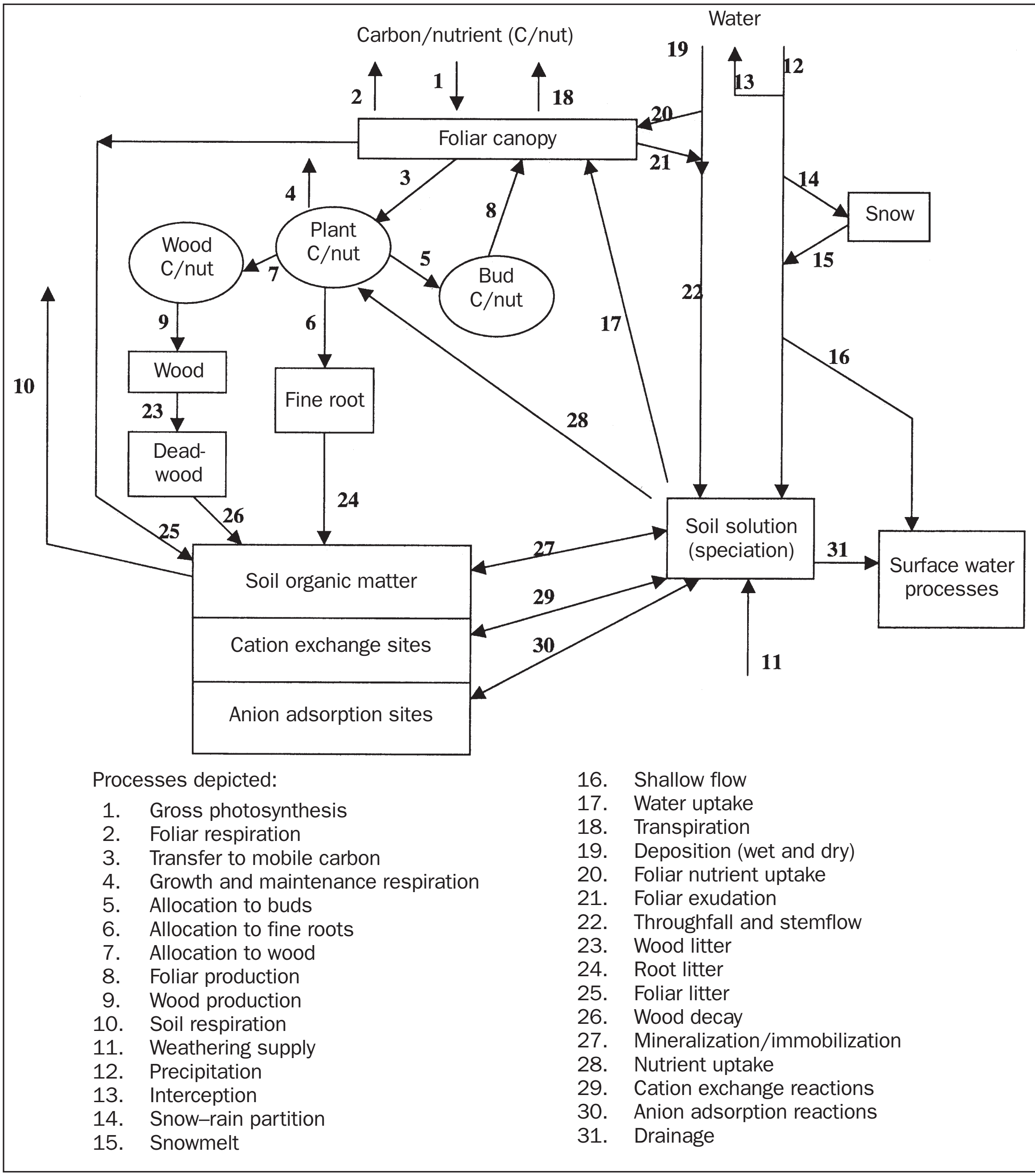

Figure 3. Structure of the PnET-BGC model illustrating the compartments and flow paths of carbon and nutrients within the model. From Gbondo-Tugbawa and colleagues (2001).

and altered to evaluate variation in both state and variable–stochastic factors. This alteration is consistent with our flexible, question-driven approach to defining the ecosystem. A quantitative, well-validated model like PnET guides us from a conceptual discussion of different factors to a more realistic evaluation of their importance. The model can be extremely useful for designing and synthesizing complex experiments involving ecosystem manipulation.

We are modifying the PnET models to address the effects of snow depth on soil freezing and nutrient loss in forests at HBEF. Much of the analysis in the ongoing project on snow and freezing (described above) has focused on responses in the soil solution. Previous work suggested that nutrient uptake (figure 3, process 28) was reduced, resulting in an increase in drainage losses (figure 3, process 31), and that, surprisingly, mineralization (figure 3, process 27) was not altered. New work is addressing the mechanisms underlying the changes in nutrient uptake, which will require modifications to several root-related compartments and flow paths in the model. The new research will also address the effects of freezing on nutrient release from organic matter and litter, which will require modifications to the compartments and flow paths in the model that relate to soil organic matter and litter.

Conclusions

Our new conceptual model provides several specific benefits to HBES that should also be applicable to many other ecosystem studies. First, making a distinction between state factors and variable–stochastic factors resolves an old conceptual debate about the existence and utility of predicting an expected state for ecosystems. More practically, it motivates the production of a comprehensive list of factors that might be important controllers of ecosystem structure and function over large spatial and temporal scales. Second, we are proposing a new, flexible approach to defining what goes into the ecosystem box at the center of our conceptual diagram (figure 2). Spatial flexibility has long been a hallmark of the ecosystem approach, allowing investigators to define a wide range of spatial boundaries for ecosystem studies. Here we suggest that we can assemble the components of an ecosystem in a variable way, depending on the question being addressed. This should be a useful tool for linking specific drivers with specific services. Finally, assembling a comprehensive list of ecosystem services enhances the interactions of research with policy and management in two ways: It allows managers to identify key factors that might influence services of interest, and it allows researchers to articulate the value of their basic science questions about how ecosystems work.

The true test of a new conceptual model is whether it broadens scientific thinking about ecosystems and improves the science in the field. A new graduate student, starting work at HBEF with an interest in the snow–freeze project, recently studied the model, with its extensive lists of variable–stochastic factors and ecosystem services, and began to wonder about interactions between moose and snow. Snow influences the ability of moose to browse on saplings, and preferential browsing on hardwood saplings is a key mechanism by which moose influence the trajectory of plant succession. The student is going on to address the ways that the human aesthetic desire for moose in the landscape will interact with climate change, which influences snow depth and the vigor of the deciduous species favored by moose browsing—the kind of complex question that is on the frontier of ecosystem science and management. To the extent that the new model helps to motivate the development of complex questions like this, it is a success.

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References cited

Aber JD, Driscoll CT. 1997. Effects of land use, climate variation and N deposition on N cycling and C storage in northern hardwood forests. Global Biogeochemical Cycles 11: 639–648.

Aber JD, Ollinger SV, Driscoll CT, Likens GE, Holmes RT, Freuder RJ, Goodale CL. 2002. Inorganic N losses from a forested ecosystem in response to physical, chemical, biotic and climatic perturbations. Ecosystems 5: 648–658.

Amundson R, Jenny H. 1997. On a state factor model of ecosystems. BioScience 47: 536–543.

Bormann FH, Likens GE. 1967. Nutrient cycling. Science 155: 424–429.

———. 1979. Pattern and Process in a Forested Ecosystem. New York: Springer-Verlag.

Botkin DB, Janak JF, Wallis JR. 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology 60: 849–872.

Canham CD, Cole JJ, Lauenroth WK, eds. 2003. The Role of Models in Ecosystem Science. Princeton (NJ): Princeton University Press.

Carpenter SR. 1998. The need for large-scale experiments to assess and predict the response of ecosystems to perturbation. Pages 287–312 in Pace ML, Groffman PM, eds. Successes, Limitations and Frontiers in Ecosystem Science. New York: Springer-Verlag.

Carpenter SR, Turner M. 2000. Opening the black boxes: Ecosystem science and economic valuation. Ecosystems 3: 1–3.

Cooley KR. 1990. Effects of CO_2-induced climatic changes on snowpack and streamflow. Hydrological Sciences 35: 511–522.

Daily GC, Ehrlich PR, Goulder LH, Lubchenco J, Matson PA, Mooney HA, Schneider SH, Woodwell GM, Tilman D. 1997. Ecosystem services: Benefits supplied to human societies by natural ecosystems. Issues in Ecology 2: 1–16.

Driscoll CT, et al. 2001. Acidic deposition in the northeastern United States: Sources and inputs, ecosystem effects, and management strategies. BioScience 51: 180–198.

Federer CA. 1979. A soil–plant–atmosphere model for transpiration and availability of soil water. Water Resources Research 15: 555–562.

Gbondo-Tugbawa SS, Driscoll CT, Aber JD, Likens GE. 2001. Evaluation of an integrated biogeochemical model (PnET-BGC) at a northern hardwood forest ecosystem. Water Resources Research 37: 1057–1070.

Golley FB. 1993. A History of the Ecosystem Concept in Ecology: More than the Sum of the Parts. New Haven (CT): Yale University Press.

Groffman PM, Driscoll CT, Fahey TJ, Hardy JP, Fitzhugh RD, Tierney GL. 2001. Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. Biogeochemistry 56: 135–150.

Holling CS. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4: 1–24.

Holmes RT. 1990. Ecological and evolutionary impact of bird predation on forest insects: An overview. Pages 6–13 in Morrison ML, Ralph CJ, Verner J, Jehl JR Jr, eds. Avian Foraging: Theory, Methodology, and Applications. Los Angeles: Cooper Ornithological Society. Studies in Avian Biology 13.

Holmes RT, Sherry TW. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: Importance of habitat change. Auk 118: 589–609.

Holmes RT, Schultz JC, Nothnagle PJ. 1979. Bird predation on forest insects: An exclosure experiment. Science 206: 462–463.

Holmes RT, Sherry TW, Sturges FW. 1986. Bird community dynamics in a temperate deciduous forest: Long-term trends at Hubbard Brook. Ecological Monographs 56: 201–220.

———. 1991. Numerical and demographic responses of temperate forest birds to annual fluctuations in their food resources. Proceedings of the 20th International Ornithological Congress 3: 1559–1567; 9–16 December 1990, Christchurch, New Zealand.

Holmes RT, Sherry TW, Marra PP, Petit KE. 1992. Multiple-brooding and productivity of a Neotropical migrant, the black-throated blue warbler *(Dendroica caerulescens),* in an unfragmented temperate forest. Auk 109: 321–333.

Holmes RT, Marra PP, Sherry TW. 1996. Habitat-specific demography of breeding black-throated blue warblers *(Dendroica caerulescens):* Implications for population dynamics. Journal of Animal Ecology 65: 183–195.

Hornbeck JW, Martin CW, Eagar C. 1997. Summary of water yield experiments at Hubbard Brook Experimental Forest, New Hampshire. Canadian Journal of Forest Research 27: 2043–2052.

Huggett RJ. 1995. Geoecology: An Evolutionary Approach. London: Routledge.

Jenny H. [1941] 1994. Factors of Soil Formation: A System of Quantitative Pedology. New York: Dover.

———. 1961. Derivation of state factor equations of soils and ecosystems. Soil Science Society of America Proceedings 25: 385–388.

Johnson C, Driscoll C, Siccama T, Likens G. 2000. Element fluxes and landscape position in a northern hardwood forest watershed ecosystem. Ecosystems 3: 159–184.

Likens GE. 1992. The Ecosystem Approach: Its Use and Abuse. Oldendorf (Germany): Ecology Institute.

———. 1998. Limitations to intellectual progress in ecosystem science. Pages 247–271 in Pace ML, Groffman PM, eds. Successes, Limitations and Frontiers in Ecosystem Science. New York: Springer-Verlag.

Likens GE, Bormann FH. 1995. Biogeochemistry of a Forested Ecosystem. 2nd ed. New York: Springer-Verlag.

Likens GE, Driscoll CT, Buso DC. 1996. Long-term effects of acid rain: Response and recovery of a forest ecosystem. Science 272: 244–246.

Likens GE, et al. 1998. The biogeochemistry of calcium at Hubbard Brook. Biogeochemistry 41: 89–173.

Likens GE, Butler TJ, Buso DC. 2001. Long- and short-term changes in sulfate deposition: Effects of the 1990 Clean Air Act Amendments. Biogeochemistry 52: 1–11.

Matson PA, Vitousek PM, Schimel DS. 1989. Regional extrapolation of trace gas flux based on soils and ecosystems. Pages 97–108 in Andreae MO, Schimel DS, eds. Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere. New York: John Wiley.

Mitchell MJ, Driscoll CT, Kahl JS, Likens GE, Murdoch PS, Pardo LH. 1996. Climatic control of nitrate loss from forested watersheds in the northeastern United States. Environmental Science and Technology 30: 2609–2612.

Noble IR, Dirzo R. 1997. Forests as human-dominated ecosystems. Science 277: 522–525.

Odum EP. 1983. Basic Ecology. Philadelphia: W. B. Saunders.

Ollinger SV, Aber JD, Reich PB, Freuder RJ. 2002. Interactive effects of tropospheric ozone, nitrogen deposition, elevated CO_2 and land use history on the carbon dynamics of northern hardwood forests. Global Change Biology 8: 1–18.

O'Neill RV. 2001. Is it time to bury the ecosystem concept? (With full military honors, of course!) Ecology 82: 3275–3284.

Pickett STA, Cadenasso ML. 2002. The ecosystem as a multidimensional concept: Meaning, model and metaphor. Ecosystems 5: 1–10.

Pickett STA, Parker VT, Fiedler P. 1992. The new paradigm in ecology: Implications for conservation biology above the species level. Pages 65–88 in Fiedler P, Jain S, eds. Conservation Biology: The Theory and Practice of Nature Conservation, Preservation and Management. New York: Chapman and Hall.

Reuss JO, Johnson DW. 1986. Acid Deposition and the Acidification of Soils and Waters. New York: Springer-Verlag.

Rodenhouse NL, Holmes RT. 1992. Results of experimental and natural food reductions for breeding black-throated blue warblers. Ecology 73: 357–372.

Schuur EAG, Chadwick OA, Matson PA. 2001. Carbon cycling and soil carbon storage in mesic to wet Hawaiian montane forests. Ecology 82: 3182–3196.

Sillett TS, Holmes RT, Sherry TW. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288: 2040–2042.

Strong AM, Sherry TW, Holmes RT. 2000. Bird predation on herbivorous insects: Indirect effects on sugar maple saplings. Oecologia 125: 370–379.

Tansley AG. 1935. The use and abuse of vegetational concepts and terms. Ecology 16: 284–307.

Walters CJ. 1998. Improving links between ecosystem scientists and managers. Pages 272–286 in Pace ML, Groffman PM, eds. Successes, Limitations and Frontiers in Ecosystem Science. New York: Springer-Verlag.

Williams MW, Brooks PD, Mosier A, Tonnessen KA. 1996. Mineral nitrogen transformations in and under seasonal snow in a high-elevation catchment in the Rocky Mountains, United States. Water Resources Research 32: 3161–3171.

Wilson MA, Carpenter SR. 1999. Economic valuation of freshwater ecosystem services in the United States: 1971–1997. Ecological Applications 9: 772–783.

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