

Range and Richness of Vascular Land Plants:

The Role of Variable Light



PETER S. EAGLESON

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Front cover: Spong trees moving toward the light at the ruins of Ta Prohm, Cambodia. Film image courtesy of Beverly G. Eagleson. Digital image by James M. Long of the Massachusetts Institute of Technology.

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To my dearest Bev, who has taught me how to live and to love and, in so doing, has inspired my work and enriched my life beyond measure

In Memoriam

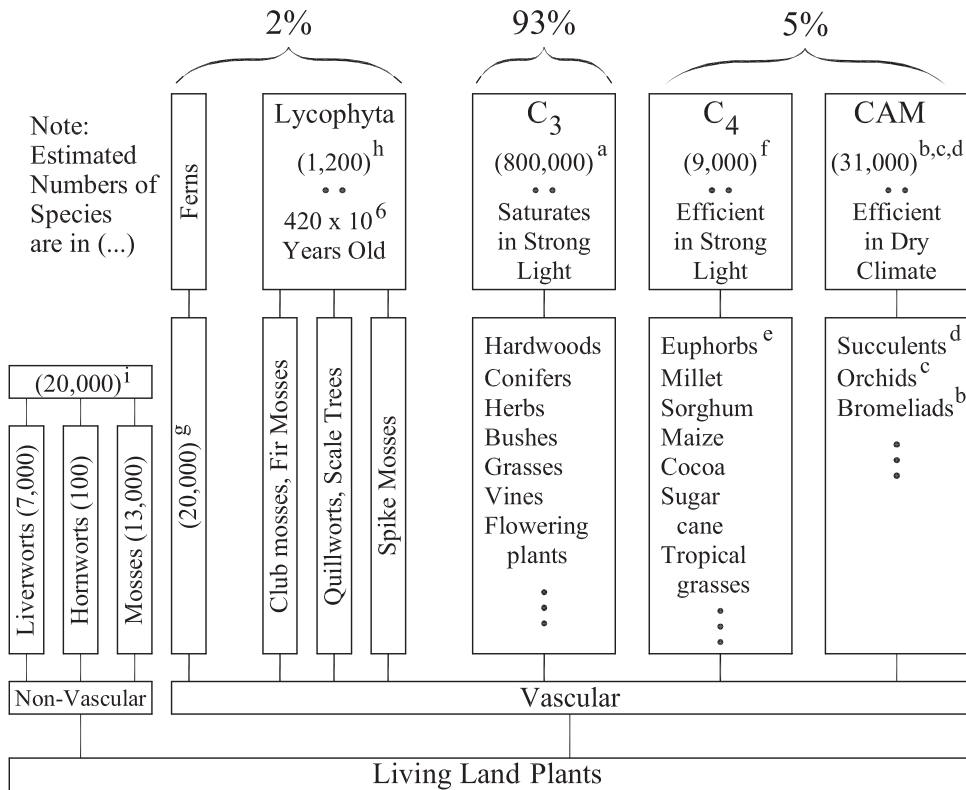
Helen Sturges Eagleson (1900–1989), mother, binder of childhood wounds, cultivator of intellect, supporter of ambitious dreams, guide through the minefields of male adolescence, and setter of the standards for life, who, through continuing personal sacrifice, single-handedly prepared her children for early and productive independence.

Arthur Thomas Ippen (1907–1974), teacher, advisor, advocate, professional exemplar, colleague, surrogate father, and dear friend, whose unfailing confidence and support placed a Massachusetts Institute of Technology career within the author's grasp and whose foresight, in the early 1960s, directed that career toward development of the neglected hydrologic sciences.

Ecosystem Research Needs

We lack a robust theoretical basis for linking ecological diversity to ecosystem dynamics. . . .

Carpenter et al. [2006, p. 257]



Estimated global numbers of vascular land plant species: The key to analytical formulation of local species range and richness as a function solely of incident light lies in finding a robust one-to-one connection between species and a biologically optimum value of intercepted shortwave solar radiation. Such a connection exists at the intersection of the asymptotes of the photosynthetic-capacity curve of the leaves of C₃ vascular land plants, and this illustration demonstrates the global dominance of this photosynthetic pathway. Keyed letters indicate the following Web sites: a, <http://www.bio.umass.edu/biology/conn.river/photosyn.html>; b, <http://en.wikipedia.org/wiki/Bromeliaceae>; c, <http://en.wikipedia.org/wiki/Orchidaceae>; d, http://en.wikipedia.org/wiki/Succulent_plant; e, <http://science.jrank.org/pages/6418/Spurge-Family.html>; f, <http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/C/C4plants.html>; g, <http://en.wikipedia.org/wiki/Ferns>; h, <http://en.wikipedia.org/wiki/Lycopodiophyta>; and i, <http://www.discoverlife.org/20/q?search=Bryophyta>.

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Foreword

This immensely creative and original book addresses one of the most important problems in evolutionary biology and ecological theory, namely, the observed decrease of species richness with increasing latitude and the accompanying increase of the latitudinal range of individual species. Professor Eagleson starts from the hypothesis that climate is the key conditioning of the above two gradients and that the answer for a theoretically solid explanation of the variability of species range and richness may lie in their links with the spatial and temporal variability of climate. Thus the ambitious goal of this book is to establish the bioclimatic basis of local community structure. This is indeed a challenging objective that may resist a generally applicable explanation to specific situations because of the infinite variety of conditions that may affect a particular species. Recognizing this, Eagleson focuses on the magnitude and gradient of the maximum possible local species richness: an equally challenging goal, which if solved, will bring to light a number of patterns found embedded in immensely complex ecological systems.

Focusing on the forests of the middle and high latitudes, whose growth is basically limited by light, Eagleson develops a theoretical, analytical, bioclimatic explanation of the variability of species range and richness over the midlatitudes. This book presents a theory and framework of analysis that provides synthesis and promotes understanding of the structure and diversity of ecological communities.

Local climate experiences fluctuations throughout time and acts as a causative agent for a succession of optimally supported species. From a bioclimatic function relating a key plant characteristic, the projected leaf area index, to the controlling climate variable, shortwave radiative flux, Eagleson proceeds to derive a theoretical prediction of the range of C_3 plants as a function of latitude that agrees extremely well with the observations available from the North America continent.

The maximum possible local species richness is assumed to be controlled by the local disturbances of shortwave radiative flux, which are, in turn, estimated by Eagleson via the statistical structure of local cloud arrivals and their shortwave interception. Again, the theoretical maximum thus estimated compares very well with the zonal richness observed for C_3 plants in North America.

In summary, the author provides compelling evidence that the biogeography of plants over middle and high latitudes can be theoretically explained by the space-time patterns of the shortwave radiative flux. Professor Eagleson's book is a most original and exciting monograph that comprehensively explains an extremely important and challenging problem of ecosystem science.

The approach and style of the book is one based on the best tradition of scientific research. The enormous complexity of the problem does not distract the author from his goal of finding an explanation founded in solid theoretical principles. Eagleson is not afraid of making simplifying assumptions that will then allow for analytical constructs leading to quantitative understanding of a general type. The assumptions are carefully stated, and the results are thoroughly tested against large amounts of data.

Professor Eagleson has written a book whose influence will only increase with the passage of time. This monumental work will forever change the way that ecologists, hydrologists, climatologists, and geographers study a set of fundamental phenomena lying at the intersection of their sciences. Researchers in all those disciplines will be at the same time challenged and inspired by the search for quantitative explanation and by the creativity continuously displayed throughout the book. The beauty of the analysis is probably its greatest intellectual appeal.

Peter S. Eagleson has continuously led hydrology into new and exciting territories throughout the last 50 years. He has eloquently said:

We need to get away from a view of hydrology as a purely physical science. Life on earth also has to be a self-evident part of the discipline. In particular, I'm thinking of vegetation and its powerful interactive relationship with the atmosphere, at both a local and a global level. In attempting to get the full picture, we must not be afraid to express the role of plants in our mathematical equations [*Hanneberg, 2000*].

This wonderful book is science at its best: It attempts to get the full picture and succeeds beautifully in this effort! It is for me a privilege to introduce it to the scientific community.

Ignacio Rodríguez-Iturbe
James S. McDonnell Distinguished University Professor
of Civil and Environmental Engineering
Princeton University

Preface

This is a research monograph and not a textbook. Here I demonstrate analytically how the observed, opposing, latitudinal gradients in the average range and richness of local vascular land plant species are (outside the moist-tropical zone, at least) driven primarily by the local temporal and spatial variability of shortwave radiative flux at the canopy top. (The term “richness” as used here means the local number of different vascular land plant species unlimited by the size of the area sampled.) The hypotheses are simplistic but are nevertheless convincingly accurate in extratropical latitudes when tested against observations over the continental land surfaces of the Northern Hemisphere, the only areas tested here.

Species geographical range and local richness lie at the interface of two complex sciences, biology and geophysics, each having its own established techniques and traditions of analysis. A rigorous, general explanation of range and richness covering all the many microclimates of Earth and the myriad species evolved in accommodation thereto seems impossible at this time; the number of variables is daunting, and the necessary observational detail is unavailable. This is, or at least was, in earlier years, a common situation in many branches of engineering, and a variety of useful approaches exist to deal with such complexity. We must first agree to seek a limited rather than generalized solution; that is, ask a different and less demanding question! Here I will then need to limit the independent variables (climate and soil variables, in this case) to the one or two reasoned to be most important and be willing to accept the resulting restricted accuracy and/or geographical applicability of the findings. We shall see in chapter 1 that if the fundamental biophysical relation between the observable independent (climate) variable(s) and the dependent (species) variable is locally quasi-linear, then we need know neither its sense nor its true mathematical form; we can derive an approximate probability distribution of the local species

and proceed to an approximate and restricted solution of the original problem. This process is an example of “reductionism” (see the epigraphs on the section I, II, and III opening pages) and forms the basis for the work described herein.

This volume contains a substantive section (section II) preceded by an overview (section I) and followed by both a recapitulation (section III) and a set of supportive appendixes (section IV). Because it is a research monograph rather than a textbook, the volume more or less follows the path of discovery, describing what does not work as well as what does, and why, for the failures are often as instructive as the successes.

Section II begins with the presentation, in chapter 2, of latitudinal distributions of the mean, variance, and latitudinal gradient of the annual zonal SW flux at canopy top during the growing season, for continental land surfaces in both North America and in the entire Northern Hemisphere, as derived from NASA satellite observations and generously prepared for use here by my longtime Massachusetts Institute of Technology colleague and friend, Dara Entekhabi.

In chapter 3, I employ a local linearization of the bioclimatic function (derived in the appendixes from simplified biological behaviors) relating a physical property of separate C_3 species to their saturating SW flux. This permits derivation of the standard deviation of the local frequency distribution of species as being directly proportional to the standard deviation of the local annual SW flux and thus, from local flux observations, to the associated “standard deviation of latitude,” as measured in degrees. These transformations provide the scale by which to estimate local range. Latitudinal oscillations in both the mean and variance of the observed local seasonal SW flux give “point-by-point” predictions of range that are wildly oscillating. However, elimination of these local flux oscillations in favor of flux gradients reveals underlying linear trends and range gradients, yielding close agreement, in both North America and the Northern Hemisphere, with the widely referenced North American observations of *Brockman* [1968] over their full span of 41°N latitude.

Chapter 4 employs the role that ground-level SW flux variations play in both seed germination [*Pickett and White*, 1985] and the follow-on stressing of the emergent species to estimate the potential number of local species, acknowledging that the actual number of local species will be less than the potential by virtue of that unknown (and/or unaccounted for) myriad of special local conditions referred to earlier. I derive this potential from local temporal variations in the pixel-scale atmospheric interception of solar radiation (and hence in the heat) during the growing season, when represented as a stationary time series of independent and Poisson-distributed arrivals of cloudy periods. Assuming the total energy intercepted annually by the random number of annual cloud events to be gamma distributed (this assumption does not weaken the analysis substantially as the gamma distribution can represent a variety of shapes), the shape parameter, κ , of the latter must be estimated. I do so from existing similar analyses of local North American rainstorms and, with it, obtain

the first two moments of the cloud disturbance frequency as an inverse function of the variance of the local annual SW flux. From these moments, I estimate the maximum number of (assumed normally distributed) local annual stressful disturbances to be approximated as their mean plus (at 99% probability mass) 2.5 standard deviations therefrom. This formulation predicts quite closely the maximum envelope of the observed number of local vascular plant species over the 48° of latitude in North America encompassed by the work of *Reid and Miller* [1989]. The theoretical relation of local range to local richness is found to be inverse through the derived nature of their separate dependencies on the variance of local annual SW flux, thereby corroborating the observation of *Rapoport* [1975].

Chapter 5 presents a set of paired summaries of the major issues considered along with the associated conclusions derived herein, plus mention of a few promising related, but unresolved, problems.

The appendixes are devoted to reductionist modeling of the bioclimatic process by which radiation drives the conversion of carbon dioxide into solid plant matter. Because of their predominance, at least in the humid and shady habitats [e.g., *Ehleringer and Cerling*, 2002], I consider only vascular plants having the C_3 photosynthetic pathway and examine their behavior at two scales: individual leaf (Appendix A) and homogeneous canopy (Appendix B). It is in Appendix A that I draw heavily on my previous hypotheses [*Eagleson*, 2002]. There I (1) review the generalized geometry of the classic leaf-scale C_3 photosynthetic capacity curve, (2) identify the principal species variable to be the projected leaf area index and the principal climatic forcing to be incident SW radiation, and (3) arrive at a generalized bioclimatic function at leaf scale that relates local C_3 species to average local incident SW radiation in the growing season such as to maximize unstressed productivity. Appendix B expands the leaf-scale development to the full homogeneous canopy.

In Appendix C, I find and verify, using a small sample of data from the literature, that the leaf-scale bioclimatic function is applicable across both of the considered scales, provided that the CO_2 supply and demand are both maximized and equal. I call this the “evolutionary equilibrium hypothesis” and suggest it as a possible quantification (only for the case of C_3 plants, of course) of so-called punctuated equilibrium [*Eldredge and Gould*, 1972; *Gould and Eldredge*, 1977]. Except for Appendix A, the monograph is new work.

My interest in the geographical distributions of species range and richness was stimulated by the writings of *Stevens* [1989] and *Wilson* [1992], who left me with their sense that the problems were related, were among the great theoretical problems of evolutionary biology, and at those times, were unsolved. Accepting this as a personal challenge, I began this work in 2002 and was delighted to find them still unsolved as late as 2006, at least [*Carpenter et al.*, 2006]. With this monograph, I hope to convince the reader that, at least for C_3 plants at North American latitudes, this is no longer the

case. I also hope to convince the reader that the science of ecology, lying as it does at the interface of biology and Earth science, has much to gain from practitioners skilled in mathematics and physics (and from their cousins in engineering science) as well as in the usual chemistry and biology.

My apologies for the difficult (if not impenetrable) notations brought on at least in part by the need to average in four dimensions.

Peter S. Eagleson
Cambridge, Massachusetts