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ESSAY REVIEW

Eagleson's optimality theory of an ecohydrological equilibrium: quo vadis?

T. J. HATTON,* G. D. SALVUCCI† and H. I. WU‡

**CSIRO Land and Water, Perth Laboratory, Private Bag, PO Wembley WA 6014, Australia, †Department of Geography, Boston University, Boston, MA and ‡Department of Industrial Engineering, Texas A&M University, College Station, TX, USA*

Introduction

Hydrology and ecology have in common an almost complete lack of fundamental theory unique to those fields. That is, there are few theorems which are always given pre-eminence where conflicts arise among modelling constraints (*sensu* Dooge 1992). Therefore where the potential exists to identify and express basic, novel principles in either of these sciences, it should spawn general interest and debate. The purpose of this essay is to review and discuss a theory that bridges both ecology and hydrology, but has had apparently little impact on those fields since its publication more than 13 years ago. Given changing perceptions of where these sciences are heading, in this essay we argue that this theory offers powerful, useful and credible paradigms for both of these fields of research, and perhaps an apotheosis for the emergent field of ecohydrology.

Although increasingly quantitative, ecology remains largely descriptive and empirical, with the development of theory still at a stage of defining concepts and relationships. Pomeroy, Hargrove & Alberts (1988) noted that those few general principles emerging from ecology (e.g. successional theory, Liebig's 'law' or the stability–diversity relationship) are still contentious. Even the much-touted hierarchy theory (Allen & Starr 1982; O'Neill *et al.* 1986) is perhaps better termed an analytical framework, in that it is essentially a tool for structuring mathematical models to simulate multiscale phenomena (Shugart & Urban 1988). Formal statements of relationships exist in ecology, but originate in the chemistry or mathematics of mass transfer, or are derived entirely from the theory of evolution and properties implicit in that theory (McIntosh 1981); it is questionable as to whether ecology has any fundamental theory of its own (Loucks 1981; Peters 1991). Whittaker & Levin (1977) went so far as to assert that ecological theory should focus more on 'the analysis, interpretation, comparison and modelling of cases rather than widely applicable generalization'. This statement perhaps reveals a different meaning to the term *theory*, as used in ecology, than in more traditional science philosophy (e.g. Popper 1959).

Possibly because modern hydrology is also a relatively young scientific discipline, the development of its theory is in a state equivalent to that of ecology. It is ironic that Bras & Eagleson (1987) used ecological terminology when describing the science of hydrology as a 'vacant niche'. Klemes (1988) argued that modern hydrology was driven chiefly by technology as opposed to theory. Dooge (1992) stated that while for many years he had considered that 'there was no fundamental theorem in hydrology which would pervade the whole of hydrologic theory', he concluded that at least the lumped form of the continuity equation qualifies as a pre-eminent principle in hydrology.

An interesting coincidence of perspectives on this situation has appeared in recent ecological and hydrological literature, independently drawing parallels to the need for, and development of, statistical mechanics in physics. This theoretical strategy was developed as a means to overcome the inherent limitations of analytical mechanics in complex systems by instead studying the emergent properties of aggregates of large numbers of interacting objects. Most ecologists recognize the infeasibility of aggregating the myriad independent observations of organism and interaction into an ecosystem model that reveals larger-scale phenomena; in fact, this reductionist approach ('bottom-up' *sensu* Caldwell *et al.* 1993) is often seen as the antithesis of ecosystem science, but is implicit in much of biology (Shugart & Urban 1988). While ecologists recognize that large-scale phenomena can be reduced to biological and physical laws, this does not imply the ability to start from those laws and reconstruct an ecosystem. 'Top-down' approaches, linked hierarchically to our understanding of mechanism at finer scales, is now a dominant paradigm for the way forward in ecology (O'Neill *et al.* 1986; Levin 1993).

Philosophical and practical problems with the bottom-up approach in hydrology have been discussed for some time (Woolhiser 1971; Beven 1989; Hauhs 1990; Barnes 1993; Wheater, Jakeman & Beven 1993; Hatton, Dawes & Waker 1994). Dooge (1986) suggested that in hydrology's efforts to develop theory for large systems, perhaps we should 'attempt to find simple equilibrium laws at the macroscale in much the same way as in the statistical mechanics approach', and offered a few historical examples of where this had been (successfully) attempted, e.g. Horton (1945), Shreve (1966), Gupta & Waymore (1983), Rodriguez-Iturbe & Valdes (1979) and

Ealgeson (1978s, 1982). Dooge (1988) offered a more complete review and theoretical discussion of the use of statistical mechanics and the concept of maximum entropy in hydrology. Nevertheless, much of modern hydrology is characterized by the adaptation of point scale physical models and the transformation of parameters to a larger scale of application.

In this context, the work of Peter Eagleson and colleagues (Eagleson 1978a–g, 1982, 1994; Eagleson & Tellers 1982; Diaz-Granados, Valdes & Bras 1984; Eagleson & Segarra 1985; Arris & Eagleson 1994; Salvucci & Entekhabi 1994a,b, 1995) is particularly relevant in that it bridges ecology and hydrology in a statistical–dynamic approach which derives large-scale hydrologic behaviour based on a hypothesized equilibrium between the hydrological and biological components of ecosystems. Using probability density functions for climatic variables in combination with simplying assumptions about hydrologic processes justified on a mechanistic basis, Eagleson (1978a–g) was able to derive the statistical distributions of hydrologic response on the basis of five key surface parameters (three related to the soil and two to the vegetation). By adding three ecological constraints to the theory (discussed at length below), Eagleson (1982) asserted that the space- and time-averaged hydrologic response could be inferred from a knowledge of climate and the extent of the vegetation cover, even with little direct knowledge of soil properties. Further, a knowledge of the hydrologic response of a system can inversely provide insight into the structure and function of the vegetation-soil system. Thus at once we have a predictive, testable theory of relevance to both ecological and hydrological systems at scales involving levels of natural complexity which otherwise preclude a 'bottom-up' approach. So why has this theory not been adopted, tested or applied to any significant extent outside of the group from which it originated, while it is apparently consistent with the research directions advocated by visionaries separately in both ecology and hydrology?

This essay has three major objectives. The first is to recapitulate Eagleson *et al.*'s basic ideas, commenting on how the assumptions and implications of the theory relate to other ideas in ecology, hydrology and geomorphology. The second objective is to review the impact of these ideas and to discuss why they have not had more influence. The final objective is to assess the relevance and attractiveness of the theory to current research challenges in ecology and hydrology, and to suggest how the theory might be modified for specific applications.

The equilibrium water balance

The ecological optimality hypotheses are posed within Eagleson's statistical–dynamic model of equilibrium water balance (Eagleson 1978a–g), a one-dimensional representation of soil moisture dynamics. The model statistically aggregates over the high-frequency temporal variability in climate forcing (e.g. storm intermittency) to solve the partitioning of annual precipitation into yield and evaporation in terms of the temporally effective, vertically averaged equilibrium soil moisture. Appreciation and evaluation of the subsequent ecological hypotheses (Eagleson 1982) used to relate vegetation cover to soil and climate depends on an understanding of the structure of the general model (Eagleson 1978a–g), which we briefly review as follows.

The land-surface moisture dynamics are represented by the concentration-dependent diffusion equation (i.e. Richard's equation). Eagleson (1978c) modified Philip's (1960) solution to this equation to incorporate a distributed vegetal root sink, and introduced the Brooks & Corey (1966) model of unsaturated soil hydraulic properties to express storm and interstorm surface fluxes in terms of soil parameters (see below), time and relative soil saturation. These modified solutions were then averaged over the ensemble of surface boundary conditions arising from a Poisson arrival of rainstorms (Eagleson 1978b). These storms, of exponentially distributed intensity and duration, and the mean potential evaporation rate applied during the interstorm period, form the climatic forcing in the model. In this way, the dependence of the expected value ($E[]$) of the surface fluxes, i.e. storm infiltration ($E[I_j]$) and interstorm bare-soil exfiltration ($E[E_{sj}]$) on climate are found. The moisture extracted by the root sink is transpired at some proportion, k_v, of the bare-soil potential evaporation rate, providing a simple, species- and climate-dependent parameterization for the expected value of the interstorm evapotranspiration rate ($E[E_{vj}]$).

The soil moisture diffusion processes occurring in the root zone are assumed to dampen the weather-induced variation in surface boundary conditions resulting in a steady-state lower boundary condition representative of the expected values for the percolative (v) and capillary rise (w) fluxes (Salvucci & Entekhabi 1994b). These steady-state bottom fluxes and the event-based surface fluxes are then transformed into annual means by summing the product of the event flux and number of events with the product of the steady flux and the mean season length.

The mean annual water balance is determined by imposing continuity of these annual mean fluxes through the soil column; the soil moisture value at which this condition is satisfied is the equilibrium soil moisture, s_0. This water balance condition may be stated:

$$\begin{aligned} E[P_A] = {} & E[ET_A\,(s_0, \text{climate, soil, vegetation})] \\ & + E[R_{gA}\,(s_0, \text{climate, soil})] \qquad \text{eqn 1} \\ & + E[R_{sA}\,(s_0, \text{climate, soil})] \end{aligned}$$

where P_A is annual precipitation (cm), ET_A is annual total evaporation (sum of bare soil evaporation and

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transpiration, weighted by respective areal fraction covered (cm), R_{sA} is annual infiltration excess surface runoff (cm), R_{gA} is annual groundwater runoff (cm) and s_0 is equilibrium soil moisture concentration.

The dependence of these fluxes on climate, soil and vegetation is expressed through the following 14 physically meaningful (and realistically obtainable) parameters: climate, where e_p is time-averaged potential bare-soil evaporation rate (cm s^{-1}), T_A is annual average temperature (°C), m_{tb} is mean time between storms (s), m_{tr} is mean storm duration (s), κ is shape parameter of gamma distribution of storm depths, m_{PA} is average annual precipitation (cm) and m_τ is mean length of rainy season (s); vegetation and land surface parameters, where M is vegetated surface fraction (cover); k_v is potential transpiration efficiency relative to bare soil evaporation and h_0 is surface retention capacity (cm); soil parameters, where $k(1)$ is saturated effective intrinsic permeability (cm^2), c is pore disconnectedness index, n is effective medium porosity and $\psi(1)$ is saturated soil matrix potential (cm).

Through comparison with detailed numerical flow simulation under a variety of climate and soil conditions, the statistical dynamical model represented by equation 1 has been shown to provide an analytic alternative to numerical simulation of effective moisture flow (Salvucci & Entekhabi 1994a). The above-water balance framework, consisting of one equation and 14 parameters, is less useful than it would be if some or all of the below-ground (soil) parameters could be eliminated by invoking additional constraints (equations). The ecological optimality hypotheses of Eagleson (1982) provide these constraints.

The ecological optimality hypotheses

Eagleson (1982) proposed three ecological optimality hypotheses regarding the expected state of vegetation in a natural, undisturbed ecosystem in an equilibrium state:

1. Over short time scales (say, within one or a few generations), the vegetation canopy density (M) will equilibrate with the climate and soil to the value at which equilibrium soil moisture (s_0) will be maximized; the value of this optimal canopy density (M_0) can be found as:

$$\left.\frac{\delta s_0}{\delta M}\right|_{k_v,\ \text{climate, soil}} = 0,\ M = M_0\,. \qquad \text{eqn 2}$$

Provided M and k_v are independent, this is equivalent to minimizing evaporation and can be written:

$$\left.\frac{\delta E[ET_A]}{\delta M}\right|_{k_v,\ \text{climate, soil}} = 0,\ M = M_0\,. \qquad \text{eqn 3}$$

2. Over longer time scales (a few generations), species will be selected whose potential transpiration efficiency (k_v) result in the maximum equilibrium soil moisture. Mathematically,

$$\left.\frac{\delta s_0}{\delta k_v}\right|_{M,\ \text{climate, soil}} = 0,\ k_v = k_{v0}\,. \qquad \text{eqn 4}$$

3. Over much longer time scales (commensurate with landscape evolution), vegetation will alter soil physical properties toward equilibrium values at which the optimal canopy density (M_0) of equation 2 is itself at a maximum value (because at maximum M_0, the potential for biomass growth, assumed proportional to canopy water use $M \times k_v \times e_p$, will be at a maximum). The soil physical properties assumed to change in accordance with this long-term optimization are the saturated intrinsic permeability, $k(1)$, and the soil pore disconnectedness index, c. Mathematically:

$$\left.\frac{\delta M_0}{\delta k(1)}\right|_{c,\ \text{climate}} = 0 \qquad \text{eqn 5}$$

and:

$$\left.\frac{\delta M_0}{\delta c}\right|_{k(1),\ \text{climate}} = 0\,. \qquad \text{eqn 6}$$

The long-term equilibrium canopy density for which equations 5 and 6 hold simultaneously is considered the climatic climax density M_0*. Simultaneous use of equations 3–6 and the water balance equation 1 reduces the original set of one equation and 14 parameters to the original equation and 10 parameters (all but two above ground).

It is worth noting that even without the ecological constraints on the formulation, three parameters found almost universally in ecohydrological models (soil depth, available water-holding capacity and plant rooting depth) are avoided entirely. This is not because of their ultimate irrelevance to process in nature, but because of the extreme difficulty of estimating these parameters across a landscape. Nor are the parameters which are included in the model real in any ultimate sense; they are effective parameters which control the rates of inputs and outputs and enable a representation of the dominant behaviour of the system.

Relationship to other ideas in hydrology and ecology

It is useful to ask how consistent Eagleson *et al.*'s assumptions and concepts are with mainstream hydrological and ecological research, and to trace the roots of these ideas in works that predate Eagleson (1978a–f) and Eagleson (1982). The basic modelling approach to the water balance was not, in any fundamental sense, novel to hydrology. In recognizing that we must retain in our models the underlying (deterministic) physical processes while acknowledging uncertainty in the spatial and temporal configuration of the system, Eagleson (1978a) proposed a framework which replaced (real) spatial complexity with an idealized deterministic configuration of physical elements which preserved the essential hydrological relationships among responses. Further, the input climatic variables are recognized as fundamentally stochastic and are thus represented as probability distributions. As Eagleson (1978a) noted, this approach is known as *derived distributions* in applied statistics and as *statistical mechanics* in applied mathematics and thus as an approach is well established in the modelling literature in general (e.g. Wymore 1967) and hydrology specifically (e.g. Eagleson 1972; Carlson & Fox 1976; Klemes 1978; Rodriguez-Iturbe & Valdes 1979; Diaz-Granados *et al.* 1984).

The scientific credibility of such approaches to applied hydrological problems must be assessed against the alternatives, in particular the deterministic, complex and dynamic numberical approaches which currently dominate the hydrological (and ecohydrological) literature and whose deficiencies have been widely discussed. These deficiencies arise over the impossibility of obtaining the data necessary to test adequately or validate models with so many unknowns in the face of natural variability (Oreskes, Shrader-Frechette & Belitz 1994), and the great uncertainties which arise in attempting to aggregate numerically processes in space and time (Bevan 1989; Wheater *et al.* 1993). Most predictive ecohydrological models attempt to couple energy, water, carbon and geochemical processes in an *a priori*, numerical book-keeping fashion in which the interactions among the diverse and complex ecosystem components are generally constrained only by conservation and/or continuity equations, e.g. the FOREST.BGC model (Running & Coughlin 1988), TOPOG_IRM (Hatton *et al.* 1992) or BATS (Dickson *et al.* 1986). In such models, any assemblage of climate, landscape and vegetation is in theory permissible, and the simulated responses necessarily obey no overriding theory of ecohydrological behaviour. For example, any combination of rainfall, soil hydraulic conductivity, vegetation cover and plant rooting depth may be specified, even if such an assemblage does not (and cannot) exist in fact. The necessarily large parameter space defined by such models results in their questionable value for application in the real world (Beven 1989, 1993; Barnes 1993). Hatton *et al.* (1994) suggested that much of the information required by these models, particularly below ground, is essentially unknowable in any direct (spatial) sense. The equilibrium framework, coupled with ecological optimality constraints, minimizes the onus of system parameterization while retaining an underlying framework based on concepts familiar to physicists, hydrologists and physiologists. However, we recognize that to a certain extent, complex physical models as exemplified above are perhaps intended for different purposes and we do not preclude the possibilities for cross-fertilization of ideas between the two approaches discussed herein. Indeed, they share common roots in the physical formulations upon which they are based and thus have the potential to exchange and build upon their respective process representations.

The idea that there is some natural balance between climate, vegetation and soil is also not new. The notion of a climax condition of vegetation at a given site [Eagleson's (1982) first two hypotheses express this notion in hydrological terms only] is at least 100 years old. Clements (1936) asserted that most of an area in a state of nature was in the climax condition and disturbed areas occupied a minor portion of the regional climax because disturbances were unusual events; if many modern ecologists see equilibrium reached rarely (if ever), much recent ecosystems modelling tacitly assumes the existence of, and trend toward, an equilibrium. Bormann & Likens (1979), for example, commented that their extended studies of ecosystem development of northern hardwoods forest at Hubbard Brook assumed the steady-state condition. Pomeroy *et al.* (1988) noted that when photosynthesis, respiration, assimilation and transpiration are measured at the ecosystem level, we see remarkably stable rates in spite of successional changes. There seems to be an element of self-regulation in ecosystem process, at least until some threshold of stress is reached and the system collapses. In general, however, there remains a dichotomy between the view of succession as a collection of population processes dependent on the life-history strategies of the component species as against the concept of a sere as an ecosystem process leading to the development and evolution of an emergent entity (McIntosh 1981). From a practical point of view, however, Bazzaz (1993) maintained that irrespective of the level of detail required in examining ecological function, conceptual aggregation is essential, because without some aggregation the task of assessing the response of ecosystems within the time frame required to assess and redress human impacts is impossible.

The idea that the development of this climax condition of vegetation is co-dependent on the development of the soil landscape [Eagleson's (1982) third hypothesis] goes back at least to Dukuchaiev (in Glinka 1927), Higlard (1914) and Jenny (1941). It is well accepted that biota influence soil and geomorphic processes and that biological and geochemical or geomorphic changes do not proceed independently (Eyre 1968; Schimel, Stillwell & Woodmansee 1985; Pastor & Post 1988; Bazzaz 1993). Eagleson (1982) argued on the basis of work by L'vovich (1979) and Eyre (1968) that, with time, vegetation modifies (moderates) the hydraulic characteristics of parent material toward values which maximize vegetation production (i.e. sandy soils become richer and more water-retentive; clayey soils become more porous and conductive). Clearly, land surfaces for which this criterion might apply must have sufficient age to reflect this moderating influence by vegetation but not so old as to develop severe limitations owing to limitations other than water. A significant example of the latter phenomenon was described by Walker *et al.* (1981), in which productivity decreased with increasing age of very old dune systems owing to a progressive loss of nutrients from the system.

Although the hydrological equilibrium idea for vegetation cover is attributed in recent literature (e.g. Nemani & Running 1989; Pierce *et al.* 1993; Hatton & Wu 1995) to Grier & Running (1977) or Gholz (1982), in Australia the quantitative form of this idea goes back at least to Specht (1972). In this latter paper, Specht used a simple water-balance equation on a monthly timestep to characterize the water-use behaviour of perennial evergreen plant communities across a wide range of sites and climates, using as inputs only potential evaporation, rainfall, the soil moisture-holding capacity, and an empirically determined coefficient relating available soil water to the ratio of actual to potential evaporation. He demonstrated that this coefficient is linearly and closely related to projected foliage cover of diverse Australian evergreen plant communities ranging in cover between 18 and 88%. Eagleson (1982) traced the idea back to Rosenzweig (1968), who argued that where water limits productivity, there may be some optimal efficiency of water utilization that is approached in both short-term succession and long-term evolution, and to Budyko (1974) and Larcher (1975), who independently proposed that there is some optimum value of leaf area index at which vegetation productivity reaches its maximum with plentiful water. This modelling constraint appears to be reasonably well accepted among ecologists and is thus something more than a mathematical convenience.

Eagleson's notions of ecohydrological optimality with respect to the balance between productivity and water use reflects other ideas about optimal behaviour from ecophysiology and ecology. The most relevant and notable of these is Cowan's (1977, 1978, 1982) paradigm connecting photosynthesis and stomatal conductance by hypothesizing an optimal behaviour defined by the availability of soil water. Cowan argued that over any given period of time, the average assimilation of CO_2 (A) could not be increased without increasing transpiration (T) over the same period. There is some non-linear relationship between A and T which defines the increasing cost to the plant in terms of water loss as the benefits from assimilation increase, the slope of which is equivalent to the unit marginal cost. Optimization requires that the plant maintain the unit marginal cost uniform in all leaves and constant in time. Although this theory is expressed at the leaf level, Cowan (1982) anticipated its application to the whole plant. Other paradigms of optimal vegetation behaviour with respect to resource availability were presented by Gutschick, Pushnik & Swanton (1988), Hilbert (1990) and Running & Gower (1991). If the idea of optimization in nature is essentially phenomenological (*sensu* Reynolds, Hilbert & Kemp 1993), it nevertheless can serve to describe a property of the system directly at the level of interest (e.g. ecohydrological response) while retaining some general understanding and representation of process.

How reasonable is the generalization that plant cover involves an equilibrium with the availability of water only? For how much of the earth's land surface does this assumption hold, as opposed to biomes in which plant cover is controlled by nutrients, temperature or radiation as well? Clearly the theory does not hold for the Antarctic, nor for ice fields elsewhere. For much of the earth, however, there seems to be a general relationship between climate and vegetation (Holdridge 1947; Mather & Yoshioka 1968) which does not need to invoke additional information, such as plant nutrition or soil type. This in no way validates the details of the Eagleson equilibrium framework, but at least suggests that the lion's share of variance in plant cover at the regional or global scale can be accounted for without invoking additional constraints on productivity other than climate. A number of geographically local studies support this idea (Grier & Running 1977; Eaglesoni & Segarra 1985; Nemani & Running 1989; Pierce *et al.* 1993; Arris & Eagleson 1994).

In a major review of controls on the distribution of *Eucalyptus* in Australia, Adams (1995) challenged the dominant paradigm, traced back to Beadle (1954), that nutrients delimit vegetation types on that continent. Adams argued that nutrient recycling supplies most of the nitrogen and phosphorus (and other nutrients) required for tree growth in forest and woodlands and therefore that water availability is the dominant control on vegetation in geologically old landscapes. This rather counter-intuitive notion was supported by a number of studies cited and by the theoretical argument that time, and its consequence for changes in climate, organisms and topographic relief, is the dominant influence and parent material a lesser influence on soil properties. This idea echoes the previously stated ideas regarding Eagleson's third ecological optimality hypothesis and is consistent with assertions by Stark (1994) regarding the diminishing influence of parent material with time as soils age. At the landscape scale, patterns of species distributions and rates of growth in a number of cited studies in Australia were related to landforms and landscape position (and their consequences to the availability of water). This is not to say that the equilibrium framework under discussion could not accommodate additional ecological constraints like nutrition, but model parsimony and the limited availability of spatial and temporal information on below-ground ecosystem properties argue that such constraints must be of prime importance before such model complications are warranted. In this sense, the value of Eagleson's theory is in the generation of an expectation of plant cover (which can be assessed synoptically via remote sensing, for example); this null hypothesis is testable and where found failing, can be a useful tool in identifying where non-climatic climax conditions exist.

The impact of ecological optimality theory on ecohydrology

The impact that Eagleson *et al.*'s parameterization of hydrological equilibrium theory and ecological optimization has had on the field of ecohydrology is limited. Papers citing this work often only refer, almost in passing, to the principles or concepts rather than their mathematical formalizations (e.g. Rambal 1987; Nemani & Running 1989; Choudhury 1991; Joffre & Rambal 1993; Pierce *et al.* 1993; Hatton & Wu 1995). Research adopting the formalizations originate almost exclusively from within the group that developed the framework (e.g. Eagleson & Segarra 1985; Arris & Eagleson 1994; Salvucci & Entekhabi 1994a,b, 1995). A notable exception to this is the SESOIL hydrological model applied by Hetrick *et al.* (1986), but note that this implementation does not include the ecological optimality constraints. In this work, the equilibrium approach to modelling the soil water balance was shown to perform as well as a much more complex numerical hydrological model. Only Chavez, Soorooshian & Davis (1994) employed the optimality ideas in hydrologic parameter estimation, but without testing their applicability.

Ecological optimality: quo vadis?

From the perspective of ecohydrology, a reading of Eagleson (1978a–f, 1982) quickly reveals a major impediment to adoption of this approach: the conceptual model is often subtle and foreign to the non-engineer and the mathematical formalization is extremely complex. The solution space is presented in a way unfamiliar to most ecologists. We argue that this lack of accessibility has hindered the impact of equilibrium theory to a far greater degree than any controversy over its assumptions or concepts.

A further impediment would appear to be the modern hydrological fashion toward complex, dynamic, distributed-parameter numerical models such as SHE (Abbott *et al.* 1986), TOPMODEL (Beven & Kirkby 1979), THALES (Grayson, Moore & McMahon 1992), TAPES-C (Moore, O'Loughlin & Burch 1988) and TOPOG (Vertessy *et al.* 1993; Dawes & Short 1994), and the tendency in ecohydrology to hybridize (and further complicate) these models with ecophysiological representations of vegetation behaviour as in TOPOG_IRM (Hatton *et al.* 1992; Vertessy *et al.* 1996) and RHESSys (Band *et al.* 1991, 1993; Band 1993). Even more ambitious were Lauenroth *et al.* (1993), who proposed linking a number of already complex ecosystem models operating at different scales. As Beven (1989) pointed out, these models have a role to play in examining the sensitivities of hypothetical systems, but they hardly add to the theoretical understanding of the real world in its true complexity. Perhaps Norman (1993) was right when he stated that 'examples of new paradigms are difficult to find because most of us are too deeply entrenched in past successes to risk much investment in the unknown'. Klemes (1986) was more scathing in his consideration of most complex hydrological computer models, suggesting less time should be spent on 'the unscientific concept of mindless fitting that dominates contemporary hydrologic modelling' and more on 'acquiring a deeper knowledge of climatology, meteorology, geology, and *ecology*' (our italics). This rather uncharitable point of view is perhaps unhelpful to those faced with providing real-world answers to complex, trans-scientific questions through the application of complex physical models in the absence of any practical alternatives. We restate our view that the development of equilibrium approaches to ecohydrological questions is not mutually exclusive of the kind of hydrological modelling exemplified above. Rather, it is complementary.

The equilibrium model is explicitly scaleless; it may apply to a plot as well as a region. Application in practice requires a system in which inputs and outputs can be measured, which implies a closed catchment. This being the case, it is vital to note that the physical parameters employed in the model are *effective* ones, in the sense that they control transfer functions at the scale of application. For example, an intrinsic permeability used (solved for) within this framework may not be identical to values of this parameter mapped anywhere within system (this is a general feature of physical parameters found by the inverse method in hydrology). Nevertheless, we know that within a sloping catchment, there are systematic spatial differences in materials related to surface erosion and deposition (Daniels & Hammer 1992), as well as the spatially systematic availability of soil water (O'Loughlin 1986); in both cases, this is owing to the lateral redistribution of water within the catchment. The equilibrium/optimality framework of Eagleson (1982) takes no account of these lateral processes and spatially systematic variations, and thus would predict a uniform cover of vegetation in catchments with known riparian areas and associated distinct changes in cover. The existing framework allows for deep drainage of soil water (local losses from the system) but makes no mention of the ultimate fate of this water when it discharges (presumably downslope). Salvucci & Entekhabi (1995) extended the equilibrium equations to idealized hillslope shapes, but in the absence of vegetation and thus without the ecological optimality constraints. More theoretical development is required to express the three ecological optimality hypotheses in a (*effective*) three-dimensional framework.

The practical need to simulate the function and form of ecosystems and to project changes in these systems as a result of human activity is greatly complicated in most landscapes by the lack of knowledge of what landscapes would look like in the absence of all disturbance by people. Even discounting atmospheric impacts, few parts of the earth's land surface approach a pristine condition. Thus, we generally have few paradigms of how a landscape *should* function in terms of its water, carbon and geochemical cycles. We have no gauge, no theory for the optimal functioning of such complex systems, nor for the likely effects of perturbing systems from this optimum. Eagleson's framework has the potential to provide this type of insight: for a given climate and soil, and in the absence of significance disturbance, the theory predicts the extent of vegetation cover and the hydrologic water balance. The potential to link these ideas with the concept of catchment health is intriguing.

Does the theory have application in disturbed environments? In principle, the model, once parameterized, can be used to examine the impact of changes in vegetation cover or soil properties. Scenario applications, however, have never been published using this approach. It would be of interest to perform the kind of predictive ecohydrology attempted by completely deterministic spatial models as in Vertessy *et al.*'s (1996) application of TOPOG_IRM to the question of the expected change in catchment water yield following forest harvesting and subsequent regrowth, or for that matter simulating the responses of any other of the 94 catchment studies of vegetation change and water yield summarized in Bosch & Hewlett (1982). In this regard, perhaps one direction that equilibrium theory can take is in accommodating the rates of ecohydrological change in systems following disturbance or climatic variability: how quickly and closely do ecosystems track the (current) optimum? How do we incorporate notions of thresholds or multiple meta-stable states into the theory? Can we characterize the short-term optimum as well as the long-term equilibrium?

The hydrologic equilibrium and ecological optimality framework offers the possibility of painting, with a broad brush, the expected degree of land cover in the absence of disturbance across large regions or even globally. The applications of this predictive capability to improved land surface parameterization of GCMs, the identification of non-climatic climax conditions, and the prescription of regional revegetation schemes is obvious. For instance, vegetation cover has a profound influence on the heat and moisture budgets of the land surface, but in current GCMs it is a prescribed boundary condition. Such prescription does not account for reaction among climate, soil, and vegetation which in fact determines such parameters as canopy density (Eagleson 1986). Furthermore, the equilibrium framework at the same time enables the quantitative and credible prediction of local and regional hydrological behaviour, with the potential to extend these predictions to the hydrological impacts of disturbance.

Physics continues to struggle with the issue of scaling process across the hierarchy of scales toward a unified theory of the forces of nature (Gross 1989) and much physical experimentation and interpretation is based on the conscious disregard of forces operating at other scales. Over a vastly more restricted range of scales and properties, the science of hydraulics has endeavoured, with much success, to scale fluid behaviour in highly idealized systems. The child of hydraulics, hydrology, has utterly failed to produce, either through aggregation or disaggregation, a theory that will allow prediction of the correct partitioning of rainfall at any scale of interest. Dooge (1992) recognized that the development of a corpus of hydrologic theory was complicated by the immense range of scales involved, and the changing appearance of phenomena when viewed from different spatial and temporal scale. It is unlikely that a search for a comprehensive scaling theory will be successful owing to the continuing dependence of hydrological response on the environmental and geological history over timescales also involving changes in climate; these external historical and geological forcings greatly limit the potential for scale-invariant representation of behaviour (Beven 1995). Adding ecological phenomena to this already complex system would seem to prescribe utterly the recognition of scale-dependent phenomena and their representation in scale-specific models.

If we cannot start with fundamental laws and reconstruct what appear as emergent properties of complex systems, then at each level of complexity the search for, and understanding of, new behaviours is necessary and appropriate. Anderson (1972) asserted that such research is as 'fundamental' in its nature as any other, requiring inspiration and creativity to just as great a degree as in lower levels of the hierarchy of complexity. In attempting to characterize the emergent properties and constraints of broad-scale ecohydrological behaviour, Eagleson and colleages pioneered a credible and quantitative approach to developing unique insights into what may appear to be hopelessly complex systems. Perhaps by pursuing, redeveloping and extending their theory, scientists may learn more about the nature of the problem itself, even if not finding the actual means to solve it. As Anderson (1972) stated so succinctly, 'more is different'.

It was the intention to explore and document the credentials, both hydrologically and ecologically, of the concepts underlying Eagleson's framework. We believe that the theory in its latest statements (Salvucci & Entekhabi 1994a,b, 1995), with the help of this manuscript, is more accessible to both ecologists and hydrologists. Furthermore, the conceptual abstractions associated with the theory are defended on a philosophical basis as appropriate to the analyses of complex systems, and in this sense may prove an apotheosis to the emerging science of ecohydrology.

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