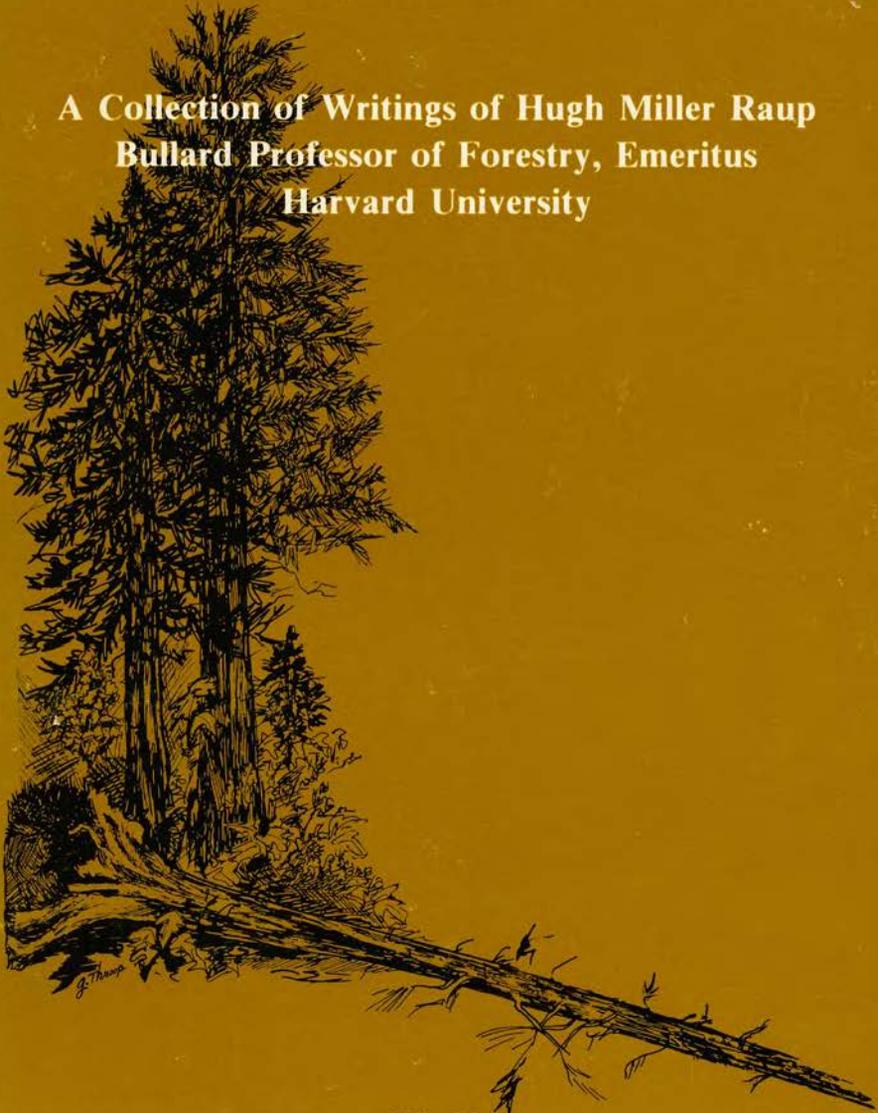


Forests in the Here and Now

A Collection of Writings of Hugh Miller Raup
Bullard Professor of Forestry, Emeritus
Harvard University



Edited by
Benjamin B. Stout

with
a fore- and afterword by Calvin W. Stillman

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*Benjamin B. Stout
Missoula, MT
March 1981*

Foreword

We speak easily of Nature, as if we could define it. We reserve the greatest respect for "natural science," as if such study were beyond the range of human foibles. We seldom reflect that all science is a human enterprise, and thus subject to the vagaries of human minds.

The term Nature always links its user to his larger world of things and of other people. Use of the term always has a subjective element, which should make it instantly suspect in the field of science.

The term Nature links the user with his larger world through implying a proper sense of order, a pattern of how things ought to be, with a status established for the user of the term, and some claim of sanctity for the general plan. The standard sanction is attribution of the plan to a Creator. This is all in the tradition of deductive logic.

Robert Redfield pointed out long ago that Man, God, and Nature exist in some form in every culture. He pointed out the variations that are possible in emphases on these terms. Among the ancient Hebrews, God was overwhelmingly powerful. Among the Mesopotamians, all three were subjected to a dominant priesthood. Among the Arapesh of New Guinea, Man is the center of concern; God and Nature set aside. Among the Zuni of New Mexico all attention is devoted to maintaining a proper balance among the three.¹

To the ancient Greeks, deities were sufficiently non-threatening that time and attention could be paid to the amenities of life, among them speculation on such practical matters as agriculture, mining, geography and astronomy. For the Greeks of the Golden Age, Nature was to be enjoyed and explored.

In the Christian world Nature as we would recognize it appears first among the early monastic brotherhoods which kept the faith alive in barren sites on the extreme western shores of Ireland. Their company was mostly sea-birds. Members of these orders travelled later throughout Europe spreading their values of piety, simplicity, and closeness to Nature. Their influence flowered in the 12th century in the person of St. Francis. Faith, Nature, and Poverty gave this young man a "unitive" experience. In the words of our time, he got it all together; he enjoyed his life.²

Personal feeling for Nature has been visible in our culture ever since. From the 12th century, leaves, flowers, and little animals appeared as decorations in European cathedral architecture. Natural landscapes crept into the backgrounds of religious paintings, ready to become central in Flanders with the Reformation in the 16th century.³ Amateurs led in the establishment of all the field natural science disciplines. Needs of collectors led to classification systems, and to the development of glass to house their treasures.⁴ With the notable exception of piety, the values of St. Francis surfaced again with Thoreau at Walden Pond, and in the stark simplicity of the tradition of children's camps in our society.

Assuming that the idea of Nature always has a place for the believer, we can predict instant appeal for any theory that relates an individual to his whole perceived world. Such seems to have been true in the mass acceptance of the tenets of ecology.

Ecology takes its place among the great idea-systems that have moved our people. It has a place for everything, including the believer. A system is implied: a pattern, any disturbance of which would destroy a whole often represented as "the balance of nature." The usefulness of ecology in analytical science is limited as is any tool; the usefulness of ecology in popular philosophy has not yet found its end.

Earlier great idea-systems trace back to Hebraic and Greek notions of an artisan God who designed our world down to its last detail, then left it to us to figure out how it all worked.⁵ The great religions that grew from these origins offered complete explanations of the human and the non-human worlds, and gave each communicant a place to belong. These religions also were vectors of systems of ethics for interpersonal behavior. Ecology offers a system with a niche for every living thing, but no ethical parameter. There are no ethics in Nature.

Many of us have been preconditioned to think in terms of such general plans. Any such plan implies a planner. As Langer has pointed out, some of the more sophisticated of us have attributed the planning role to nature itself, or to evolution.⁶

All such thinking is implicitly deductive, and in the tradition rather of theology than of experimental science. General ideas are so helpful to us in achieving individual orientations to the larger world that we are startled when a man like Hugh Raup points out their lack of congruence with reality. To work inductively and to question authority takes courage, and it takes time painstakingly to develop a case. We see the process in the papers which follow.

Raup was trained in the tradition of Henry C. Cowles and Frederick E. Clements.⁷ Their picture of the natural world comprised an orderly system of interdependent communities in which every living individual has found a pre-existing niche. The whole moved through a stately succession toward a "climax" which represented stability in the long run. Individual lives and the roles of the random were de-emphasized. Overall hung an aura of continuity and of certainty.

Robert Jay Lifton tells us that identification with on-going Nature is one of the devices we use to deal with really major stresses.⁸ This is clear in the United States in the last century, at every period of particularly rapid social change with distortions of human status. The most recent example is the rise of the "environmental" movement. This was preceded by no noticeable change in the national life-support systems. It was preceded by a general rise in affluence and opportunity, sparked by civil-rights agitation, and then by the unrest occasioned by military operations in Vietnam. As Raup himself says, the prohibition movement of earlier in this century was very similar.⁹ The flap over abortion has been attributed to similar pressures.¹⁰ Deductive orientations come ready-made as shelters for minds under stress.

Hugh Raup has spent his professional years as a field botanist. He admits to recognizing several thousand plant species when he meets them in the outdoors. His professional articles number, at last count, in the seventies. His reviews of books number in the nineties. His letters constitute a warmly personal mine of wisdom. From these materials the editor has undertaken to put into a single volume the most exciting of Raup's contributions.

We see in the development of Hugh Raup's thinking the careful field observer, the student who has read thoroughly in the past literature, and the human being interested in everything. We see concentration on each case at hand, thorough examination of the evidence, and always a search for random factors. The method is inductive.

Raup had one great model, Dean Charles Shatzer of his Alma Mater, Wittenberg College in Ohio. Others from whom he learned were Alexander von Humboldt, Andreas Schimper, Eugenius Warming, H. A. Gleason and Richard Hartshorne.

Raup writes,

I'm afraid I have never been an "appreciator" of Nature in the aesthetic sense. I've been associated with any number of people whose whole attitude toward the world around them has been primarily aesthetic, but somehow it never rubbed off. I do not know why this is so! Maybe some psychologist could tell me, but I doubt that I would believe him if he did. I guess I'm too much of a pragmatist.

I think Raup is wrong in this statement. His greatest accomplishments have been in appreciation of reality as he has observed it with his own senses. "Pure fact may be defined as that which is known by immediate apprehension alone," Northrop tells us.¹¹ Raup differs from others in his failure to emote about what he has observed. Neither does he leap to use immediately-apprehended fact to validate a general theory. He builds on what he sees. He operates as a Baconian facing a problem in natural history. He has read all the general theories, but he has a commitment to no one of them.

Raup's approach to Nature demonstrates the essence of inductive logic. He uses his senses, and leaves his emotions back in camp. He limits himself to the case at hand. He uses whatever tool of analysis seems to apply, and then tests it for validity and reliability. In using his own senses, and in thinking for himself, he uses all his aesthetic sensibilities without allowing them to sweep him away on a cloud of generalities.

Raup leaves us at the end of his career with a popular deductive theory of nature in ribbons.

*Calvin W. Stillman
Califon, NJ
November 1980*

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- ⁶LANGER, SUSANNE K. *Mind: an essay on human feeling*, vol. 1. Baltimore: Johns Hopkins University Press, 1967.
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- ¹⁰SKERRY, PETER. "The class conflict over abortion," *The public interest*. No. 52. Summer, 1978.
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Introduction

“IS THAT THE CLIMAX?”

“Is that the climax?” The question is asked in awe, in wonder, in naïveté, and in reverent expectation, by students and adults, of leaders of nature walks, naturalists, ecology professors, foresters, or anyone who leads groups of people through assemblages of trees that are past the sapling stage. Today, when environmental education is all-pervasive, and the words ecology and ecological have come into the vernacular, most literate nature lovers have heard of “the climax forest.” They assume, moreover, that the concept of vegetative climax is an absolute truth, and that if a given patch of woodland (or bog or field or whatever) can be said to have attained its “climax,” then all’s right with the world. For this means that here man’s intrusion has been minimal, and we are witnessing the beautiful culmination of a natural cycle of growth, based on an orderly succession through time, in the context of a community of organisms, all cooperating or competing within the web of ecological relationships.

*Hugh Miller Raup has argued for half a century that this concept may be mistaken: that the very question, “Is that a climax?” may be based on a series of false premises, each requiring examination. What follows are his comments, arguments, and conclusions, especially with reference to the idea of climax as it was set forth as early as 1914 by the botanist Frederick E. Clements in his Carnegie Institute publication, *Plant succession: an analysis of the development of vegetation*.*

According to Clements, vegetation tends to a steady state of age and species distribution, through successive stages. If an assemblage of plants has undergone a long period of stability without major disturbances—such as wind, fire, drought, flood, insects, disease, or human predation—it will reach, ultimately, an equilibrium with its environment which is said to be the climax. By studying the successive stages of similar aggregations of plant species, we should be able to predict the nature of the climax grouping of a given stand of plants. Unless a major disturbance should occur, this climax grouping should be self-perpetuating.

The idea of the Clementsian climax has far-reaching consequences. If the natural order is to move all vegetation to the climax, then man’s role is one of minimizing disturbance. If the natural order is less ordered and the progression to climax is not ordained, then man’s role can be one of manipulating: i.e., disturbing the vegetation so that the vegetation better serves the needs of man. Vegetation is simply converted solar energy. Disturbed vegetation converts solar energy to biomass at rates higher than undisturbed vegetation. The way people perceive vegetation has far-reaching societal consequences.

The ideas of community and succession are integral to the concept of climax. Integral to these ideas are those of scale, environmental determinism, and species.

Hugh Raup has looked at the evidence—the vegetation itself—and has attempted to understand and describe the processes he has observed. In doing so he challenges the concept of the Clementsian climax. The questions he raises will help the reader think more clearly about today's critical energy and environmental issues. Although Professor Raup's perception of the world is at odds with much modern writing about environmental problems, even those who disagree with him will find here the carefully-reasoned arguments of an alternative point of view.

Raup's arguments on several subjects are to be found throughout his published works. His assistance was sought when a search of his literature was begun. Not only did he provide suggestions as to where his writings on a list of topics could be found, he commented on the topics. The comments were in the form of a letter. Therefore, he introduces himself, as it were, at the beginning of each chapter.

There is precedent for Professor Raup writing his own introduction. His 1938 paper, "Botanical studies in the Black Rock Forest," was so heretical in the eyes of the director of the forest that a disclaimer was written as a prefatory note. Though the disclaimer bears the name of the director, it was in fact written by Raup. The director asked a colleague for help, the colleague asked Raup to write it. He did. No disclaimers are needed for this volume.

*Benjamin B. Stout, Editor
Missoula, MT
March 1981*

FORESTS IN THE HERE AND NOW

Chapter I

COMMUNITY, SUCCESSION AND CLIMAX

Hugh M. Raup was introduced to the ideas of community, succession and climax early in his educational experience. The development of his disaffection with certain aspects of these ideas and certain underlying assumptions is detailed in his letter to the editor and the selections from his published papers. The arguments are based on observations of vegetation over a wide geographic range.

LETTER FROM HUGH M. RAUP 1979

I've been trying to gauge my change in viewpoint by the change in my use of the word *community*. I read Clements and Cowles while I was an undergraduate, and all the training I got at Pittsburgh was based on the theories of community, succession and climax. While I was in graduate school I read Gleason's "Individualistic Concept, etc.," and both Schimper and Warming. But I don't think I really understood what they meant. My Ph.D. thesis was based on the work we did at Shelter Point (Lake Athabasca, Canada), and at Fort Reliance (Great Slave Lake), and clearly reflected a blend of Clements and Cowles. I thought I was seeing communities and successions everywhere!

But somewhere and sometime in those early years I began to be suspicious of Clements' emphasis on biological succession as a system for interpreting the history of the vegetation in any given spot. I think this came from Professor Charles Shatzer's influence at Wittenberg. He made me look at the whole landscape of that part of Ohio and try to see it in terms of physiographic development. I began to wonder whether any "dynamic" interpretation of present vegetation could be projected backward or forward through the changes in landform, climates and soils that we know have occurred since the ice disappeared, many of which are still going on.

This became clearer to me in the "Wood Buffalo Park years" (1928, 1929, 1930). I think the only things I saw there that I described as "successions" were the changes following fires in the upland forests, and what seemed to be going on on river floodplains, deltas and islands. I may also have thought I saw successions at upland lake and pond shores; but I

was by this time seeing evidence of fluctuating water levels in such places, particularly in the Karst topography on the gypsiferous limestone west of the Slave River.

Then I came to Harvard (1929), and discovered that there was a kind of plant geography that I had scarcely more than heard of before. It was based on the local behavior and general distribution of individual species, which required that a student must *know* the species in any area he was trying to rationalize. I had been collecting the flora everywhere I had been, and had been working up species identities as I went along, so this part of the show was not a serious problem. But what did all these “new” ideas do to our ecological theories? I think that about this time I reread Gleason, who had been questioning the whole notion of community, succession and climax on the basis of what he knew about the behavior of species. And I began to understand what he was driving at.

In 1933 and 1934 I tried to make “ecological” sense out of the Harvard Forest, and saw that I could do nothing with it until I knew what *people* had done there since the time of settlement. This sparked the land use study, which didn’t get done until 1938. In 1935 we spent the whole summer on Lake Athabasca, and saw what a changing water level could do to shore “successions.” Also we saw in that summer what really big floods could do to river floodplains and islands. I decided that “successions,” if they occurred at all, were really short-term affairs, indeterminate at both ends, and unpredictable in terms of flora and time. I see the vegetation as a thin rind on the surface of the earth, existing at the mercy of climatic and geomorphic processes and made up of whatever kinds of plants are available from regional floras. The 1938 hurricane and Brooks’ study of past hurricanes, the fire history in boreal and western forests, and plenty of other cases suggest that my general theory might have something in it.

Also in the 1930s I found out what could be done in the use of pure form in plant geography—with just the physiognomy of plants. I read Humboldt’s *Essay on Plant Geography* and a raft of other books and papers on it that very few American students have ever paid much attention to. Humboldt described “communities” of plants, but they were not the “biological” or “organismic” communities that Clements glorified. Rather they were physiognomic elements such as are seen as zones of vegetation around ponds or on mountainsides.

Perhaps the most important reading I did in the 1930s grew out of my association with a geneticist, Edgar Anderson, who was at the Arnold Arboretum from about 1931 to 1936, and also from Eric Hultén’s book on the “History of arctic and boreal biota, etc.” Anderson and Hultén made me conscious of ecotypic variation within species, which has colored everything I have done since.

Out of all this I found that I could never again be a “good” ecologist. A prominent practitioner in this field told me one time that I should not be

allowed to teach! I have written it all down here just to show you how difficult it is to say when or how I got like I am. I thought I had stopped describing “successions” by 1935, but to my amazement I find one on floodplains in “The Botany of Southwestern Mackenzie” written at about the end of the war and published in 1947. And at Black Rock (1938) I described pond shore successions.

“Community” and “association” are something else again. I used one or the other at least through the mid-1950s. I don’t think you can find the words, unless in a quotation, in any of the Greenland papers, the last of which I wrote while I was at Johns Hopkins (1967-1970), and I don’t think it appears anywhere in the paper Fred Johnson and I wrote on our Yukon stuff (1964). Why did I continue it for so long? I suspect it was for lack of a better word. I have never liked it, because it implies mysterious interrelationships for which there is no clear evidence. The same goes for “competition,” which I have avoided for a long time, and “dominant,” which implies that we know there is a competition. While I was at Hopkins I read some paleobotanical things and found their authors using the word “assemblage,” which is much more noncommittal. I am pretty sure that since the 1930s I have not used “community” in a Clementsian organismic sense, but rather as Humboldt did—to designate a mass of vegetation that has a distinctive physiognomy, color or texture.

After more than a decade of struggling with the idea of community, Hugh Raup put his thoughts on the subject into a Botanical Review paper published in 1941. The context is boreal America.

— † —

The ecological description of boreal vegetation bristles with problems of method and concept. Analyses in terms of plant associations, or attempts to arrange the associations in series, often become so complex and involved as to defeat their own purposes. Griggs, in trying to describe the arctic plant cover of the Katmai region in ordinary ecological units, found it hopelessly complex. "In the temperate zone vegetation is rather clearly segregated into more or less well-marked associations, like beech forests, oak forests, pine woods, swamps, and bogs. . . . When one goes to the arctic he naturally expects to find similar plant associations, but instead he meets a bewildering mixture of plants of all sorts jumbled together in seeming defiance of the principles of plant association learned in low latitudes" (Griggs 1934). He stresses repeatedly the difficulty of setting up a group of associations with which to generalize over any large area, pointing also to the experience of Scandinavian botanists who have set up a multiplicity of associations to describe the occurrence of a very few species. (See also Faegri 1937, for a recent review of European problems in this connection.)

I have had similar difficulties in the forested regions of the interior. The necessity for describing three kinds of white spruce forest in the same district is anomalous in the light of our rather well-defined temperate types. Again, the failure to find any phytosociological basis for generalization among pond floras is an excellent example of the same kind of confusion. Polunin described 30 odd combinations involving vascular plants on Akpatok Island, with a total vascular flora of only 129 species (1934-1935). He notes no attempt to outline communities until he has described a series of special habitats in which to look for them. A glance at the designations he uses for many of his communities indicates the difficulty he had in defining them: "Dryas-Salix-herb polygon sub-climax," or just "Forbs." Hultén apparently found similar difficulties on the Aleutian Islands.

Griggs' (1934) conclusion is that "Each of the items contributing to the belief that arctic vegetation remains in a state of flux goes to indicate that the plants of the arctic, individually and collectively, are still far from equilibrium with their environment." He thinks that the arctic vegetation "has not yet recovered from the glacial period but is still in process of active readjustment." This is consistent with my own findings in the Mackenzie basin.

Griggs reaches still another significant conclusion: that "a science of arctic ecology cannot be built up on the assumption that the place and mode of occurrence of a plant give reliable indications of its optimum habitat." Here he is in essential agreement with several other students whose work on relic species and communities is reviewed in this paper.

From Hugh M. Raup 1941a. Botanical problems in boreal American. *Bot. Rev.* 7:147-248. (All H. M. Raup entries refer to chronological listings.)

With so much confusion in the *content* of northern plant associations, their organization into developmental series, especially under the existing climatic and physiographic conditions, becomes more obscure. The difficulties in working out the history of what look like comparatively simple seres on the shores of large northern lakes has already been discussed. Similar studies in ponds, alluvial deposits, and upland forest seres suggest that the successions are not conditioned so much by biological factors as by climatic and edaphic ones. That is, the presence of a plant association in a given place is dependent not so much upon the previous existence of another one which prepared the ground, as upon the availability of the ground itself and a suitable climate. For instance, it is suggested that the Banksian pine has invaded the park-like spruce forests because a lowering of the upper limit of ground frost made possible the penetration of the rigid taproot of the pine, rather than because the spruce had modified the soil so that it could be invaded. Competition assumes far less importance in the structure of communities under this concept than it does in more temperate regions.

If the ideas outlined above are accepted, then a central theme of the theory of succession, that of the "climax," becomes difficult of application in boreal regions. One would have to concede that in much of our region no true climax has yet developed in post-glacial time. If we continue to use a concept of climax, it must of necessity be entirely theoretical, or at least highly conditioned.

Polunin seems unwilling to discard the ideas of equilibrium, climax, and seral development, in spite of the troubles he had in defining them. His statement of the problem is worthy of quotation: "Over the exposed limestone plateau which constitutes almost the whole area of the island, the vegetation is so poor as to suggest that hardly any successional advances or even marked changes (except in a few favoured localities) can have taken place since the first colonization after the final ice retreat. Consequently it is to be presumed that the *Dryas* and other main communities now seen, although they may appear to be of almost a pioneer type, will persist at least for a very long time to come. Whether they resemble true climaxes or arrested (sub-climax) stages in an *autogenic main sere*, or merely pioneer or migratory *proseres*, the majority at least of these dwarf and meager plant communities which go to make up the vegetation of Akpatok appear to be in equilibrium with the present conditions and hence relatively stable" (1935).

Cooper has been extraordinarily successful in establishing successional series in the Glacier Bay region of Alaska (1937). Here he has a clean-cut history of recent topographic change following the retreat of the glaciers, with an actual time scale covering a considerable part of it. Furthermore the climate of the region is conducive to relatively heavy forest growth. The analysis of plant communities and seral stages under such conditions becomes almost an exact science.

Although a time scale is not available, quite reasonable successional series can be worked out on floodplain and delta deposits in the northern interior (Raup 1935a). Here the change is rapid enough to show some of the earlier

stages by which the forests develop. Although Cooper can be fairly confident that the forests being produced on the older surfaces at Glacier Bay are parts of the regional climatic climax, it is doubtful if the northern interior forests can be so classified. The relative simplicity of the latter, both in flora and structure, together with their lack of uniformity, suggest that they have not yet reached the equilibrium of a climatic climax. If Polunin's concept is applied, however, with a somewhat broader interpretation of what constitutes a climax, then these forests might be regarded as actually in equilibrium with conditions in general, and could perhaps be called edaphic subclimaxes.

If recent or current fluctuations of the treeline are valid, then it may well be that an analysis of climax vegetation in the eastern arctic or subarctic would produce quite different results from one in the West. The instability and lack of organization in the Katmai vegetation described by Griggs may be replaced by relative stability in other parts of the arctic. Polunin has postulated a degree of stability at Akpatok Island, and Clarke thinks the forest line is stable in the Thelon region. Cooper has abundant proof of recent development at Glacier Bay, and I have found evidence of unstable conditions in the Mackenzie basin.

Here the matter rests at present, with no well-defined bases for generalization. Most of those who have attempted ecological description in boreal America are impressed with the difficulties in the delimitation of associations, the definition of what constitutes equilibrium in a region where associations are so poorly defined, and the reconstruction of seral development. Added to these troubles is the disturbing failure to adjust the distribution of many species to any climatic values that have yet been set up, and the evidence that northern plant communities may not actually be adjusted to known climatic features. Griggs goes so far as to suggest that some entirely new basis may have to be established before we can form a rational organization of arctic vegetation.

Floristic plant geographers have raised concepts of "conservative" and "aggressive," or "rigid" and "plastic" species; but we do not yet know how significant these categories will be when applied to the organization of plant communities. It has already been proposed that criteria of "species potentiality" will have to be used in this organization before common ground can be found between modern floristic and physiological plant geography. Ecologists have attempted to deal with the situation in the physiological terms of "ecological amplitude," but Cain (1939) thinks that this may be conditioned by the age of the species and its relative "capacity for extending its range despite the availability of apparently suitable habitats." In a later paper (1940) he suggests that the biotype depauperation of a species by isolation is more significant than age in determining its capacity to extend its range. The existence of conservatism in species has been sadly lacking of proof, but the recent findings of geneticists have set it up firmly as at least a good working hypothesis.

It is not impossible that if we are ever to understand the structure and development of boreal plant communities, with their complicated distribu-

tion of species and dominance, we will first have to learn where the species lived during the Wisconsin glaciation. Did they survive on large areas where they formed large populations in which their inherent variability could be maintained; or were they parts of limited populations which were depauperated of biotypes and reduced to a "rigid" condition? It is possible that the role of a species in the formation of a young boreal community may be determined as much by these inherent limitations as by the interaction of the multitude of external environmental factors.

Two phases of this matter must be borne in mind. First, if such a rating of potentiality for species is set up, we have to deal, not only with extremes, but also with a series of intermediate conditions depending upon the amount of depauperation that has occurred. Further, some populations that were reduced to uniformity under the influence of isolation during the Wisconsin may subsequently have managed to fuse with others and so to regain their potentialities. Second, the ordinarily accepted species set up by taxonomic criteria may not show the same abilities in migration, establishment and dominance at different points. Races which show little or no structural peculiarity, isolated from their kind by the ice, may be conservative while larger populations have remained aggressive.

In connection with their studies of speciation, Clausen, Keck and Hiesey (1940) make a comment which is significant here, although they do not go into the matter of conservatism vs. aggressiveness: "That modifications and heritable variations have been confused by many botanists is evident in the literature. There has been a paucity of evidence showing to what extent plants may be modified in different types of environment, and how modifications compare with heritable variations. These comparisons have been emphasized . . . , for such a study is fundamental to an understanding of plant interrelationships, and of plants in relation to their environments."

Concepts of conservatism, aggressiveness, and the history of the development of plant communities over long periods of time are to be applied not only in the classic approaches to boreal plant geography, but also in studies based upon the hypothesis of continental drift. It will be noted that the phytogeographic applications of the theory of continental drift are not discussed in the present paper. American students have done very little in this field, but recent papers by Steffen (1937-1938) in Germany serve to outline the current thought and research that touch upon it. E. V. Wulff's paper on "An introduction to Historical Plant Geography" (1943) should also be consulted.

With regard to recent changes of climate and their probable effects upon vegetation boundaries, there are some ecological aspects that need elucidation. As previously stated, Griggs believes that the present treeline in Alaska is not to be correlated directly with contemporary climatic factors, but rather that the forest has lagged behind the change in its favor, and is but slowly advancing to a position of actual adjustment. This idea of "lag" in development is not a new one in phytogeography. Cowles (1901) utilized it in his analysis of vegetation in the Chicago region, and Clements (1934) uses it in

discussing the "Relict Method in Dynamic Ecology." Rübél (1935; see also Faegri 1937) has tried to reduce it to a factorial interpretation in his paper on "The Replaceability of Ecological Factors and the Law of Minimum." Hutchinson (1918) has suggested that the deciduous forests of Ontario have lagged behind climatic changes in their movement northward, and await the further development of soils suitable to them. I have postulated somewhat similar conditions in the central part of the Mackenzie basin (1930a), and have suggested also that the forest boundaries in southern New England have shown a tendency to persist after climatic changes have occurred (1937b).

The fundamental issue has been stated by Deevey (1939) in his discussion of my studies in southern New England: "The concept of widespread and continued persistence of forests not adjusted to the prevailing climate logically leads to a negation of ecological theory, and Raup's hypothesis must be construed to include only local areas of relic vegetation." If ecological theory postulates the continued adjustment of vegetation to climate, then Deevey is right; but if the interpretations set forth in the preceding paragraphs are correct, we must postulate conditions wherein vegetation is very often *in process* of adjustment, and actually existing with only partial adjustment. That such conditions need not be local is shown by the large-scale fluctuations of the treeline.

It should be noted in this connection that Hultén arrived at similar conclusions on climatic adjustment in his study of the boreal distribution of species (1937b). In fact the idea is inherent in the persistence hypothesis which has been discussed elsewhere in this paper.

To show that the idea of community generates questions independent of geographic area, we turn now to notes reporting on visits to forests in tropical America. These were written in 1950. The "Research Department" to which Raup refers is a department of the United Fruit Company; the observations were made in Honduras. In this selection Professor Raup suggests a system by which shade-intolerant trees could be perpetuated in a forest.

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A sound basis for the silvicultural management of the Research Department's timber tree plantations and naturally regenerating forests should be looked for in studies of the natural behavior of the species involved. By the "natural behaviour of the species" is meant their preferences in soils and climates, their rates of growth under varying conditions, their means of natural regeneration and the success with which they accomplish it on differing sites, the degree to which they prune themselves if growing in the open or if in competition for space and light with other species, their susceptibility to disease and insect pests, the length of their normal life spans, and the behaviour of their growth rates from seedling stages to maturity. To these things must be added their behaviour as members of communities of trees, particularly in mixtures of two or more species. Such mixtures may prove to be desirable but they cannot be formed artificially until the mutual compatibility of their component species is determined.

Overshadowing all of these problems is a larger and composite one. The Research Department is developing forests which are artificial in form and context. They are not under control in the sense that agricultural crops are at man's command, for control in this sense would necessitate answers to the questions posed above, with experience in their application. The tree crops in Honduras, whether planted or naturally generated, are essentially wild crops. Their success will be determined by factors that for the most part are not controlled, and the Research Department's success in making them profitable will depend upon how cleverly it can adjust the natural growth of the trees to its own uses on one hand, and to the natural laws governing the forests on the other.

Partial answers to many of the above questions have already begun to appear in plantations and controlled natural forests. For instance, the wide replication of experimental plantings under varying conditions of soil and climate is beginning to indicate soil and climatic preference among the species. Some species are clearly able to prune themselves even when growing in the open, and probably can be planted with wide spacing at the outset. A few data on regeneration capacity are beginning to appear, and there is some evidence of relative compatibility wherever mixtures occur.

This information is a mere pittance compared with what is necessary, and large acreages of Honduran mahogany, teak, primavera, and many others are growing apace. They will not wait for management plans to develop from the

From Hugh M. Raup 1950b. Notes on reforestation in tropical America II. Unpublished.

slow accretion and interpretation of data on the natural propensities of the species. In the absence of such information the only source of guidance available is the behaviour of the native woodlands of the region—their composition, origin, developmental history, probable future successional trends, and their behaviour under the hand of man. Management plans for the plantations, for instance, will be conditioned by whether or not the trees are “tolerant.” By “tolerance” is meant the species’ ability to regenerate itself by the development of seedlings or root suckers under the canopy made by its own crowns. The only indication we can get of this ability, with our present knowledge of the trees, must be found in the wild forests where the species are now growing naturally.

The following remarks on natural trends in vegetational development are based upon such observations as I have made in the natural forests of the region. Most of these observations were made in the older hardwoods at Lancetilla and in the Cienega tract at Agua Azul, and in the pine forests at Los Dragos, Agua Azul, and Trincheras.

THE OLD FORESTS AT LANCETILLA

The basis for the following notes was primarily in observations made in an old forest on the hillside that borders the Lancetilla valley on the east. The old forest has been protected for many years because it occupies land which produces the water supply for the town of Tela.

It was necessary at the outset to identify most of the principal forest trees. Such data as I have on this were made possible by the assistance of Mr. Robert Armour, who is in charge of the Lancetilla garden, Mr. Paul Allen of the Research Department in Costa Rica (who happened to be visiting Lancetilla at the time), and a native Honduran boy whose knowledge of the trees proved to be extensive and remarkably accurate. Also we had available Dr. Paul C. Standley’s excellent description of the forest, published in his *Flora of the Lancetilla Valley, Honduras* (1931). See Table I for a list of the trees noted.

This forest is a “high” one, commonly regarded hereabout as primeval tropical rain forest. The tallest trees probably reach heights of 150 feet, sometimes with clear lengths up to 70 feet. They are mostly straight, some species with buttresses six or more feet above the ground. The largest ones tower as individuals high above the main canopy, and are commonly widely spaced on the ground (50 to 100 feet apart). The trunks and crowns support a wealth of epiphytes, and are festooned with lianas. The main canopy is of tall Monaca palms and a miscellany of smaller hardwood trees that usually have straight, clean boles. The Lancetilla palm is abundant in the lower undergrowth, as are many lesser woody plants and climbers. There are not many herbs. Ferns and aroids are common, however, on the ground and on the trunks of trees. The shade is dense.

Fallen trees rot and distintegrate very rapidly on the ground. When the larger trees fall they leave huge openings in the canopy not only by their own disappearance, but by dragging down with them all the lianas attached to their

Table 1: Trees noted in *Flora of the Lancetilla Valley, Honduras*

Tall Trees, forming the main canopy or extending above it.

Barba de Jolete	<i>Pithecolobium arboreum</i>
Sangre	<i>Virola guatemalensis</i>
Papo de Viejo	
Laurel	<i>Cordia gerascanthus</i>
Paletto	<i>Dialium diverigatum</i>
Bursera	<i>Bursera simaruba</i>
Urraco	<i>Licania platypus</i>
Aguacatillo	<i>Nectandra?</i>
Ceiba	<i>Ceiba sp.</i>
Quita calzon	
Tango	<i>Zollernia Tango</i>
Tempisque	<i>Sideroxylon capiri</i>
Varillo	<i>Calophyllum Reko</i>
Silion	<i>Lucum izabalensis</i>

Smaller Trees and Palms

Lancetilla palm	<i>Astrocaryum cohune</i>
Paterno	<i>Swartzia pamamensis</i>
Mahao	<i>Heliocarpus Donnel—Smithii</i>
Mombin	<i>Spondias Mombin</i>
Strangling fig	<i>Ficus sp.</i>
Fruta de danto	<i>Cynometra retusa</i>
Ja—Ja	<i>Rollinia sp.</i>
Cacao	
Monaca palm	

Additional Species, not seen by me, but derived from Standley's lists

Honduras mahogany	<i>Swietenia macrophylla</i>
Spanish cedar	<i>Cedrella mexicana</i>
Honduras roseweed	<i>Dalbergia Cubilguitzensis</i>
Masica	<i>Brosimum terrabanum</i>
Masicaran	<i>B. costaricanum</i>
Carbon	<i>Gaurea excelsa</i>
Sapote	<i>Calocarpum mammosum</i>
Zapotillo	<i>C. viride</i>
Vochysia	<i>Vochysia</i>
Rhedia	<i>Rhedia</i>
Ciruelillo	<i>Astronium graveolens</i>

crowns and by breaking lesser trees that are under them. Openings thus made seem to close quickly. The root masses turned up by the fall of large trees are relatively small. One that I saw in an opening rather recently made was only three feet high and wide, and the hole left in the ground was correspondingly small and only about a foot deep. A reason for this might be that the roots of a tree would rot away very quickly after the tree died, so that when the trunk finally fell, there would be little woody material left to heave up the soil. A hummocky surface on the forest floor, so common in very old temperate

woodlands and due largely to windthrow, scarcely exists in the old forest at Lancetilla. Mr. Allen told me, however, that he had seen such hummocky surfaces in high forests elsewhere in the American tropics.

Throughout our examination of this forest we tried to find the canopy trees in the understory. There were plenty of seedlings, often found with the seeds still attached, but we could not find these species occurring as small trees. A possible exception was Paeto, but in this case the young tree was at the side of a ravine where it got considerable light from the side. We could find little or no evidence, therefore, that the forest is regenerating itself with the species of its present canopy. Although seedlings are being produced on the forest floor, they do not survive. If any regeneration is going on, it is probably in the accidental openings caused by fallen trees.

The above observations suggest, it seems to me, the conclusion that this forest is made up essentially of species which, in this setting, are "intolerant." Their seedlings seem unable to compete successfully for light, water and soil nutrients with the parent trees. This is in contrast with the hardwood forest on the Cienega tract at Agua Azul, where a considerable proportion of the species (some of them the same as those listed above) are able to do this. It is entirely possible that if vigorous seedlings were present in an opening caused by the fall of a very large tree, they might by rapid growth reach the canopy before it closed again.

The vega† at Lancetilla, now planted to timber trees, was formerly banana land, and presumably before that it was used for milpa†† agriculture. All of the valley sides, with the exception of the protected forest described above, are now in milpa cultivation or are in various stages of guamil††† development following cultivation. During my observation of the plantations, described elsewhere, I saw no less than 12 of the 34 species noted as occurring in the hillside forests. These were all growing in guamil of one sort or another, some at the lower slopes of the hills, and a few in thickets along the river. Of the 12, nine can be classed with the high canopy trees. These 12 species are as follows:

Sangre	Spanish cedar
Laurel	Sapote
Bursera	Vochysia
Ceiba	Mahao
Tempisque	Strangling fig
Masica	Monaca palm

One of the clearest conclusions reached to date by the Research Department is that all its principal native plantation trees (Honduras mahogany, Honduras rosewood, Spanish cedar, primavera, ciruelillo, frijolillo) must have sunlight above them if they are to thrive. The plantations include an abundance of experiments in "tolerance" to support this

†A flattish valley.

††Rotational agriculture.

†††Early brush stage in succession following abandonment of land.

conclusion. To the above list could be added, therefore, cirulillo, Honduras mahogany, Honduras rosewood, and possibly Barba de Jolote.

There is little doubt that still more of the canopy species of the high forest could be found in guamil in the Lancetilla valley provided a serious search were made. Those I saw were noted in passing.

Standley (1931) questioned the primeval quality of the high forest at Lancetilla. He based his doubt upon the occurrence of potsherds in the soil of the forest floor, and upon the presence of cacao, sapote, and avocado. All of these species are grown by the natives for their fruits, and have been grown since Mayan times. When to these facts are added the apparently almost universal "intolerance" of the canopy species, and the apparent failure of the forest to regenerate itself with the species now growing there, the conclusion may be inescapable that the present cover is the initial forest growth after milpa agriculture. The present large trees must have grown up more or less together as a part of the guamil that came into the abandoned fields. In fact a considerable portion of them are to be seen doing it now in other parts of the Lancetilla valley.

Before such a conclusion can be reached, however, it will be necessary to prove, by much more observation than I was able to make, that the forest is not regenerating itself. It is possible to develop the idea of regeneration through openings made by falling trees, particularly if the extremely rapid growth and early maturity of tropical trees is taken into consideration.

Thinking along these lines is usually done with temperate zone forests in mind. Here the trees commonly grow to great age before they die of natural causes, in our eastern American forests as much as 300 years. Any given spot in these woodlands, therefore, is likely to be opened up to overhead sunlight by a falling tree only once in, say, 300 years. Openings made in this way commonly introduce intolerant species to a forest in which they would not ordinarily occur. It is impossible by existing means to determine the ages of the large tropical trees. Their known rate of growth as young trees is so great, however, that we are justified in assuming that they reach maturity and great size in relatively short times. I think it not unreasonable that some of the large trees at Lancetilla were seedlings scarcely more than 50 years ago. Dead and fallen trees are not uncommon in this high forest, indicating that the life span is being completed by many of them. If the above estimate of age should be correct, a given spot on the forest floor might be open to light once in 50 years, or six times as frequently as a spot in a temperate forest. Further, the hole made by the falling tropical tree would be much larger than one so made in a temperate forest, and the intolerant seedlings could get up into the canopy much more quickly than could a white pine in a northern forest. Further study will be necessary before it will be possible to say whether a forest of intolerant trees can regenerate itself by such means.

The above theory does some violence to the current concept of the "climax" forest. The latter is usually thought of as composed principally of species which are so tolerant of shade and other forms of competition that they can perpetuate themselves more or less indefinitely on a given site, and can

eliminate intolerant species. Here I have conceived of a forest of intolerant species in perpetuity.

Whether such a forest actually exists or not, I think the above reasoning may serve to explain the widespread occurrence on the Central American rainforests of the intolerant "rare woods" such as mahogany, rosewood, and Spanish cedar. The Research Department has been concerned with the question of whether or not its plantation-grown trees will produce lumber of quality comparable to that of the wild stands. I believe that most of the wild mahoganies, rosewoods, cedars, and other trees of commerce have had their beginnings in the open, either in guamil or in blowdowns, and their wood should not be much different from that of plantation-grown stock. Recent tests have shown that this is the case.

The ideas of Clements and others were not considered to be limited by geography. In what follows, Hugh Raup reminds his audience at a meeting of the Ohio Academy of Science that there are problems with Clementsian ecology. It should be noted that E. Lucy Braun arranged the session at which this paper was read. It was Miss Braun who described so elegantly the forests of the Cumberland Plateau and who coined the term "mixed mesophytic." The paper from which this excerpt is taken was published in 1951.

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Some of us have tried to work out plant successions outside of the temperate zone. To put the matter mildly, we have had difficulties in applying the ideas derived from our training and experience in the temperate regions. We have found that the farther we go, phytogeographically, toward the Arctic or the Tropics, the greater the difficulties become. It is only natural that we should carry our methodologies and assumptions with us as we go, and it is also natural that we should be loathe to discard or seriously modify them when we find them inadequate.

One of the first problems is the application of idea of dominance to complex communities. In the arctic and alpine tundra we have communities of relatively few species, but when one tries to describe them in terms of dominance or primary species he finds himself merely listing a considerable part of the flora. Antevs (1932) had this difficulty when he was describing the alpine communities in the White Mountains of New England and Polunin (1934-35) found it extremely difficult to do at Akpatok Island. Polunin's (1948) recent study of plant communities in the Eastern Arctic resolves itself into a compendium of variable species complexes that reappear with endless variety in one locality after another. It was this that Griggs (1934) was talking about when he said that the tundra flora of Alaska acted like a ruderal or weedy flora with no apparent rhyme or reason in its local assemblages. In all of these cases, we see a prime characteristic of temperate vegetation non-existent or very poorly developed in the Arctic.

Another of the attributes of plant communities, successional development, also becomes extremely difficult to document and prove as we go away from the temperate zone. Vegetational change does occur naturally, but to establish it within a "biological" definition, or in terms of any physiographic progression with which we are familiar, commonly becomes impossible.

In the boreal regions of America, we deal with topography which in many cases is extremely youthful. Water tables and lakeshores fluctuate much more than they do in the temperate zone. One wonders what would happen to our ideas of the development of vegetation on the shores of Lake Erie if the water level of this lake should rise eight or ten feet every 50 years or so and then return to its former level; but that is what happens at Lake Athabaska. Whole lake basins composed of myriad small bodies of water interspersed with swamps and bogs are having their ground water levels reduced by the erosion of friable barriers such as glacial moraines. Other lakes are being formed as

From Hugh M. Raup 1951c. Vegetation and cryoplanation. *Ohio Jour. Sci.* 51:105-116.

“thaw lakes” in areas underlain by perennially frozen ground (Hopkins 1949). Such bodies of water appear, develop marginal vegetation and then disappear when the vagaries of seasonal thaws open underground drainage channels. Ice-push is enormously effective in modifying shore forms, and is a factor which is insignificant in most of the temperate zone. The result is that vegetation around lakes and ponds in the far north commonly gives but little indication of regular successional stages in the development of organic deposits.

Perhaps the most nearly authentic natural successions in the North, with the exception of a few secondary ones, are on river islands and floodplains. Here again, however, excessive flooding due to damming by ice and driftwood is so common that it becomes difficult to infer natural biological successions.

Evidences of succession in the Arctic, when they are carefully examined, commonly prove to be so fragmentary and so isolated in the total context of the vegetation that they cannot be strung together into recognizable trends toward equilibrium.

The publication of E. Lucy Braun's Deciduous Forests of Eastern North America is an important milestone in American forest ecology. Raup's 1952 review of the book included his concerns about the idea of community and the effect of the community idea on an author who adopts it, even one so eminent in her field as Professor Braun.

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Modern ecological plant geography, particularly as it has grown in America, has been concerned primarily not so much with the simple geography of vegetation as with the development of vegetation. This emphasis upon vegetational change is to be seen in the very fabric of the science. Although some of its roots are to be found in European work of the late 19th century, it has had its largest development in America during the past 50 years. Its primary design first appeared in the work of Cowles in the region around the southern end of Lake Michigan. It was based in large measure upon an area of correlation elaborated by Cowles and his students—a correlation between the development of vegetation and the development of land forms. A primary impetus for it seems to have come from the contemporary studies of the cycle of erosion by the physiographer, William Morris Davis.

Ideas developed in the Chicago school were quickly picked up by many students in the Middle West and the Great Plains region. The most articulate of these students was Frederick E. Clements, who developed the idea of plant succession to such an extent that it has become the organizational base for most American ecological plant geography.

Particular emphasis upon the development of vegetation has led inevitably into a maze of problems, the statements of which have become burdened with an impenetrable tangle of facts and assumptions. Once completely imbued with the idea of development, one has a strong tendency when looking at a stand of vegetation to see it not for what it is, but for what it has been, or for what it is becoming. Dr. Clements once told me, while commenting upon the work of a contemporary ecologist, that I seemed to be able to see only what was on the ground in front of me. This was meant to be a disparaging remark.

When existing reality thus becomes so transitory, the way is open for endless theorizing on what may happen in the course of development. The plant ecologist attempts to bring order out of this chaos with the concept of "climax." It is assumed that all vegetation is developing toward some kind of more or less stable equilibrium, or has already arrived there. This does not solve the problems, because it becomes necessary to define climaxes.

Decision on what constitutes a climax rests upon our capacity to understand the relationship between a forest and its habitat, and to project this relationship over time. It is safe to say that with our present knowledge we are unable to state the relationship by processes of analysis and synthesis. Our

From Hugh M. Raup 1952, *Deciduous forests of eastern North America*, by E. L. Braun. Review in *Ecol.* 33:304-307.

knowledge of the genetics and ecology of the individual species of trees is so slender, and our inability to measure and synthesize the multitude of external environmental factors is so marked, that the method of analysis and synthesis seems for the time being impracticable. Even if we were able to draw up such relationships for individual species, we would still be far from our goal because of the complex nature of most communities.

The element of time introduces still further difficulties, particularly in the study of forests, for it becomes necessary to project our imperfect knowledge of the interactions of trees and their habitats over comparatively long periods of time in order fully to define climaxes.

In the absence of tangible results from analysis and synthesis, therefore, we look for indications of climaxes in what we can reconstruct of the precolonial forest, or in whatever trends of development we can detect in existing second-growth stands. To make these methods workable, however, we have to assume a certain amount of stability in general forest-habitat relationships. It is common practice to proceed with cases of forest succession as though the climate were a relatively stable influence within which changes occur at such a slow rate that they are almost imperceptible. The same is commonly thought to be true of most physiographic processes which affect land forms and soils. Out of these areas of relative stability come our concepts of climatic and physiographic climaxes. Climatic and physiographic changes do occur, however, some of them gradual and others cataclysmic. Correct definitions of climax by these methods therefore rest upon the assumptions that we know the rates and effects of gradual changes; and if the changes are cataclysmic, that we know what they are and can place them in time sequences.

In spite of the fact that Dr. Braun carefully defines her terms and concepts at the beginning of the book, some readers will have difficulty with Part II. Throughout her description of existing and precolonial forests, she has inserted the concept of the climax, and has attempted to place all existing forests in a climax or in some developmental sequence leading to one. She describes her forest regions in terms of forest climaxes, and in so doing she has raised all the problems that surround the definition of climaxes. For those who have found it difficult to utilize the theory of climax, her insistence upon it may be a source of distraction when they read her superb descriptions of the forests. It might have been better had she reduced her discussion of the deciduous forest regions to simple geographic descriptions, and placed her interpretations of succession and climax in an additional chapter of Part III.

One of the most remarkable papers of Raup's entire bibliography was published in 1975. In this paper he essentially says that his data interpretation in his dissertation and certain subsequent papers of nearly a half century earlier is faulty. The paper was published in 1975; it had been in preparation since 1926.

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When this study was begun in 1926, major emphasis was placed on the "development of the vegetation." The units of study were to be "communities" or "associations" of plants described in terms of form and floristic content. The "development" was largely confined to the theory of succession among communities, leading to more or less stable climax or climaxes. Time scales for the processes were not clearly defined, but it was assumed that the present state of the vegetation could be rationalized by projection of these processes backward to the disappearance of the last glacial ice.

The vascular flora of the region was not well enough known in 1926 to cover the needs of such a vegetational study. This applied not only to the less common species but also to many abundant ones which, as "dominant" species, gave form and character to "communities." Consequently the collection and identification of the species was the first necessity. Between 1926 and 1935 the known vascular flora of the region was thus increased by about 30 percent. Most of the new records were range extensions, for the region has very little endemism.

My earliest papers on the region reflect the above frame of reference (1928, 1930a&e, 1935a). After the field season of 1935 this frame became almost wholly inadequate.

A determined effort was made to use "communities" or plant "associations" as the basic units of study. This could be effective only if the assemblages of species, or at least of the so-called "dominant" species, were largely repetitive within such habitat complexes as could be defined with the knowledge and facilities at hand. Because the identity of the "communities" rested upon floristic composition, it was thought that they probably had some form of internal organization among mutually compatible species which added validity to their use as study units.

Wide variation in species composition of the shore assemblages began to appear in the early work on Great Slave Lake (1927). Seventeen small bodies of water were studied on Fairchild Point, a peninsula about 10 miles long in this lake. Each of these ponds was unique, either in the arrangement of its vegetation zones or in the "dominant" species composition of the zones. The field seasons in the Wood Buffalo Park (1928-1930) brought out even greater variability, not only among the many ponds and small lakes that were studied, but also within habitats on the shores of individual bodies of water. A lake about 10 miles long on the upland west of the Slave River required eight transects for a fair sampling of its shore vegetation. Twenty-eight different

From Hugh M. Raup 1975. Species versatility in shore habitats. *Jour. Arn. Arb.* 56:126-163.

“communities” of vascular plants were described in these transects, involving 20 “dominant” species. Field experience strongly suggested that in the region as a whole the study of more pond and lakeshores would yield more different “communities,” more zonal variations in the vegetation, and additional “dominant” species.

The use of the “community” or “association” as the basic unit for the study of the shore vegetation became extremely doubtful. Nonetheless, these terms continued to be used (1934, 1935), and the complexity was in part avoided by annotated descriptions of assemblages believed to be “typical” of the various habitats. Maximum confusion was reached in the 1935 season when many shores around the whole of Lake Athabaska were examined, particularly those of the intricate lagoon systems on the south shore. Here no two of the hundreds available for study seemed to have the same “community” structures and contents.

The idea of orderly successional development among “communities” had to be greatly restricted in space and time. The last cover of glacial ice did not retreat steadily, but in stages so that land surfaces available for colonization by plants were of varying ages. Owing to the general topography of the region and the geography of its drainage systems, there had been large variations in the levels of its major lakes and in the development of its floodplain and delta systems (Raup 1930a, 1931, 1946, and Cameron 1922). Lengths of time during which physical habitats could remain relatively stable, and in which long-term biological successions could have occurred began to be notably shortened. A high water level seen at Lake Athabaska in 1935 was maintained throughout the growing season, and effectively drowned all the shore “successions” that were described in prior years. The frequency of such floods has been estimated recently by Stockton and Fritts (1973), and it is not unlikely that time periods during which the shores of this lake can remain physically stable are shorter than the life spans of most of the perennial plants that make up the shore vegetation. If this is the case, successions in this vegetation are reduced to fragments which, if they exist at all, have indeterminate beginnings and ends.

The extent to which analogues of these findings can be seen in the shores of smaller upland lakes and ponds is unknown. Many of these smaller water bodies are held up by morainic dams, which were deposited at different times, have varying materials, and erode at different rates. Extreme cases occur in the karst topography west of the Slave River, where fluctuations in pond levels of 10 to 30 feet are not uncommon, giving rise to curious “duplications” of shore zonations at different levels in the same sinkhole. Here the fluctuations are due to unpredictable changes in the movement of ground water through the underlying cavernous gypsum.

With the failure of the “community” as a viable, repetitive unit for study and rationalization of the shore vegetation, and with the greatly restricted use of biological succession for interpreting the development of this vegetation, it became necessary to construct some other frame of reference. The present paper explores the use of the species as the basic study unit. There is abundant precedent for this in the literature of floristic plant geography (cf. Raup 1942c,

Wulff 1943, Cain 1944, Böcher 1954). But there is less precedent in ecological plant geography, which has been concerned primarily, during the present century, with the structure, physiology, and "dynamics" of "communities" (cf. Gleason 1926, Cain 1947). The use of species as study units has been greatly stimulated since the 1920s by research on ecotypic variation within species and by the realization that taxonomically defined species contain biotypes and ecotypes that behave differently in their relations to environments (Turesson 1922a&b, 1925, 1927, 1929; Hultén 1937b, Clausen, Keck and Hiesey 1940; Mayr 1964). The implications of this research for the geography of plants were rather thoroughly reviewed by Cain in his *Foundations of Plant Geography* (1944).

In the present paper the term "community" is replaced by "assemblage," which carries fewer connotations of relationships among species that are unknown or nonexistent. The terms "primary" and "secondary," though not common in ecological literature, are not new in the sense in which they are used here. They were so used by Hultén in his *Flora of the Aleutian Islands* (1937a).

In 1972 Hugh Raup spoke to the Ecology Program Seminar at Rutgers University. He reviewed the history of the idea of community and some of the consequences to be found in that body of knowledge we call plant ecology. To a group of graduate students whose educations had been guided by ecologists who accepted the idea of community, Raup's remarks were shocking, if not heretical.

In the foregoing papers we have had the evidence laid out. In this paper we have the elder statesman not only reviewing the evidence but also putting it in an historical and ideological context.

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About 1900 there appeared a curious offshoot from the physiological plant geography I have been speaking about. It was, in its earliest form, peculiarly American, and was led by two men: Henry C. Cowles at the University of Chicago, and Frederick E. Clements who was then at the University of Nebraska. For Warming and Schimper as I have said, the basic units of study in their physiological and community geography were individual species. Cowles and Clements dropped the species as units of study, and substituted "communities" of species, which they also called "associations" or "societies." Why they did this has never been satisfactorily explained. With Cowles it seems to have been a tacit decision, made without comment, but Clements spelled it out in a book on research methods in plant ecology, published in 1905. I can only suggest a couple of reasons for their doing it. Taxonomy was just at this time in something like doldrums. Its practitioners had retreated into their closets, shuffling names and specimens and making confusion for anyone trying to use species as study units. Mendelian inheritance had just been rediscovered, and had not yet begun to revitalize the field. For a second reason I have wondered whether these men didn't sense what Livingston and Shreve eventually came to, that results from experimental studies of species would be so long in coming, and so uncertain, that they could not live long enough to make use of them. Perhaps they thought they could short-cut the business by dealing in larger units in which they could generalize the relations of plants to environment. Whatever their reasons for the decision, it was momentous, for it bent American plant ecology and plant geography into a channel it still follows.

Early in their careers these two men took off in another direction which was fraught with large consequences. Cowles had been a student at Harvard when the famous physical geographer, William Morris Davis, was at the height of his powers as a teacher. Davis had developed his "cycles of erosion" and "peneplanation." Cowles picked up this idea and applied it to the development of plant associations on river floodplains. As he went down over a series of floodplain terraces into a river bottom he went gradually from well-developed forests on the higher surfaces to younger communities on lower ones, and finally to a few "pioneer" species growing on sand and mud bars along the river itself. He thought that as a river gradually eroded its channel it left its floodplain terraces at higher and higher levels above the water so that

the higher ones gradually got above flood levels and became stable habitats for plants. The communities he found at these higher levels he thought had developed by what he called "successions." Major emphasis was placed on the capacity of the vegetation to alter its own habitat so that it would be followed by different communities in a regular, predictable sequence until it arrived at a sort of balance which would contain the "highest" form of vegetation that the region could produce. This vegetation would then persist by reproducing itself in perpetuity. Eventually it was called the "climax community" in the succession. Cowles proposed all this in a paper published in 1901 on "The Physiographic Ecology of Chicago and Vicinity; a Study of the Origin and Development of Plant Societies." He had published shortly before this (1899) a treatment of vegetational development on the Indiana Dunes at the south end of Lake Michigan. Though Cowles himself did not publish much more along this line, he fostered a galaxy of students who did. Clements picked up the ideas very quickly, and began applying them to all vegetation, making succession to climax the central theme of American ecology and plant geography for many years to come. This is the essence of the "dynamic ecology" that is emphasized in most American textbooks and research papers. It was the ecology and ecological plant geography that I was taught when I went to college and graduate school. Most of the ecologists I knew when I was in school either had studied under Cowles or under his earlier students. Most of the current crop of American teachers in ecology and geographic botany are in the same line of ideological descent. It is now so deeply entrenched in our educational programs that children get it from the first grade on.

The theory has several characteristics that account for its popularity. First, it is eminently teachable. It has a kind of internal logic that is easy to understand and use. It allows people to make predictions about what will happen to the vegetation in a given area if it can remain undisturbed. Once the successional stages have been worked out, and if you know or think you know what the climax is for your region, you plug in your data, turn the crank (nowadays you switch on the computer), and out comes the answer to where you are in the successional process. Foresters and conservationists love it, because it will run backward as well as forward. The supposed climaxes for most of the country are widely regarded as already known. Because Americans are believed to have pretty well devastated their country, we need only look backward through the system to see what we have lost and what we have to do to get it back.

Another attractive thing about the theory was that it had an abundance of words that were peculiar to it and sounded as though they meant something. When Clements elaborated it he invented the words to go with it, so that there was a ready-made jargon with which to talk or write about it as obscurely as desired.

Throughout this period there were a few voices crying in the wilderness, but there were very few, and not many people heard them. For some reason not entirely clear, zoogeographers and animal ecologists were not enthusiastic. Clements had a few supporters in Britain, Europe, South Africa, and in some

parts of the tropics, but with a few exceptions, only parts of his theory were accepted overseas. The whole theory had some fundamental weaknesses in its foundations, which were, in fact, merely assumptions. The plant association, or community, which replaced the species as the basic unit of study, was not definable in space with any degree of precision. It was nearly always fuzzy at the borders where it overlapped its neighbors. Clements had a lovely word for this overlap—it was the “ecotone” between communities. In many of the commonest types of vegetation, such as upland forests, one had to be careful in his mapping lest he end up with more territory in ecotones than in communities. H. A. Gleason, one of those voices in the wilderness, saw this early in the development of the theory and said so. He made another devastating remark at the same time. He said that because the plant association could not be defined in space, neither could it be in time. This seriously questioned the whole idea of succession. Clements merely went on describing associations as though they were real organic units. This was his “organismic” concept of the association, in which he endowed it with a life of its own, from birth to maturity, to senility and death when it was replaced by the next stage in the succession.

The idea of natural succession and climax have turned out to be especially vulnerable. That successions occur seems unquestionable. Anyone who has a garden or a farm for a few years knows this. They start with weeds, but if the gardener is solvent, and has any pride, he doesn't let them get very far. Many natural successions, particularly those involving forest trees, take a long time to develop. This might run into several centuries. Ecologists began describing forest successions in this country only 60 or 70 years ago. One has the right to ask how they did it. A favorite thesis subject for graduate students in this country for many years was on the filling of shallow ponds and lakes by vegetation growing outward from the margins. The concentric zones that appeared in this vegetation were of different species content and were considered to be natural communities. It was believed that the accumulation of humus and other detritus in the outermost community so changed the habitat that the next community to landward would invade it, while the outermost would move farther out. This would go on in all the zones, and the surrounding mesophytic vegetation, usually trees, would also advance. The student then made a nice successional diagram (I have made many of them) showing how the pond or lake would eventually be filled and covered by the climax community. Cowles set the general pattern for this along the rivers near Chicago. How were all these things done? By a simple device that should have been detected and squelched long before it was. It was the substitution of space for time on some gradient like that of moisture, and it was assumed that one zone must be developing into another. Who could say they were not? No one, unless he could sit with a notebook and watch for a century or so. My personal experience leads me to think that most of the successions worked out in this way were spurious. I know that mine are.

The idea of the “climax community” has also come in for a great deal of criticism. I think I can best discuss this in terms of a specific case. The climax

vegetation, as I said earlier, came as a result of a long-term succession of communities beginning with invasion of bare ground by groups of "pioneer" species which did not reproduce themselves on the same ground. Rather they were superseded by the invasion of another community that profited by changes in the habitat caused by the life and death of the pioneers. This process of change was believed to go on until a final community would appear and remain essentially unchanged until some major climatic event occurred. In forest successions at least, the process itself made mandatory certain characteristics for the final or climax stage. First, it had to be made up of forest tree species that were able to reproduce themselves on their own ground. Seeds that fell from the mature trees had to be able to germinate and grow up successfully under the shade and in root and nutrient competition with their parents. In foresters' terms they were the "tolerant" species. Second, the trees in the climax forest had to be, at any point in time, of all ages, ranging from seedling to old age. Third, in order to produce this forest climax by the successional process described, there had to be a long period of time during which the site remained relatively undisturbed. It had to be long enough to cover the life spans of not only one, but of several generations of trees. In our northeastern American forests, as well as in many others, this time period would easily extend to a millennium.

On a map of the eastern American deciduous forest climaxes, published by Dr. E. Lucy Braun in 1950, most of New England north of central Connecticut is covered by "Hemlock, White Pine, and Northern Hardwoods." The primary species in this group are hemlock, American beech, sugar maple, and yellow birch, with white pines scattered here and there. It is consistent with one of the basic requirements of the climax, because these species, with the exception of the pine, are the most tolerant of the trees we have in this region. The scattered pines were thought to be due to "accidents" such as lightning strikes or occasional violent winds that would blow down a large tree or two and open the way for the less tolerant pine to get started. At the Harvard Forest in north central Massachusetts we are well within the region of this climax. Some fleeting doubts about the validity of it began to appear among our Forest's people in the early 1930s, long before Dr. Braun's map was published. They were based on a *History of Worcester County, Massachusetts*, published in 1793 and written by one Peter Whitney, a clergyman who was born in the Town of Petersham in 1744 and spent his early life there. This is the town in which most of the Harvard Forest is situated. It is in hilly country, with relatively narrow valleys and lowlands. It was settled in 1733, only 11 years before Whitney was born. We know from our studies of land use history that the early settlers were subsistence farmers who cleared very little land because they had no external markets for farm produce. As late as 1771, 38 years after settlement and when Whitney was 27 years old, only eight or nine percent of the town's forest land had been cleared. Whatever ideas Peter Whitney had of this forest, they were certainly based almost entirely on what was there when the first settlers came.

The history was written by towns, and for each town Whitney gave a brief

description of the forests it contained. His note on Petersham is as follows: "On the high lands the growth of wood is oak, more chestnut, and a great deal of walnut of later years. In swamps and lowlands, there is birch, beech, maple, ash, elm, and hemlock." This description would do remarkably well for the present forest cover, but it is indeed far removed from that theoretical climax. It was not primarily of tolerant trees.

The hurricane of 1938 devastated vast areas of forest in New England, and greatly stimulated our studies of forest history. Young trees up to 20 or 30 feet high were not much affected, but most of the mature trees went down. We now know that there have been four hurricanes of similar proportions within the last 500 years, at intervals that are much less than the life spans of the trees. The evidence for the blowdowns was in the forests and in their soils. When a large tree is uprooted, about half of its root system is ripped up and stood on edge. A mass of soil from the A and B horizons is brought up with the roots, and then gradually falls or is washed down to form a mound of earth. There results from this an inversion of soil horizons which can be detected long afterward by a good soils man. Walter Lyford, our soil scientist at the Forest, who has been probing our soils for many years, tells me that he has never dug a pit four feet long and three feet deep without finding inverted horizons due to the uprooting of trees. Usually these have been unaccompanied by any evidence of uprooting on the surface of the ground. We conclude from this that hurricanes were prevalent in our region long before those we have surface evidence for, perhaps as long as there have been trees there.

The supposed climax forest of tolerant trees was not in our region when the first white settlers came to it, and now we cannot believe it ever was there. One of the basic requirements for its development—hundreds of years with no serious disturbance—probably has never been realized. The third requirement, that the forest should be all-aged, must also go by the board. It was noted in our forest, long before these more recent studies, that all our stands, even the oldest of them, were essentially even-aged, either completely so or by well-defined age classes. Knowing what we now do about their history we realize that they had to be even-aged because all the trees came up at about the same time after the last hurricane or after cutting.

We are left with no criteria for prediction as to what will happen in these forests in the future. There is no question that there have been biological and soil changes, for we have documented them, but whatever successions may have occurred have been fragmentary, of short duration and with unpredictable beginnings and ends. No tree appears ever to have lived out its life span. The climax, for us, has disappeared into pure speculation, as have long-term biological successions in our forests.

The controlling agent in our woods has been wind—a factor that is purely physical, entirely outside the vegetation, and immune to any biological influence. Fire is another such agency, but has not had any appreciable effect in the Harvard Forest area. However, where coniferous trees form a large part of the cover, fire wrecks the general theory of succession and climax as wind does with us. Coniferous forests, wherever found, are nearly all even-aged or

have definable age classes. They are notoriously flammable. Patches of woods in all the boreal forest region, stretching across this continent from Newfoundland to Alaska, and I suspect in those of Northern Eurasia as well, that have not been burned in the past 200 to 300 years are exceedingly rare. I do not think it possible to turn up the soil in all that region without finding charcoal. The same is true for our western mountain forests and for the conifer forests of our southeastern states. Fire has been so much a part of the natural habitat in such forests that we have no idea of what they would be like if they were not burned periodically.

Chapter II

SCALE

Our language confounds our discussion of scale, and because of the confounding we find ourselves in intellectual cul-de-sacs. A small-scale map encompasses a large area. A map of the vegetation of a continent (small scale) is of little help when one tries to understand local distributions of species. Because we tend to forget scale problems and because Raup is one of a few who have discussed them, we include his discussions.

LETTER FROM HUGH M. RAUP 1979

Though I have talked a lot about scale I have written about it only a few times. Probably the best of these is in the Greenland papers, where the organization of the cited literature is based on scale.

Raup implicitly extends the concept of scale from space to time. Here, scale is measured by disturbances. The scale of arctic vegetation, in time terms, is between freezes which injure plant roots. In New England forests this time scale is between fires, or between devastating winds. A discussion of this will be found in Chapter III, in a paper on the relation of vegetation to the instability of the site.

Raup has said that he has talked a lot about scale and written about it sparingly. Such is the case. In this section we have two additional excerpts. In a Greenland paper the literature review is organized on the basis of scale. We examine only the discussion of scale per se.

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Organized ideas on the vegetation of the whole of Greenland began with Warming. He published an account of this vegetation in 1888, and an English version appeared in 1928. When his general ideas on arctic vegetation (1909) were applied to the fjord region of Northeast Greenland most of the landscape came under the type he called “fjaeld-mark,” or “fell-field.” Lesser areas, particularly in the southern districts, were covered by “dwarf-shrub heath,” “mat-herbage,” “mat-grassland,” tundra bushland,” and a form of “low moor.” It is also possible that something resembling what he described as “moss-tundra” is found there. Because so much of the landscape is characterized by his “fell-field,” this and the relations it bears to the other types have given rise to most of the vegetational problems of the region.

Warming (1909) characterized “fell-fields” mainly by the small stature of their plants, and by the fact that the *soil is never completely covered by plants*. He said that: “The cause for the poverty in individuals does not lie in the soil itself, for this indubitably contains a sufficiency of nutritive substances and water, and could certainly produce luxuriant vegetation *were sufficient heat* supplied. Between climate and vegetation there evidently must be a certain constant relation of such a kind that no more seeds or other propagative organs germinate or develop into plants than just suffice to maintain the vegetation at the standard once established.” Further, to the controlling influence of the heat factor he stated “On *high mountains in Europe* and in *arctic countries* fell-fields prevail where the mean temperature of the warmest month is below 6°C.” He thought that at somewhat lower latitudes fell-field was “confined to unfavourable localities, while plants on more favourable sites produce a closed formation.” Presumably the reverse would also be true, and at higher latitudes, within the fell-field region, “closed formations” should be found on the “more favourable” sites. Warming rationalized the occurrence and distribution of these “favourable” and “unfavourable” sites on the basis of local water supply, snow cover, soil, slope and exposure.

The mean temperature of the warmest month at Mesters Vig is approximately 6°C (6.2° Av. for 1953-1961; cf. Washburn 1965). Although

From Hugh M. Raup 1969b. The relation of the vascular flora to some factors of site in the Mesters Vig district, Northeast Greenland. *Meddel om Grøn.* 176(5):80p.

there is considerable local variation, and a regional gradient from the outer coasts to the inner fjords, it is probable that most of the fjord region would satisfy Warming's temperature requirement for fell-field.

In this description of fell-field as vegetation in which the ground was not completely covered by plants, Warming did not define precisely what he meant by "covered." The most densely vegetated "heaths," herb-heaths and "low moors" in the Mesters Vig district, when studied carefully, did not show more than 90 percent coverage. It can be assumed that this amount is well within the range of variation allowed by Warming (1928) for "complete" coverage by vascular plants. The coverage proportion at which the vegetation becomes fell-field by his definition must also be assumed for application in the Mesters Vig district. If about 60 percent (again vascular plants) is chosen, between 60 percent and 70 percent of the land surface probably would be in fell-field, and the remainder under denser vegetation.

Another element of uncertainty is in the thin organic crusts which are prevalent at Mesters Vig. Much of their content is dead, but there are blue-green algae in them, occasional lichens, and a few living fronds of mosses and hepatics. Whether they should be included in the plant "cover," in the sense of Warming, is unknown. Because of their thin populations of living plants they have been included in "fell-field" for purposes of the present discussion. Vegetation of somewhat similar nature was described by Böcher (1933) in Southeast Greenland as of "snow-patch" origin. However it was observed at Mesters Vig emerging from the snow in early summer, simultaneously with "heaths," "low moors," and the bare soil of the "fell-field."

Warming generalized the vegetation in terms of form and communal structures. His basic units of study and mapping were not so much taxonomically defined species as physiognomic or biologically interpreted life-forms, or formations and communities made up of these forms. He generalized site factors into units that would be roughly commensurate with his major units of vegetation.

Our investigations in the Mesters Vig district have dealt with a small geographic area (about 110 sq. km). Within this space our actual detailed studies have covered much smaller areas (ranging from a fraction of one hectare to two-three hectares). These operations have required maps of large scale, and have entailed great difficulty with definitions of, and boundaries for, types of vegetation and sites. They have placed a premium upon knowledge of behaviour patterns, not only of the poorly defined vegetation types but also of the better defined taxonomic species. They have also required measurements of site factors at commensurate scales.

A major difference between the Mesters Vig studies and those begun many years ago by Warming is one of *scale*. In general, the last 60 years have seen increasing refinement in our knowledge of Greenlandic species, types of vegetation, and sites, with mapping possible at increasing scales. In the same period there has occurred a parallel increase in the specialization of the students carrying on the research. Warming appears to have kept his site and vegetation scales commensurate, but later students, with a few exceptions,

have lost this habit. A search of the literature for material useful to the Mesters Vig studies is therefore much concerned with matters of scale. Research that has brought investigations of either vegetation or site to relatively small areas, using large map scales, is more desirable than that for large areas using small scales. Such research at large scales is likely to have used, also, the more clearly definable and precisely measurable units of vegetation and site. Most useful is research in which *both* clearly definable vegetational units and environmental variables have been measured and compared *in the same areas on commensurate scales*.

By far the most immediately useful papers in the literature reviewed in this paper were published between 1931 and 1945 by the Danish botanists who worked in Northeast Greenland in the 1930s. These papers contain the basic taxonomic and geographic information on the flora, and the local arrangement of the flora to form the plant cover. Although their descriptions of sites are not entirely adequate for present needs, their voluminous and precise notes on the vegetation and its behaviour are nearly all at the species level. Therefore the majority of them are usable for analyses of site relations at large scales.

Second in order of significance to the Mesters Vig problems, useful for methodology rather than directly, are a few recent papers on the vegetation of northern and western Alaska. These studies correlate the behaviour of species with site in small areas at large commensurate scales.

Next is a series of studies in Greenland and other parts of the Arctic in which the scales used for vegetational analyses are at variance with those used for the attendant sites. In some cases detailed morphological and physiological studies of individual species were made, but the authors described the sites in such general terms that it is now impossible to place their plants in realistic habitats. Contrasting cases are mainly those in which a "community concept" of vegetation was used for analysis where the sites were described in great detail. Here the basic vegetational units were usable only at relatively small scales while the sites were being studied at large scales.

This excerpt on scale captures the essence of scale argument. It also shows how Professor Raup perceives the links between ideas and the paths areas of study follow. A review of a pessimistic book was the context for these remarks.

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Ecologists can be criticized for their persistent disregard of the significance of *scale*. It is possible that the difficulties conservationists have got into with their time scales stem from this failing. Organisms, including man, live at “microscales” in time and space, limited by their life spans and mobility. Man customarily makes detailed and often intricate short-term models of reality that are effective in guiding current operations, but they remain at “microscales.” Conservationists and ecologists commonly extrapolate these to “macroscales,” though we have not yet learned to make models on these scales without over-simplification. The simplification becomes so great that the resulting models give no guidance for further research or action. Ecologists took this course many years ago when they substituted the community for the species as a basic unit of study, and more recently when they began to emphasize the assumed natural productivity of land.

From Hugh M. Raup 1971. *The environmental revolution*, by Max Nicholson, review in *Jour. Ecol.* 59:312-316.

Chapter III

PHYSICAL DISTURBANCE OF PLANT HABITATS

A paradox is found in our thinking about vegetation. Every gardener disturbs the habitat of the plants either before or after planting. Almost everyone from Clements on has considered stability when thinking of plants (vegetation) not tended by man.

In the excerpts that follow we have Professor Raup's developing awareness and appreciation of the amount of disturbance found in wild environments.

LETTER FROM HUGH M. RAUP 1979

My papers are so full of material on disturbance that it is hard to miss. I've even talked about it as a "cataclysmic theory of vegetation." I suppose I have written about it most specifically in "Vegetation adjustment, etc.," "Vegetation and cryoplanation," the papers on the sand dunes, the Honduras manuscript, and in the Greenland papers. The last are *mainly* about disturbances of one kind or another.

It didn't register much in the first five or six years of our field work in Canada. Of course I saw the effects of fire everywhere, but didn't know enough about it to see its broader meaning. Large changes of water levels in sinkhole ponds in the Wood Buffalo Park made an impression, but they were so localized that I didn't think of them as anything but "special cases," which is really what they were. I often think, with considerable embarrassment, what I must have missed in those early years. I didn't even know that frost heave, mass wasting or patterned ground existed, or how to recognize Indian artifacts even if they were in plain sight. I must have walked over all these things hundreds of times.

As I said earlier, I couldn't make any sense of forest "types" in the Harvard Forest in the early 1930s, and realized that it must be due to human disturbance. It wasn't until 1935 that the idea began to gel, when I saw the effects of occasional high water in Lake Athabasca. It was, again, a "special case," but if the ecologists could be so wrong about it as they seemed to be, they might be wrong about a lot of other things. Then I saw how wrong Bray was on the presettlement forest of the Hudson Highlands, using straight Clements in his reconstruction. The 1938

hurricane and Peter Whitney's history of Worcester County did away with climax theory in forests that were not so easily burned as the boreal and western mountain forests.

For glacial geologists, plant geographers and ecologists a high point of the 1950s was a symposium organized by Dr. E. Lucy Braun for the Ohio Academy of Science meeting. There, Hugh Raup spoke about vegetation and cryoplanation; the following excerpt is from that paper. C. S. Denny and John Goodlett talked about their work along the glacial border in Pennsylvania. The 1950s may have been a quiet decade socially; in eastern plant geography circles it was a time of great excitement.

Your editor, fresh from graduate school, was one of the fortunate ones who attended the meeting in Columbus. Following the meeting, Dr. Braun arranged a field trip into southwestern Ohio. I shall always remember her astonishment when Raup and Denny pointed out to her a deltoid fan that was likely the result of solifluction or congeliturbation. She, in her quiet, regal manner, exclaimed she had been over the ground a number of times and had never seen the fan. That day she had a different introduction to the idea of disturbance and its influence on vegetation.

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With the ideas of dominance and succession so difficult to apply in the North, it behooves us to re-examine some of our basic premises with regard to the relations between the development of vegetation and the development of landforms. Dominance and succession are both basic attributes of vegetation in the temperate regions, and I have suggested above that they both arise from a degree of physical stability which in turn is a fundamental attribute of the land surfaces. We are entitled to ask whether there can be something wrong with the physiographic premises upon which we are basing our work in the boreal regions.

The student of landforms brought up in temperate America, when he goes into the boreal regions, sees a great variety of forms with which he is totally unfamiliar. He is apt to be as bewildered as a northern botanist who makes his first excursion into the tropics. Our physiographer has learned that it is possible for rocks to be cracked by frost. But he has never seen such active frost riving as he sees in the Arctic and Subarctic. Large boulders are commonly broken into little pieces by frost, with all the fragments lying about in the vicinity. He will see massive angular boulders lying about a central core. With heavy machinery he could put them back together to form a rock as big as a house, and he is forced to the conclusion that the frost riving he sees now is child's play to what must have occurred in the past.

He comes upon great fields of rock, called "block fields," that are composed of large boulders, many of them angular, and obviously formed by the break-up of still larger ones. No physiographic process that he has ever heard of in the temperate zone is adequate to explain them.

The land surface is marked by a multitude of terrace forms. Some of these are several feet high and many feet long. Others are tiny affairs, only a few inches high and wide. If he has the time to dig trenches through such terraces,

From Hugh M. Raup 1951c. Vegetation and cryoplanation. *Ohio Jour. Sci.* 51:105-116.

he finds that many of them are still active in formation and movement.

On more or less level surfaces he is confronted with curious polygonal arrangements of materials. The polygons may be composed of fine or coarse material, and they may vary in size from the width of his hand to many feet. On slopes he finds long stripes of loose stone trending at right angles to the contours, and on very gentle slopes he finds these stripes merging into a series of combinations with the polygonal arrangement. A surprising proportion of the stones will be found to be standing on edge. On high mountain slopes, he will see remnants of bedrock standing up above the general level-like monuments. These remnants are exfoliating actively, breaking up under the influence of frost. They have a configuration in profile which is utterly strange to him, because, although they are rapidly disintegrating, there is no talus accumulation at their bases. In fact, they are apt to show some overhang at the base. The surfaces of the gentle slopes below these monuments are strewn with rock fragments that have fallen from them, and it is obvious that the fragments are moving away downslope from the bases faster than they can accumulate.

He will be impressed by the relative insignificance of stream cutting and deposit. Floodplains are small in breadth and depth. There is very little evidence of these processes except where great glacial streams issue from the mountains. Another striking feature of the landscape is the broad rounding of slopes. The general contours of these slopes are not those that we have learned to associate with downcutting by streams.

From all of these observations, our student of landforms gets the impression that the surface materials of the land are in motion, slow motion though it may be. He must also conclude that this motion has been more active at some time in the past than it is now. He soon begins to associate most of these features with the action of frost upon the soils.

Each year in the boreal regions the ground freezes to great depths. In many parts of the Arctic and Subarctic there is perennially frozen ground beneath the surface. In fact, it is now computed that about one-fifth of the Earth's surface is underlain by perennially frozen ground (Jenness 1949). During the spring of each year the surface materials thaw out. But there is a relatively long period during which the temperature fluctuates diurnally around the freezing point. Each time the water in the soil freezes it expands; and the effective expansion is in a direction at right angles to the freezing surface. When the soil thaws again its particles fall vertically, so that if the surface has any slope, they tend to move downgrade. It is obvious that if freezing and thawing are to be effective, there must be a supply of water. One of the characteristics of freezing soil is that it can absorb and hold much more water than unfrozen soil. It has a tendency to absorb water as it freezes. Consequently many frozen soils are waterlogged so that when they thaw they are almost fluid and have a tendency to flow downslope *en masse*. This greatly enhances the rate of movement of materials.

From the standpoint of vegetation, one of the principal results of this process is instability. The soils, even under forest or heavy turf, will move,

often in masses. The result is the physical dislodgement of growing plants. This process is so widespread in arctic and subarctic lands that its effect upon vegetation is of primary significance. In thinking about the development of plant communities on such surfaces, we must become accustomed to thinking in terms of a relatively permanent physical instability of the soils.

It appears clear that the very bases upon which our concepts of dominance and primary biological succession have developed—the relative stability of surfaces—do not exist over wide areas in the boreal regions. It follows that vegetational dynamics in general for these regions must be developed upon a new conception of landform dynamics.

The study of arctic and subarctic landforms is still in its infancy, though rapid progress is now being made. The United States Geological Survey, through its Alaska Terrain and Permafrost Section, has been concentrating on the problem during the past three or four years, and we are beginning to find some order in the chaos of newly-observed facts. New aspects of the problem, however, are appearing constantly, and undescribed landforms due to frost are turning up each time a party goes into the field. There is beginning to appear, however, a concept of the molding of the landscape by the frost action. It is called “cryoplanation,” as opposed, perhaps, to peneplanation in temperate regions (Bryan 1946). Soils that owe their form and texture to frost action are now being called “congeliturbates,” and the process that forms them is called “congeliturbation.”

Some curious reversals of our commonly accepted ideas have developed. On a steep mountain slope, for instance, we are accustomed to thinking of small rocky stream channels and gullies as the most unstable plant habitats. In the Arctic, on the other hand, such stream channels, though they are very poorly represented, turn out to be the most stable habitats, for the presence of even a small running stream has a tendency to lower the water table slightly and so cut the supply of water to the surface soils immediately along its banks. The principal effect of this is to lessen the activity of frost, so that the materials along the banks of the stream actually stay in place for longer times than those on surfaces without streams.

Forests that develop on actively moving slopes are more or less unstable, depending upon the degree of slope and drainage of the soils. The mortality in such forests is high, because when masses of soil move they have a tendency to tear the root systems of the trees loose from their intimate soil contacts. If the break is not too serious the trees can recover, but many of them do not. It is not uncommon to find 25 percent of the standing trees in a forest dead. Examination of growth rings shows that the trees have been subjected to this influence repeatedly. The evidence is in sudden suppressions of growth, with subsequent gradual adjustment. Usually no two trees show the same series of suppressions, even though they may be within ten feet of each other, because the soils move in finite masses which may be only a few feet in diameter. A characteristic of these forests is the large number of leaning trees which have been tipped over by the movement of the soils.

In the region as a whole, the only soils that are capable of developing a

degree of mesophytism as we know it are those that are very well drained.

In many parts of the temperate regions where subaqueous erosion and deposit have been the rule we are accustomed to find hill slopes deeply gullied, with the surfaces modified by outcrops of bedrock that produce talus accumulations below and coves above. The deformational processes have produced extensive sorting of materials, both vertically and laterally, so that water tables are highly irregular in their relation to the surfaces. At the same time the rate of leaching and the development of soil profiles have been rendered highly variable from place to place. These are all variations in site, which are reflected in vegetational differences that appear in both vertical and horizontal arrangement.

One of the outstanding features of vegetation on slopes that are highly modified by cryoplanation processes is its lateral and vertical uniformity. Such variety as it possesses is so local and uniformly distributed that its effects are submerged in the mass. Examination of the soils on these slopes shows a very great uniformity in texture and in the position and behaviour of the water table. Although the soils may be extremely unstable physically, the instability is so evenly distributed that an aspect of uniformity in the vegetation is maintained. The processes of cryoplanation, then, seem to have a strong tendency to form relatively smooth slopes upon which the sorting of fine and coarse materials is local and of small areal extent.

It is justifiable at this point to ask whether or not these findings in the study of boreal landforms and vegetation are of any immediate use to us who are concerned with problems at or near the glacial boundary. The effects of frost action are quite obviously a function of climate, and it is entirely justifiable for us to assume that climates in front of the advancing and disappearing glaciers were intensely cold. We are justified in looking, therefore, for the effects of this climate and its attendant frost action in the soils and topography in both the glaciated regions and beyond the glacial border. We probably must also insert in our sequence of events the development of postglacial vegetation a period of time during which there must have been instability of soils and vegetation similar to that now occurring in the Arctic and Subarctic. The length of this period of time is as yet unknown.

Interpretation of our modern vegetation in terms of the periglacial climates should be approached circumspectly, and with full understanding that even in the Arctic where congeliturbation is still active and a major factor, its relation to vegetational dynamics is very imperfectly known.

I have suggested that it is necessary for us to insert in the sequence of postglacial vegetational changes a period of time during which the soils were unstable due to frost action. The cover of vegetation in this period had to be of plants capable of withstanding the instability. We have only small inklings of the floristic character of this vegetation. If we follow the classical interpretation of glacial and postglacial events we would assume that the plant cover was tundra and composed of arctic species. In this, however, we would be faced with our failure, to date, to find good evidence of an arctic tundra flora at the bases of our American peat profiles. We can get some suggestions,

perhaps, by looking at the behaviour of modern boreal flora with relation to stable and unstable soils.

The most important division in the boreal vegetation is that between forest and tundra, whether the latter be alpine or on the arctic plain. The timberline is generally regarded as a climatic phenomenon, and its fluctuations are thought to reflect climatic changes. In view of our growing knowledge of boreal soils it is possible to interpret the timberline as a zone of transition from relatively stable to relatively unstable soils, and to look upon the climate as having an indirect effect through its influence upon congeliturbation.

The white spruce, as a species, seems to cross the arctic isotherms at will. It can be found hundreds of miles north of the recognized timberline. Such northward projections, however, are on stream banks and narrow flood-plains, or on sandy outwash plains where frost action in the soil is minimal or non-existent. The timberline itself might be thought of, then, as the zone in which the spruce can survive in numbers on the uplands due to the gradual southward amelioration of the extreme instability of the tundra soils. On the other side of the timberline, whether it be southward or at lower elevations on mountain slopes, the spruce fails to survive wherever congeliturbation is unusually intense.

By 1956 Professor Raup was in a position to summarize over a quarter century of observations of vegetation. Geographically the observations were made from the arctic to the tropics.

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In this paper I shall present briefly some personal experiences in the study of vegetation. Geographically, these experiences have a wide range, from northwestern Canada and Alaska to the forests of New England, and to the tropical forests of Central America. Having described the experiences, I shall try to say what I think they mean to current thought on the nature and development of natural vegetation, and to our present conceptions of the manipulation and use of native plant life.

The first case history to be presented took place many years ago when I was beginning my first serious field work at Lake Athabaska, in northern Alberta and Saskatchewan. Lake Athabaska is about 200 miles long. Its shores are extremely varied, with shelving sandy beaches, steep rocky cliffs, and broad marshes. The shores have a variety of plant life usually arranged in some kind of zones extending from the open water offshore to the neighbouring uplands.

One of the most commonly used illustrations of plant community structure and succession is the zonation on pond and lakeshores. Water lilies and pondweeds in shallow water are gradually building up peat and catching silt and sand around their root stalks. As the muck gradually nears the surface, other plants that like this kind of place, with its peaty substratum and shallower water, gradually take the place of the water lilies. Usually these are cattails or some kind of bulrushes. A little nearer the shoreline the sedges and cattails have so changed the substratum that they cannot live there any more, and perhaps some grasses can take their place. I described these things in great detail at Lake Athabaska, showing their neat zonal arrangement and the orderly change or succession that was presumed to be going on. My wife was along collecting lichens and mosses, and she quickly found that there was a fine zonation of these plants also. It was particularly evident on vertical cliffs where different coloured lichens made horizontal bands on the rock faces above the water level. Having been taught that wherever possible one should be accurate and have actual figures and measurements, we carefully measured the heights of all the zones above the level of the lake (Raup 1928a; L. C. Raup 1930).

We went back to Lake Athabaska six years later, seeing again the things we had described, and describing many more. Then we went back a third time, nine years after our first trip. In that field season we discovered that nearly everything we had described previously had vanished completely. Sometime during the three years that had elapsed since we had last seen it, the water level in the lake had risen no less than 6.5 feet, as shown at the places we had made our careful measurements. A large part of the watershed that drains into the

From Hugh M. Raup 1957. Vegetational adjustment to the instability of the site: in *Proc. 6th Techn. Meeting, Internat. Union Conserv. Nat. & Nat. Resources, Edinburgh 1956*. 36-48. London.

lake is in the northern Rocky Mountains, where snow and weather conditions had combined to send an extraordinary amount of water into the lake in a very short time. How often this sort of thing happens we do not know with any accuracy. From talking with the oldest inhabitants, the nearest we could come to it was at intervals of 40 or 50 years.†

At Lake Athabaska, every so often, the whole system of shore vegetation is simply drowned and eliminated, and the plants have to start over again. If there is any succession at all, it is in little fragments that never make any real progress, at least in the way it is assumed that they do. The water lilies had been growing in shallow water offshore, the bulrushes and cattails in shallower water, the sedges and grasses on the wet shore itself, each of them for the simple reason that it had found for itself a place best suited to it. These simple observations could be refined to great detail; but to take the next step and say that because the different communities were growing next to each other they were developing from one into the next, would be going beyond the facts, and into pure speculation.

It can properly be asked, "There must have been evidence of such extraordinary high water on Lake Athabaska. Why didn't you see it?" The answer is, "I did see it." I described it and took pictures of it—large driftwood high on the old beaches, and undercut banks high above the existing water level. But I was so entranced with the theory of succession that I bent all these facts around so that they would fit the theory—I thought they were evidence of unusually big storms, or a gradual though permanent lowering of the lake level.

My second case will deal with some observations of tundra vegetation in northwestern America. When looked upon as a community of species the tundra is extremely variable in floristic composition and in the forms of the plants that make it up. Nearly all those who try to describe tundra communities attempt to use the familiar methods that have been worked out for temperate zone vegetation. First they try to describe the tundra communities in terms of dominants. But they quickly learn that when they have listed the primary species in a patch of tundra they have put down the names of about half the total flora of the patch, perhaps a dozen or fifteen species. For purposes of description such a method becomes hopelessly unwieldy, and defeats its own purpose. They find that tundra communities commonly do not have clearly defined dominants, but rather are apt to be miscellaneous aggregations of species growing together in what appears to be a disorganized mixture. Recourse may be had to statistical analyses of the frequencies with which species occur, but these often seem only to accentuate the randomization. If competition is present, it has not led to the dominance of any particular group of especially well-adjusted species. If our students want to find different combinations, all they have to do is move on a few feet and they are likely to find them.

†Documentation for these changes of lake level, and estimates of their frequency since 1810, have been published by Stockton and Fritts (1973).

Not being able to find dominants, they have still greater difficulty in finding successions of dominants. The seemingly disorganized patchwork of variation will not fit together in any developmental sequences with which they are familiar. With succession so poorly defined in the tundra, the idea of climax becomes almost unusable.

In the early 1930s Dr. R. F. Griggs read a short paper on "The Problem of Arctic Vegetation" at a winter meeting of the Zoological Society of America in Boston (Griggs 1934). Dr. Griggs had the same troubles with the description of tundra communities that others had had, but in his short paper he went a little further and made a simple though highly pregnant observation. He said that in the tundra the plants were acting like weeds in the garden. They seemed to be all jumbled together with the individual species giving little evidence of dominance. The arctic plants do act like weeds in their community behaviour and this has been causing much of the difficulty in the describing of the communities. Dr. Griggs did not go much beyond this, except to point out that the weed-like behaviour of the arctic plants constituted a real problem, and possibly a basic one in the study of arctic vegetation.

There exists in the alpine and arctic tundra lands one of those basic natural phenomena that loom so large and are so all-pervasive that they are apt to be missed. It is frost-heaving in the soils, and it occurs with an intensity that is beyond anything we know under temperate climates. Some of the more obvious results of it are the various kinds of patterned ground that are now being studied in detail by geomorphologists (Troll 1944; Washburn 1950). Not only are there those large manifestations, but also a vast number of small ones, down to those which affect the positions of the least mineral and organic fragment of the soil.

Frost-heaving, and mass movements of soil under the influence of frost, are so common and widespread that they seem to govern the behaviour of most of the plants (Hopkins and Sigafos 1951; Raup 1951c; Sigafos 1951, 1952). The roots of the plants are torn loose physically from their soil contacts, and only those that can stand this sort of thing can survive. The frost-heaving is so frequent that it occurs within the normal life span of all plants that live in the tundra. Consequently, no small group of species ever gets a chance to develop dominance, and no natural biological succession ever continues long enough to reach any kind of equilibrium or climax.

Dr. Griggs was more nearly right than he knew when he said that arctic plants behaved like weeds in a garden. A garden is mechanically stirred each year by cultivation. Tundra soils are stirred as effectively, if not more so, by freezing, thawing and mass movement. It is probable that some dominance and succession is to be found in the tundra. They are to be expected especially on well-drained soils such as sand and gravel. But even here the successions are apt to be only fragments, so varied locally that they cannot be arranged in any kind of patterns, in either space or time. In short, a basic characteristic of tundra vegetation is that it is essentially unstable. And we have every reason to believe that it has been able to maintain itself under these circumstances for a

long time.

The third kind of experience I shall describe took place in Honduras, in Central America. The jungle forests of this region have been for many years an enormous source of wealth, largely because of the presence in them of the so-called rare woods of commerce, such as mahogany, rosewood, primavera, balsa, and Spanish cedar. Most of these fine timber trees are now gone from areas that are accessible, and a large business concern with wide interests in the American tropics has been engaged, during the past fifteen years or so, in an elaborate reforestation programme. It has put some 10,000 acres into tree plantations, and it was only natural that it should concentrate upon the woods best known to commerce. For instance, about 4000 acres were planted to mahogany.

Wild mahogany is normally found scattered through the older jungle forests, and because these forests were assumed to be ancient and stable, or "climax," it was further assumed that mahogany plantings should be made in the forest, where this species was thought to have been able to come up naturally. Therefore lanes were cut, or rather, "tunnels," through the jungle, and vigorous mahogany nursery stock was set out and carefully protected. These plants refused to grow; they either died or merely languished. To save any of them the forest canopy had to be destroyed by one means or another. At the same time, mahogany that had been planted in the open grew rapidly.

A good many years ago an able naturalist, Dr. Paul C. Standley of the Field Museum of Natural History, made a careful survey of what is known as the Lancetilla Valley in northern Honduras (Standley 1931). On the high slopes bordering this valley there are some old woods which have been rather carefully preserved because they cover a watershed district serving one of the nearby coastal towns. This forest has long been regarded as very old and stable. It is composed of gigantic jungle trees and a tangle of lesser vegetation, the whole thing illustrating what has been described as the climax. Ranging through this forest, and high on the slopes, Standley found some trees that were practically unknown in Central America outside of cultivation. A corresponding experience would be to find an old pear tree growing in a mixed forest on a New England hillside. He found not only the trees, but by scratching around in the soils he turned up pieces of old pottery.

Another curious fact that can be observed rather easily by anyone who knows a few of the common tropical trees is that in abandoned fields, species that make the rare woods of commerce are apt to seed in naturally. First there appears a dense tangle of shrubs, woody vines, and short-lived trees. Then, scattered here and there, appear individual mahoganies and Spanish cedars. They come into the old fields, along with a lot of other things, much like white pine comes into some New England fields.

Most of the country people in the tropics live by a peculiar kind of agriculture. It is a kind that is widespread throughout both the Old and New World tropics, and is caused by the fact that most of the upland soils are extremely poor in mineral nutrients due to excessive leaching by long-continued heavy rainfall. Agriculture under these conditions becomes a rather

temporary affair, semi-nomadic in character. A farmer will cut and burn two or three acres of jungle and immediately plant a crop of corn. But very soon, perhaps within five or ten years from the time he makes his first clearing, he has to abandon that field and clear another patch of jungle.

This sort of thing has been going on for generations of farmers. All one has to do to realize its extent is to look at any landscape in the hill country of Central America. The view shows a patchwork of little farms in all stages of use and abandonment. This is not a modern phenomenon, but is as old as tropical agriculture. It is in the land of the ancient Mayan civilizations of Central America. We know that they were far advanced, with highly developed cultures, at least two thousand years ago; and there is evidence that populations were considerably greater than they are now (Morley 1946).

A traveller from the temperate zone has no difficulty in applying the theory of the climax to the high jungle. To his eyes it seems to satisfy the basic requirements of the climax. In spite of great local variation in its composition, as a whole it seems to be remarkably uniform over large areas, clothing hill and valley alike with its dense tangle of trees and climbing vines. Its individual trees are so large that the traveller from the north can hardly conceive of their not being of great age. With all this comes the impression of stability and timelessness. In the situations I have described, however, the facts all point in the other direction, and the supposed ancient jungle emerges as an "old-field forest," the major trees of which came in as pioneers on abandoned agricultural land.

I have no idea how widely this interpretation can be used in tropical America, but I believe it to be prevalent in western Honduras. It should be given some attention in all attempts to work out developmental trends in tropical vegetation.

For my fourth and last case study I come to the forests of New England. There are in New England some fifty commercially valuable or potentially valuable kinds of forest trees. They occur in a great variety of combinations. The Society of American Foresters, in its published descriptions of existing forest cover types, mentions between 30 and 40 of these combinations of species in the New England area alone, and many more could be described (Society of American Foresters 1940). Because the combinations, or communities, are difficult to define, they are even more difficult to map. A realistic map of them would have to be made on a very large scale.

Several generalized maps of New England forests have been attempted, but they do not begin to do justice to the situation (Society of American Foresters 1956). It is possible to find, in any one of the types commonly outlined, not only wide variations in its own composition, but also representatives of its neighbours. About the best we can say is that we have an almost kaleidoscopic patchwork of species combinations scattered over our landscape, and that going from south to north we pass by almost imperceptible changes from the oak and hickory forests of southern Connecticut to the mixture of spruce, fir, maple, beech, and birch in northern Maine.

There is some sense to the local distribution of certain types. Every

experienced woodsman knows that in central Massachusetts spruce is likely to be found in bogs, and that red maple and yellow birch grow most abundantly in upland swales. He knows that he can expect to find pine in abundance on excessively drained sands and gravels. But these situations are more or less marginal. On the upland loam soils, where he finds the greatest variety of trees and the best growth, there is more of mystery. He knows there are differences between upper and lower slopes, between north- and south-facing slopes, or patchwise without any apparent relation to slope, exposure, or to anything he knows about the soil. He knows that certain readjustments occur following cutting, fire, or clearing, but he quickly learns what they are and what kinds of trees are involved.

The commonest explanation for the extreme variability in these forests is the destructive activity of European settlers in the 17th and 18th centuries. Between 1620 and the second quarter of the 19th century about 40 percent of the land surface in New England was cleared for agriculture. The most extensive clearing was in the three southern states, in the non-mountainous parts of New Hampshire and Vermont, and in the southern third of Maine. Land that was not cleared was cut over for lumber and pulp, and much of it subsequently burned over. All of the pre-colonial forest has long since been gone from the three southern states, and only isolated and inaccessible fragments of it remain in the three northern ones.

Following prevalent American theory, it has been assumed that the pre-colonial forest was in a "climax" condition—that it had achieved a sort of "dynamic equilibrium" over vast areas as a result of millennia of natural development *in situ*. A certain amount of variation has been allowed in it due to major differences in soils and terrain—"edaphic climaxes" or "pre-climaxes" (Nichols 1935). Shorn of all its technical verbiage, the theory holds that the forest as we know it now is not in a truly "natural" condition, but that each battered part of it is in some temporary, passing stage of slow development toward the more stable and uniform condition that preceded its destruction by the white man. This idea is deeply entrenched in our current ecological and silvicultural thinking. Even the nature of the climax is reconstructed, by invoking the theory of tolerance; from it we learn that hemlock and the so-called "northern hardwoods" (beech, sugar maple and yellow birch) made up the climax in most of New England north of Connecticut and Rhode Island (Braun 1950).

But when we apply some simple historical methods and find out what the pre-colonial forest actually was, we find that it was by no means in equilibrium, at least not within the carefully worked out concept of what the equilibrium or "climax" should be. In fact, the more we learn about it the more evident it becomes that the old forest was not far different from what we have now. There is every reason to believe that it was nearly as variable over the landscape as it is now, and we believe that its species composition has changed but little. Probably there were more large trees in certain habitats than we now have, though we believe that the number of very old trees was never great. Further, such evidence as we have indicates that individual stands

of trees in the pre-colonial forest were essentially even-aged or contained well-defined age-classes, and that the ages varied greatly from one stand to the next (Cline and Spurr 1942). Evidence for these things comes from a variety of sources—early descriptions, land-use studies by which old wood lots can be identified, and, most important, studies in the woods themselves.

The complexity of our forests has, of course, gone through a period of intensification due to land use. Historical studies in the “town” of Petersham, Massachusetts, in which the Harvard Forest is situated, show that most of the pre-colonial forest remained essentially intact until the last decade of the 18th century (Fisher 1933; Cline and Lutz 1947; Raup and Carlson 1941b). Clearing for agriculture then went forward rapidly, made economically feasible by the establishment of inland industrial communities. By 1830 between 60 and 70 percent of the land surface in the “town” was devoid of forest. Agriculture failed rather suddenly during the third quarter of the 19th century, due in large measure to the extension of a transportation system into the rich farm lands of the American middle west. The result in Petersham, as in most of agricultural New England, was wholesale land abandonment. Abandoned fields in our part of the New England usually acquire naturally-seeded stands of white pine, for which seed sources are nearly always at hand. The pine becomes commercially mature in 50 to 60 years. When cut over, as nearly all of it has been in the last half-century, this land does not reseed itself to pine, but is quickly covered by native deciduous trees which have already established themselves under the maturing pine. Analogous old-field sequences, with different timing and different species of trees, are definable in other parts of New England.

Within the matrix of the prevailing deciduous forest cover of much of southern New England, therefore, are stands of trees growing side by side that have had entirely different histories in the last 200 years. One group contains the old woodlots that were maintained as such throughout the agricultural period. Because of the sprouting habits of our deciduous trees, and in spite of repeated grazing and cutting in these woodlots, we have abundant evidence that their composition has not changed a great deal since colonial times. Immediately adjacent are lands that were cleared in the middle or late 1700s, remained in pasture for perhaps a century, produced a crop of naturally seeded white pine, and are now back in deciduous forest which also has appeared naturally. A striking fact is that unless there are accompanying and sharply defined differences in soil or terrain in the present stands, though they differ so greatly in history, are scarcely distinguishable from one another in structure and species composition.

It seems clear that the present complex pattern of species distribution and frequency, even though it has to be interpreted locally in terms of land-use history, is of long standing and must be pushed far back into pre-colonial time. I propose that we should not be diverted from the solid core of fact derived from what we can see now in the New England forests, with all their complicated diversity.

It has occurred to me that the nature and distribution of forest types in New

England bears a fascinating resemblance to another kind of vegetation that I have described here—the arctic tundra. As in the tundra, we have a huge number of species-combinations scattered patchwise over the landscape. There is no wide expression or continuity of dominance, and our attempts to apply the theories of succession and climax become purely speculative in the face of the hard, historical realities.

In the tundra we have what appears to be a pretty good reason for the lack of organization and continuity in the vegetation. It is the frequent physical disturbance of the site by frost action. Do we have any disturbing influences in our New England forests that could produce the seemingly disorganized patchwork of types and age-classes which now exists and apparently was the rule in the pre-colonial forests as well? In the tundra the disturbance comes every year, or oftener, but there we are dealing with small unit areas and relatively short-lived plants. Suppose we project this to another scale in space and time, with large areas, and with large plants whose life spans reach from 200 to 400 years. Can we find evidence of disturbance in New England that would be effective on this scale?

We have no frost action in temperate zone soils that is severe enough to disturb forest vegetation. In some places soil erosion by running water creates havoc, but there are vast areas in northeastern America where erosion is and always has been insignificant. Archaeologists who have studied the problem intensively tell me that the New England aborigines were for the most part nomadic hunters. Only in what are now our three southern states was agriculture developed to any extent. Even there it was highly localized, and never extensive. It seems impossible that clearing of the forest for agriculture by the pre-colonial Indians could ever have caused the tangled pattern of forests that existed throughout New England.

Pests and diseases must always have ravaged the forests, but there is a strong argument against their ever having been a major disturbing influence. Evidence in the forests proves that the disturbing agencies, whatever they were, affected all kinds of trees at the same time. Pests and diseases, on the other hand, are always more or less selective, destroying certain species and leaving their immediate neighbours intact.

Wherever coniferous trees make up a considerable portion of the forest, fire is destructive and relatively frequent. Most of the great coniferous forest belt that reaches from northern New England to Alaska has been burned repeatedly, and nearly every stand in it is in some stage of rehabilitation following fire. So far as we now know, there were Indians living in this forest throughout most or all of post-glacial time. Bush Indians whom I have known and travelled with seem to have no particular dread of fire. They do not put out their camp fires; nor, I suspect, did their ancestors. In fact, I believe that with some historical research we could prove that there were many more forest fires in pre-colonial time than after Europeans arrived on our continent.

I shall not explore further the disturbing effects of fire, though I think they are of major significance in accounting for the vegetational patterns in the spruce-fir country. But there are large areas in New England that seem never

to have suffered much from fire. In central Massachusetts we can find little or no evidence of general or widespread fires in the recent or distant past.

The great hurricane of September 1938 was enormously destructive to forests in New England, laying waste thousands of square miles of our woodland (Brooks 1939). Most of the damage was done by the uprooting of the trees. In the nature of things, most of the trees that went down were comparatively large, with well-developed root systems. Each root system that was dislodged brought up with it a mass of earth, ranging in volume from one to many cubic yards. Where this mass came out of the ground there is a pit from one to two feet deep. Some of the uplifted soil has rolled back into the pit; but most of it, with the gradual rotting away of the root system, is being dumped in a mound-shaped mass at the side of the pit and downwind from it. Large areas of land in the path of the hurricane are now copiously sprinkled with these mounds and pits in various stages of development. The mounds, as they gradually form by the disintegration of the root systems, have a characteristic outline and structure. They have buried the pre-hurricane forest floor on which they fell, and this forest floor remains under them as a well-defined humus layer. The pits have a tendency to collect dead leaves which become waterlogged in fall and spring, to form a rather deep layer of unincorporated humus (Lutz 1940; Griswold and Lutz 1939).

The hurricane of 1938 was no respecter of species. It destroyed all kinds of trees at the same time, in some places blowing down whole forests, and in others leaving only fractions of them standing, either as individual trees or small groups. Thus our stage is set for the development of even-aged stands, or of stands composed of well-defined age-classes. The fickle behaviour of the wind has given us irregular or patchwork distribution of the damage and of the developing age-classes. Thus the hurricane has left us forest patterns that have some of the major characteristics of the pre-colonial patterns, particularly the even-aged stands that do not seem to be placeable in theoretical sequences of development. Even though it came as a completely unexpected catastrophe, we now know that this hurricane was preceded by others fully as severe (Perley 1891). Perhaps such winds have furnished the major disturbing agency for which we have been looking.

Having learned to see the mounds and pits in process of formation, we now realize that we have been walking over old ones on the forest floor for years without knowing what they were. A little digging in the old ones exposes the same structures that we see in those formed in 1938 (Goodlett 1954; Stephens 1955a&b). The pits have thick humus layers, the mounds sometimes show ancient buried soil horizons, and we commonly find in the mounds themselves remains of the trees that made them. The mounds are especially evident on cleared land that has not been stirred by ploughing. Cultivation easily obliterates them. One of the best demonstrations we have of them is in old trees that are perched on stilt-like roots. These trees grew from seed germinated on the tops of mounds when the latter were fresh, with soil held high in the air by the root systems that were torn up. Roots from the new seedlings penetrated these masses of earth, taking, in the aggregate, the

somewhat flattened pyramidal form of the masses through which they grew. Later the upper parts of the mounds were washed away, leaving the roots exposed, often with stones and boulders locked among them.

Again, having learned to recognize them, we have found the mounds nearly everywhere we have looked in the forests of eastern North America. In many places it is almost impossible to walk through a forest without climbing over them. A large percentage of the major trees in any given stand of old woods are found to be growing on the mounds. Almost never do we find them growing in the pits.

At the Harvard Forest Dr. Earl P. Stephens has been investigating the mounds and pits in some detail (Stephens 1955a&b). Much of what I am presenting here is derived from his work. We find the mounds there in great numbers, and they now appear to fall into several well-defined age-classes. Some formed in 1938 overlie others formed many years earlier, and these in turn overlie still others of greater age. Many of them we can date with great accuracy by counting the growth rings of trees growing on them. One of the most prominent age-classes in our woods dates from a major blowdown that we know to have occurred in 1815 (Perley 1891). We can document, in all, four major hurricanes in the last 500 years.

Here is a source of instability that seems to have been effective throughout our region. Not only have the forests been destroyed or decimated, but also it seems clear that our soils have been physically disturbed to depths considerably greater than our ploughs have ever reached. The extent and intensity of the disturbances are, of course, extremely variable locally due to the vagaries of the wind, and regionally due to the regional distribution of the storms.

In the Arctic the physical disturbance of the vegetation and its habitat is due to frost action, and occurs frequently, even annually or several times within one year. In southern New England it appears to be due to wind, and occurs every century or so. In northern New England and eastern Canada physical instability due to windthrow is probably less frequent than farther south, but fire has a relatively larger effect. All of these disturbing influences are sufficient to curb the development of dominance, and to halt theoretical natural successions long before they approach climaxes. In both the tundra and the forest they are frequent enough to be within the life spans of individual plants, whether the latter be tundra herbs or forest trees.

It is quite possible that the apparent dominance we see in our older, more mature forests has been arrived at, not through any intricate biological competition over a long period of time, but rather because certain trees were able to germinate and grow quickly on mounds of fresh mineral soil formed by the uprooting of their predecessors. Whether they are tolerant or intolerant seems to be of little consequence. Nor is there any implication that the plant community they form is a kind of organism in itself, with a lifespan involving youth, maturity, or decadence.

We know that there are forest successions in New England, for we have documented them thoroughly in our studies of sequences on abandoned farm

land. But again allowing for differences in map and time scales, and considering the poor expression of dominance and climax, it looks as though these forest successions, even though a hundred years in length, are merely fragments like those we find in the tundra.

I have described four cases in which the ideological tools with which I went into the field turned out to be entirely inadequate, or at least so dull and cumbersome that they required more time and energy for repair and adjustment than for use. These tools are embodied mainly in the ideas of the plant community as a more or less finite natural body, developing dominants within itself through competition; natural biological succession among dominants and communities to form well-defined and predictable sequences; natural succession culminating in climax, or dynamic equilibrium, which is thought to remain relatively stable until the climate is altered. I could add many similar cases from my own experience, and I am sure that still more can be gleaned from the experience of other students.

Among the cases described, one aspect is common to all, and I suggest that it has fundamental significance. The ideas of community structure and the expression of dominance, that of biological succession, and finally that of climax, are based largely upon the assumption of long-term stability in the physical habitat. Remove this assumption and the entire theoretical structure becomes a shambles. This is precisely what has happened in all of the cases. In the tundra the disturbing agent is frost in the soil. In the New England forests, both before and after the coming of Europeans, it has been fire and windthrow. In Central America man himself seems to have been a singularly efficient disturber of the tropical forests for at least two millennia. In the little shore communities at Lake Athabaska merely a periodic high water level in the lake was sufficient to undo the theoretical sequence of events. In all of these cases the disturbances have been so frequent and so generally effective that the expected "climaxes," or "equilibria," recede into pure speculation. Natural successions either do not occur at all or are limited to such incomplete fragments as can be accomplished between upheavals.

When I look at these botanical phenomena naïvely, without benefit of preconceived notions derived from projections of theory beyond the facts, I see the plant community as a relatively loose aggregation of species, visible in the landscape, but not precisely definable in space or time. This is the "individualistic" concept of the plant association propounded by Gleason many years ago (Gleason 1926). I see the community, not as the product of long-term, slow development in a relatively stable physical habitat, but rather as the product of repeated major disturbances by factors largely external to the vegetation. I must think of such disturbances, not as unusual departures from the normal, but as a part of the normal itself.

Such fragments of order as I can see in the changes that occur are then looked upon merely as readjustments within existing patterns. Many of these patterns, even local ones, and even though they may be poorly defined, seem to be remarkably persistent. The species of which they are made seem capable of rehabilitating themselves against devastating odds. When the vegetation is

looked upon in this light, its basic unit for study becomes the species or one of the racial subdivisions of the species. Basic plant geography becomes floristic, and basic ecology is the "autecology" of the species. The last is merely sound morphology and physiology applied to the living plant in its natural habitat.

I do not know how far these ideas can be carried beyond my own experience, but I propose that they should be tested elsewhere. There is some evidence that they are widely applicable in eastern North America. Part of this evidence is direct, and comes from field observations (Goodlett 1954; Hough and Forbes 1943; Stearns 1949). More of it is circumstantial, and is derived from the ever-increasing dependence upon statistical methods for the description of communities and the changes that occur in them.

It may be that nothing we, as invading Europeans, have ever done to our eastern forests, short of their complete removal, has exceeded in sheer catastrophic upheaval what Nature herself has done to them repeatedly. There is reason to believe that the rich vigour and variety they displayed to the early colonists were being maintained through recurrent disruption of any trends they may have had toward dominance and equilibrium, and through the recurrent release and enrichment of their soils by fire and windthrow.

My knowledge of our natural range lands is not adequate for proper judgement, but I suspect that the same could be said of them. I had supposed that if stable habitats were to be found anywhere they would be in the grasslands of the Great Plains. But Professor James C. Malin of Kansas University, in a searching review of the natural history of the North American grasslands, has described a galaxy of disturbing factors that seems to have kept that vegetation in a state of flux from time immemorial (Malin 1956). To express his view he has borrowed a term from the physical sciences, and suggests that the grasslands constitute an "open system" of vegetation.

The application of such ideas in silviculture, and in game and range management, can remove a great many of the shackles that seem to restrict our thinking in these fields. Perhaps we need have far less fear of disturbing balances in soils and vegetation than we are accustomed to. This fear has served to limit many useful experiments in manipulation.

In trying to understand the vegetation I have ceased to expect it to form itself into neat communities that will fit my theoretical constructions. Likewise I do not expect it to follow theoretical sequences of change for which there is no precedent in reality. Rather, I feel the need to know the secrets of its incredible powers of recuperation and persistence in the patterns in which I find it. Greater knowledge of these powers, and better understanding of the way in which they function, should make possible a more efficient use of natural vegetation. Perhaps a long stride in this direction can be taken if the vegetation is conceived of as a complex, fluctuating system wherein there is endless, essentially indeterminate change, and wherein capacity for readjustment, rather than extreme vulnerability, is given primary emphasis.

Raup has said that his papers are full of discussions of disturbance. Such is the case. We have already seen some of the arguments that are in this paper. It is included to show that assumptions accepted as fact can have long-term, significant influences on actual operations.

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The stated plans for research and operations at Black Rock Forest were based on a series of interlocking assumptions. These assumptions were integral parts of the American ecological theory and conservation thought of the time. They were not even mentioned in *Bulletin 1* (of the Black Rock Forest [Tryon 1930]) because they were generally accepted as truisms or sound guiding principles.

The first basic assumption was that there actually had been a more productive forest on this land prior to settlement. Embedded in this assumption was the concept of the “forest primeval,” which has played a highly significant role in all of American conservation thought. The second assumption was that this former productive forest had been destroyed, devastated and debased by western Europeans after they came to America in the 17th century. Then came the assumption of the biological and economic feasibility of the rehabilitation of this forest under sustained-yield management. This was a cornerstone of what Hays (1959) has called the “gospel of efficiency” upon which American forest conservation was founded. Sustained yield rested in turn upon four other assumptions which I shall discuss later.

Because so much of American theory and concept in forest ecology and conservation has rested upon these assumptions, I shall examine them in the light of our present knowledge, using our two experimental forests as illustrative case histories.

THE ASSUMPTION OF THE PRE-SETTLEMENT FOREST

The author of *Bulletin 1* had found a description of the pre-settlement forest of the Hudson Highlands. This description came from a paper published in 1915 by W.L. Bray on “The development of the vegetation of New York State.”

Bray believed “that New York was found to be a great forest region; that a vast blanket of humus material had been spread over the land, hill-top as well as valley; that upon bare rock, great boulders . . . as well as broad rock surfaces, a matrix of organically rich soil had been built up so that forest trees grew upon it . . .” He conceived that this forest had been produced by a long period of successional and soil development, *in situ*, and that “it had in large measure reached a stage of stability or equilibrium in which a certain permanency of forest type is maintained . . .” He called this stage the “climax.”

He wrote further that “Under present conditions — i.e., through the activities of human agency — a great deal of the . . . Hudson Highlands . . .

From Hugh M. Raup 1964b. Some problems in ecological theory and their relation to conservation. *Jour. Ecol.* 52(suppl.): 19-28.

[has] been thrust back into the earlier stages of vegetation history. This has been brought about largely through the destruction of the humus blanket or organic cover built up by the vegetation." He went on to say that "despite the prevalence of xerophytic habitats, the action of vegetation had, by the beginning of the era of cultural interference, brought almost the whole of this territory into a condition of moderately constant water supply and of heavy, large growth vegetation if not of climax forest." To account for the existing condition of the Highland forests he proposed "that the protective effects of forest cover — the organic soil blanket — have been so far degraded that the vegetation shows an undesirably strong tendency toward xerophytism."

Here, then, was the basic ecological data used to rationalize the research and operating plans for the Black Rock Forest. An ancient, rich, more productive forest had been present when the settlers came. Its rehabilitation was a major aim of the institution for many years.

It occurred to me when I began some studies at the Black Rock Forest in 1936 (Raup 1938), that if exploitation and fire had altered the woods to so great an extent, the local geographic boundaries of compositional types ought to show a certain amount of coincidence with the outlines of felled or burned areas. Further, I thought there ought to be some physical evidence of the erosion and deposition of humus and mineral soil called for by the assumption. On the contrary, the type boundaries tended to cross the old boundaries of cutting and fire areas at random. Careful studies of humus soils in deep, cup-like valleys gave no evidence that they had ever been augmented by additions from above (Scholz 1931). The mineral soils on the steep upper slopes showed no signs of accelerated erosion except in a few places where wagon roads were made at right angles to the contours (Denny 1938). Individual old trees ranging in age up to 300 years were found throughout the forest, on all kinds of sites, from the tall, straight stands of the lower slopes to the bush-like stands of the hilltops. Wherever found they matched the species and growth forms around them, thus suggesting that neither the types nor the sites had changed much during their lifetimes.

Then I found the earliest description of the Hudson Highlands we have, written by Robert Juet, mate on Hendrik Hudson's discovery ship, the *Half Moon*. While the ship was anchored for a time in what is now called Newburgh Bay, just north of the Highlands, the people aboard her could see some of the hilltops and northerly slopes that are now part of the Black Rock Forest. On Sept. 30, 1609, Juet wrote (1841), "The thirtieth was fair weather, and the wind at southeast a stiff gale between the mountains. We rode still the afternoon . . . The mountains look as if some metal or mineral were in them; for the trees that grew on them were all blasted, and some of them barren with few or no trees on them." Here is an eye-witness view of the northerly slopes and summits of the Highlands in pre-settlement time indicating that they looked about as they do now, with their bare rock, stunted forests and xerophytism.

Cases of this kind are becoming numerous in studies of American pre-settlement vegetation, but I have space for brief mention of only one other. A

“climax” forest of similar structure was described for the upland moderately drained loam soils of northern and central New England, with various forms of “physiographic climaxes” on excessively or very poorly drained soils (Nichols 1935; Braun 1950). We now know from historical studies at the Harvard Forest that this upland climax did not exist in north central Massachusetts (Stephens 1955a&b; Raup 1954, 1957). The general disposition of species and species groupings in the landscape that we now see, as well as the form and age structure which we find in our older stands (80 to 130 years), are essentially those found by the first settlers who came to our area in the second quarter of the 18th century.

THE ASSUMPTION OF FOREST DEVASTATION

The pre-settlement, rich, productive forest described with such apparent authenticity by Bray for the Hudson Highlands had lost most of its significance as a base upon which to plan the research of the Black Rock Forest. The pre-colonial woodland reconstructed for the lands of the Harvard Forest in Massachusetts also proved useless for realistic management. I hardly need say that the collapse of these reconstructions forced a reassessment of the assumption of devastation by invading Europeans in the 17th and 18th centuries, for the essential features of the devastation were already there when the first settlers arrived. Rehabilitation of the forests, in the sense formerly used, ceased to be a major aim of management. Rather, the datum for research and development became the existing forests.

SOME PROBLEMS IN ECOLOGICAL THEORY

Thus far I have defined some specific instances of the failure of ecological theory to function realistically when applied to the management of forests. It is proper that we should look critically at this body of theory before going on to the concept of sustained yield.

American ecology, though it was built upon the physiological ecology and plant geography of Warming and Schimper, was turned very early into studies of vegetational dynamics by Cowles and Clements, its principal founders. Cowles, greatly influenced as a young botanist at the turn of the century by the work of Davis, Salisbury and Chamberlain in the burgeoning field of geomorphology, quickly developed his “physiographic ecology.” This involved processes of interrelated geomorphic and biologic change, but with time intervals of physical habitat stability during which long-term successions among communities of plants could develop. Some of the successions had long-lived trees in them, and beginning with pioneers on newly-formed ground, went on to relatively stable associations (climaxes) that would last until major physiographic or climatic changes slowly altered them. Clements greatly elaborated these ideas, but made no change in the essential theory. Both men emphasized the community, almost exclusively, as the basic unit for the study of vegetation.

With their ideas of community, succession and climax, supported as they were in a widely accepted physiographic framework, our plant ecologists had a formidable analytical tool. It was internally logical, and eminently teachable. The assumption was made that nearly every stand of vegetation was in some stage of development — from something that it had been to something that it was becoming. Time, in potentially large units, was built into the assumption through the concept of slow physiographic and climatic changes that permitted long periods of relative stability in the site. At the beginning of the 20th century there was very little vegetation left on our continent which had not felt the hand of invading western European man, or was thought to have felt it. From this it could be further assumed that the white man's disturbances of the vegetation were traumatic, and the first major ones that had occurred in a very long time, perhaps in millennia.

By the free use of analogy and inference, and the arrangement of communities on gradients of varying mesophytism, long-term predictions of what each stand would become were rather easily made. A curious property of this engine of analysis was that it would run backwards as well as forwards. Because for any given region there was, *a priori*, a climax, and because this climax was self-perpetuating, its species had to be those capable of regeneration that would produce the climax. In the case of forest these were the "tolerant" ones. Such a forest would by definition be a very old one, all-aged, and it would, in the north temperate regions, have a heavy ground cover of humus. The heavy, productive forest that was described for the Hudson Highlands in pre-settlement time was so constructed simply by projecting the theory backwards.

Plant successions are thoroughly documented, in vegetation that has been naturally or artificially disturbed. But I believe I am correct in saying that wherever old American forests dating back to pre-settlement time have been studied historically they have failed to satisfy the requirements of the self-perpetuating "climax." One of the most important of these requirements is that the trees shall be all-aged. However, a universal feature of our old forests is that they are even-aged or have one or more well-defined age-classes in them. This phenomenon is known in so many parts of the continent, and in so many types of forest, that we cannot ignore it. We know of no way to account for it other than by the occurrence in pre-settlement time of disturbances that destroyed or decimated whole forest stands.

Real evidence for these pre-colonial disturbances is now accumulating. In much of eastern United States and eastern Canada wind has been a major disturbing factor (Stephens 1955a&b; Goodlett 1954; Raup 1954; Denny and Goodlett 1956). Its importance in the northwest coastal region is indicated by the forest destruction resulting from the great storm of the 12 October 1962. Wherever coniferous trees form a large part of the North American forests, fire has been the principal cause of disturbance (Lutz 1956, 1959). Malin (1956) has described the influences that kept our grasslands in a disturbed state for countless years before the coming of the fur traders and settlers.

Thus there was fundamental instability in the site; and here at the base of

our ecological theory was a serious flaw, for many sites were assumed to remain relatively stable over long periods of time. The prevalence of even-aging by stands or age-classes in the pre-settlement forests indicates that the frequency of the disturbances has been great enough to preclude all but fragmentary successions whose dimensions have been indeterminate. Furthermore, the proportional species content and basic structure of the vegetation of an area at any point in time has been more likely the product of the last major disturbance than of necessary relationships within a community.

I propose that the vegetation under these circumstances be conceived of as an open system, and that its behaviour is a function of the behaviour of the species or ecotypes that were available to it as it emerged from the last major disturbance of its habitat. Our understanding of it will depend upon our knowledge and interpretation of the history, geographic distribution and tolerance of the species, projected against site complexes in which we can see some order along gradients in space at points in time. Understanding of its behaviour over time, as well as much of its present condition, will depend upon how well we can analyze such indeterminate fragments of development as we can see projected against the uncalibrated uncertainty of the site as a whole.

Professor Raup began writing about disturbance over a quarter century ago. His most recent discussion of disturbance came at a symposium at the Field Museum in Chicago in 1980. The very fact that he was asked to speak at the symposium suggests, as does a perusal of paper titles in recent issues of ecological journals, that his early recognition of the importance of disturbance in plant geography and ecology is finally being appreciated.

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Vegetation forms a very thin rind on the surface of the earth. Parts of it, large and small, have been injured, disrupted, or destroyed by forces from outside itself. Seeing these disruptions in our foreshortened scales of space and time, we commonly think of vegetation as fragile, and the word "irreversible" has been applied to disruptions made in it. But the vegetation has lived its entire life, from its remotest ancestors, at the mercy of the forces exerted upon it by the earth below, the climate above, and by the voracious creatures it lives with. It makes us wonder how it has managed to survive.

The vegetation is made up of myriads of units we call species, each of which has its own line of descent. This in itself gives the vegetation an immense diversity in form and inheritance. Each species is made up of populations of individuals among which there is further diversification. The plants in these populations are so alike in form that we have to group them into single species. They may be genetically uniform, but most are not. They are believed to contain from one to many heritable characters called "biotypes" which have arisen through gene mutations, chromosome doubling, or by processes not yet understood. These characters are thought to be the "raw material" from which environmental relationships are made. In a freely interbreeding population they can be passed around. Groups of them called "ecotypes" are believed to be formed by genotypic responses to particular habitats within the total geographic ranges of the populations (Anderson 1936; Bradshaw 1972; Clausen et al. 1940; Hulten 1937b; Mayr 1964; Turesson 1922a&b, 1925). Evidence that these ecotypes exist has been found in every species population that has been studied intensively. For example, the Douglas fir of our western forests ranges from northwestern Mexico to northern British Columbia, and in altitude from sea level to 10,000 feet. It is estimated that its ecotypes are so many and so segregated that seed for plantations, if the latter are to be successful, cannot be moved more than one degree of latitude from its point of origin, or to a climatically equivalent altitude (Camp 1956).

I have lived for many years in a small Massachusetts town called Petersham. It was settled in 1733 by farmers who lived by a subsistence agriculture for about two generations (Raup & Carlson 1941). The land in the township was completely forested when they came except for a few ponds and wet meadows. By 1970 only about 12 to 15 percent of the forest had been cleared, but by 1850 fully 75 percent of it had been entirely eradicated. Both the population and its prosperity declined rapidly after 1850, and there was

From Hugh M. Raup 1981. Physical disturbances in the life of plants. Reprinted with permission from *Biotic crises in ecological and evolutionary time*. 39-52. Academic Press.

widespread abandonment of farms. Only about 15 percent of the land is now clear.

The presettlement forest was mainly of hardwoods such as oak, ash, maple, chestnut, birch, etc., with a small admixture of conifers such as white pine and hemlock. When the farm fields were abandoned they were naturally seeded to dense, nearly pure stands of white pine which grew to merchantable size in about 50 years. Most of it was logged off between 1900 and 1920. The pine did not reseed itself after logging, but was followed by the same species of hardwoods that the farmers had dug out by the roots a century earlier. This case can be duplicated, using different time periods and species, in most of southern and central New England and in many parts of the middle Atlantic States.

Nobody did anything to help the forest accomplish its rehabilitation after this catastrophic sequence of events. It did so by using only its own capacities. Were the events unique in the lives of the trees, merely aberrant disturbances caused by the advent of European man, or had there been analogous events in the forest's past that had preconditioned it?

The New England hurricane of 1938 was disastrous to the forest economy of the region. Whole stands of mature trees, in all mixtures of species, were destroyed at the same time. Some trees were broken midway of their trunks, but most were uprooted. The uprooting of a large tree produces a distinctive microrelief feature on the forest floor, consisting of an oval mound of loose soil with a pit-like depression beside it (Stephens 1955a, 1956). The pit collects water and dead leaves to form a mass of black semi-decayed humus. In succeeding years the relief gradually flattens out. It is easily erased by cultivation, but pasturage does not remove it.

Some 62 of these mound-and-pit pairs were found in a little less than an acre on a wooded slope in the Harvard Forest in Petersham. When dissected and compared they fell into four readily perceived age classes. The youngest were, of course, those of 1938. The next oldest were accurately dated to a hurricane on 20 September 1815, for which historical records were found. The third resulted from a major storm that occurred sometime in the first half of the 17th Century, possibly in 1635 when one was described in the Plymouth Colony. A still earlier series has been dated at sometime in the latter half of the 15th Century. In areas that show no microrelief at all, soil profiles almost invariably show traces of overturned horizons, evidence of much older wind-throws that are no longer visible on the surface.

Having learned to see and interpret the mounds and pits we have found them nearly everywhere we have looked in the forested regions of the Eastern States, southeastern Canada, westward to the western lake states and to the Ozark Plateau (Stearns 1949; Denney and Goodlett 1956; Goodlett 1954; Henry and Swan 1974). No one has yet worked out historical sequences such as we have in New England, but I have no doubt it can be done.

Some observations resulting from these studies are worthy of note in the present context. Massive disturbance has been caused by wind in the forests of eastern North America, reaching far back in time. The disturbances have

caused the prevalent even-aging found in remnants of the presettlement forests, which had long been an enigma, and they have produced a patchwise distribution of age classes due to the varying paths of storms and to the fickle behavior of the winds in local areas. At least in our part of New England it is probable that no major forest tree has ever lived out its possible life-span. The hurricane history in Petersham has told us that most of the trees seen by the early settlers had to be between 80 and 130 years old, and must have looked much like our older stands do now. Our forests were, indeed, conditioned to violent disturbance long before the coming of Europeans.

The most devastating disturbances the vegetation has had in Quaternary time were the advances and retreats of the continental glaciers. The major effect on plant life in the path of the glaciers was complete destruction. Where whole species populations were in this path the species became extinct. Many boreal and temperate zone species were left with greatly reduced and disrupted populations south of the ice border (Halliday and Brown 1943). Periglacial climates led to species combinations south of the ice that were unique and no longer exist (Davis 1969). The same can be said of soils and hydrologies. It is probable that all of the vegetation of the continent was altered to some extent during the Pleistocene. The advancing glaciers destroyed not just a few whole populations, but also large portions of the ecotypic content of a great many more, leaving the latter with limited genetic wherewithal to maintain their habitat versatility. There is a great deal of evidence that the present geographic distribution of the floras of our continent, and their behaviour with respect to local habitats, are governed large measure by what happened to their species populations during the Pleistocene.

Wherever the forests are of resinous needle-leaved trees the principal disturbing agent is fire, started by lightning or by people. The Indians used fire to drive game, or to improve the forage for game, or to produce dry wood for their camp fires. Fire seems to have been universally prevalent throughout the coniferous forest from Newfoundland to western Alaska, south in the western mountains into Mexico, and in the pine forests of our southeastern states from Texas to New Jersey. I doubt that a hole can be dug in the soil under these forests without finding charcoal. The frequency of the fires in any one locality, of course, varies widely. A jack pine forest that I studied in northwestern Saskatchewan in 1935 had been burned three times in the preceding 139 years. We do not know what the boreal forest would be like if it did not burn occasionally. A Swedish forester (Sirén 1955) studying an analogous forest in northern Finland found that where it had escaped fire for a very long time—some hundreds of years—it had deteriorated as forest and had to be burned in order to restore its productivity.

I have had limited experience in tropical forests such as grow in Central and South America, westcentral Africa, and the Indo-Malayan region. For a long time they were assumed to be relatively immune to physical disturbance, but studies in the last 30 years or so have shown them to contain seemingly haphazard patterns of tree forms, age classes and species. A recent student has

attempted to explain the distribution of species and tree forms in a tropical jungle by analyses of community and population dynamics (Hubbell 1979). He found that in order to rationalize the facts as he found them he had to insert a factor of periodic disturbance.

T. C. Whitmore (1975) from studies in the rain forests of the Far East has analyzed the growth of these forests in terms of "gap phases." The gaps are openings in the forest made by disturbances of various kinds. The phases refer to stages of tree growth in the gaps, from seedling to maturity and death.

Small gaps may be caused by the death and fall of a single large tree, with a crown 50 to 60 feet in diameter. The crown might produce a gap of about 1/10 of an acre. Lightning strikes make openings as large as 1 1/2 acres. Some gaps are made by fungal or insect infestations that may kill one or a group of several trees. Mound-and-pit microrelief from the windthrow of trees is reported as common. Large gaps of up to about 200 acres are known to have been formed by single local storms. Typhoons and tornadoes have destroyed large areas of forest as they have in our country.

Land slips occur frequently on steep slopes during periods of heavy rain. Many can be seen in the landscapes as small areas of bare ground. Soil profiles exposed in road cuts show organic horizons buried by these slips.

In tropical America clearing for agriculture has been going on for at least 7000 to 8000 years, and in Malaya for a much longer time. It has been characterized by a system of shifting agriculture brought about by the low productive capacity of most tropical soils. When a clearing is abandoned after a few years of cultivation it immediately goes back to forest. The result is a random patchwork of little farms in all stages of use and abandonment, and an equally random patchwork of even-aged forests ranging from seedling stages to maturity. Here is a source of tropical forest "gaps" that may go back to the time when man first planted crops.

When I first became aware of the meaning of disturbance to vegetation I thought that if any long-term stability were to be found it probably would be in the grasslands. Then I found the work of the Kansas historian, James C. Malin (1956) who marshalled a formidable array of disturbing influences that had made a vast mosaic of species combinations in the grasslands. The most prevalent disturbances were by fire and wind. Recurring periods of drought so reduced the plant life that the soils, particularly on the high plains, could be blown out by the winds. Much of the soil on these plains is loess, originally deposited by wind. Prevalent fires, started by lightning or by Indians, burned the vegetation and facilitated the movement of the soil. The vast herds of buffalo that roamed the plains continually over-grazed them, trampling the vegetation, breaking the fine-textured soils, and making them even more susceptible to blowing. The vegetation was also destroyed in buffalo wallows and by burrowing rodents such as prairie dogs which formed large communities that often occupied several acres.

Travelers on the plains in the early 19th century, long before the advent of white settlement, left eloquent descriptions of great dust storms that probably were larger and more frequent than after settlement. Archaeological sites

show horizons of occupation separated by thick deposits of loess.

My observations on the physical disturbance of vegetation in the arctic and alpine tundras have been made in several parts of the American Arctic, but I shall confine myself to those made in the Mesters Vig district, in King Oscar's Fjord, Northeast Greenland (Raup 1965-1971).

A major limiting factor in the life of the northeast Greenland plants is simple desiccation. There is very little precipitation during the short growing season, and the prevailing winds off the inland ice are dry. Spots that remain wet during the summer are chiefly those immediately below thawing ground or below snowdrifts which linger all summer. Most of the other physical factors deterring tundra plant life are related to the presence of permanently frozen subsoil and to frost heaving. Frost heaving and lateral thrusting are present in all of the soils, varying from almost none in dry gravels and sands to an intensity in some moist finer textured soils that precludes the growth of any plants. Heaving sets up shearing stresses in the soil that are injurious or lethal to roots or rhizomes.

If water is available during the summer to bring the medium- to fine-textured soils to their liquid limit they begin to flow, even on very gentle slopes. They gradually get far enough away from their upslope sources of water to lose their fluidity and begin to pile up. Lobate structures are formed in this way. The vegetation is torn apart and built up as a part of the barrier at the front of a lobe which may be only a few inches or as much as eight to nine feet high.

Frost heaving and thrusting have given rise to various forms of patterned ground. Sorted nets and stripes are common in the landscapes. Here the soils get sorted in the process, with coarse fragments in the borders and fines in centers. In active nets the fines usually are so violently heaved that no plants can live in them. Close to the stone borders they are more stable and a few species can survive, but if their roots get into the centers they are heaved out of the ground.

There are many other geomorphic processes in the Greenland tundra that restrict the growth of plants, but most of them are more localized in the landscape than frost heaving and mass wasting. Some of them, though they are of small areal extent, cause total destruction of the vegetation. All that I have mentioned are currently effective, but they must all be seen in another time scale. There is a great deal of rather clear evidence in northeast Greenland that the climate began to be warmer and dryer in the late 1800s or early 1900s. Clayey silt soils near the shores of the Fjord that we know to have supported broad, wet, moss-sedge meadows at that time are now nearly barren, with their soils dried to brittle hardness in summer. Large active mass-wasting structures such as I have described are now found only on the higher slopes of the mountains where they still have abundant water from melting snow and thawing ground. Equally as large or larger ones are found on the lower slopes, but they are completely stabilized by desiccation. Large sorted nets at these lower levels are also stabilized, with centers covered by vegetation. Turf hummock systems, developed on long slopes constantly

irrigated by perennial snowdrifts, show progressive desiccation and deterioration in their lower portions, suggesting a general retreat of the snowdrifts. Windblown sand from broad beaches on the seashore has polished adjacent rock faces, leaving only remnants or outlines of lichens that formerly grew on them. Heavy sea ice from the polar basin that comes down the coast in the East Greenland Current began to recede northward in the late 19th century, opening the northeastern fjord region to shipping (Koch 1945).

I have mentioned only a few of the physical disturbances that affect the vegetation but they are legion (White 1979). We have reason to think that the disturbances are not mere aberrations from some relatively stable "steady state." Rather, they are a continuing threat to the survival of the living rind that mantles the earth. They must have presented the same or analogous hazards to the remote ancestors of the present species, and our floras have been at the business of adjusting to them ever since their species first appeared.

We know all too little about how the plants have gone about this. Examples of *what* they have done are abundant, and I shall cite a few, but *how* they have accomplished them is obscure. I suspect that a large part of the answer may be in their evolution of a vast diversity among species, and a kind of "fluid" ecotypic diversity within species.

The jack and lodgepole pines, widespread in the boreal forest, do not open their cones and scatter their seed unless the cones are scorched by fire. Many of our southern pines produce thick, fire-resistant bark on their trunks. In longleaf pine there is a stage in the early growth of its seedlings when they are resistant to fire. The pitch pine, unlike most others in the genus, produces stump sprouts when a tree is killed by fire. A western variety of the white spruce, which seems to have kept its subarctic ecotypes on the foothills of the northern Rocky and Mackenzie Mountains throughout the last glaciation, appears to have spread eastward to the present timberline 2000 to 3000 years before its eastern counterpart, with its depleted ecotypes, could reach the timberline farther east. Nearly all of our many hardwood species sprout prolifically from the bases of their stumps after the trees are cut or burned. Desert species have evolved rather obvious means of living with extreme desiccation, and with windblown sand. Arctic and alpine species are geared to extremes of cold, very short growing seasons, long days, and a galaxy of lethal geomorphic processes. Every gardener knows that there is a flora of weeds, many of them with world-wide ranges (Anderson 1967). They seem to thrive on disaster, administered by sharpened sticks, or hoes, or plows, or bulldozers. They are scarcely known outside the areas disturbed by man.

In the small area of tundra that I studied in Greenland, there was an airstrip, a radio station, a mine, some housing for personnel and about ten miles of road. All this had been placed there, on an otherwise uninhabited coast, within the preceding decade. Along roadsides, at the borders of the airstrip, and around the buildings there were plants that looked and acted like weeds, but the place was so new that there were no introduced weeds of the kind I just mentioned. What we called weeds had simply moved in from the immediately adjacent tundra or had survived the disturbance in place. In my studies of the

tundra plant-habitat relations I had sorted out a group of species that could survive very little frost heaving but were able to tolerate or even thrive in the dry creep of soil on steep slopes, or burial by windblown sand, or in the erosion on the banks of small mountain streams, or in occasionally flooded sands and gravels along rivers, or in ground trampled by animals. Most of the species that were acting like weeds came from this group. I sometimes wonder whether our garden weeds were able to come out of ancient floras and take up their abode in ground stirred and trampled by man because they had been conditioned to disturbances of analogous kinds. One might suggest further, that our crop plants may have been chosen from native floras in part because they were already amenable to the kind of treatment the primitive farmers would give to them and their habitats.

It may be that we should build a new frame of reference for the study of vegetation. It should not be based entirely on its present internal structures, physiological processes and supposed communal organizations. Perhaps we should start with the inherited capacities of its species for adjustment to the lethal disturbances that come from outside agents. The frame would have a large element of randomness, but there would be no more randomness than the species have been coping with for a long time.

Chapter IV

ENVIRONMENTAL DETERMINISM

Nature or Nurture, genetics or environment, is an age-old argument. Untold numbers of experiments have shown that both are critical in making predictions about what will happen in a given site. Man persists, however, in looking to one or the other. To try to comprehend the effect of both genetics and environment simultaneously goes against the grain of a species (Homo sapiens) that has a penchant for simplicity.

In this chapter we encounter Professor Raup's arguments that we have to look at species and varieties. These, too, affect outcomes.

LETTER FROM HUGH M. RAUP 1979

Again, I'm not sure when I acquired an interest in this, though it must have been rather early. I read some "deterministic" books probably while I was still an undergraduate. Charles Shatzer introduced me to Ellen Semple's *Influences of Geographic Environment*, and probably also to Ellsworth Huntington's *Civilization and Climate*, so it must have been while I was still at Wittenberg. But at that time I was also becoming steeped in the determinism of Clements and Cowles, and didn't see that there was any problem connected with such determinism.

I suspect that consciousness of this problem came in the early 1930s when I learned what was going on in genetic studies of variation and speciation. I remember coming up at about that time with the rather oversimplified idea that at least half of the reason I found a plant growing where I did was that its parents had left it there. By this I meant that it brought with it a bunch of capacities and limitations inherited from its parents. All the local environment could do was sort out of all the plants that happened to land there the ones whose inherited ranges of tolerance allowed them to survive. The environment couldn't change those genetically fixed tolerances quickly enough to save the plant if the latter's tolerance limits didn't happen to measure up. Over a long period of time, with many generations, a species population might, out of its gene pool, or by mutation, produce plants that *could* live in that particular place.

Out of all this, and out of collecting experience, I got another idea that I have played with ever since. The theory that a species had to be adjusted to its environment always seemed to be expressed in "absolute" terms.

Survival depended upon absolute adjustment. A lot of the species I was collecting “looked” as though they weren’t particularly well adjusted. They seemed to be just hanging on. Some could even flower and produce seed. If this were true a species didn’t need to be thoroughly adjusted to survive, and there could be a range in a species’ capacity. Much of the work I did in Greenland and on the shore vegetation in northwestern Canada grew out of this idea of varying “tolerance” or “versatility.”

I suspect that the “problem” of environmental determinism “gelled” for me when I read Hartshorne’s “The Nature of Geography,” and found that the geographers had been wrestling with it for years. Semple, Huntington and their ilk fell into place. It seemed to me that Hartshorne pretty thoroughly demolished this determinism, and when he updated his book in 1959, 20 years later, he declared again that it was “dead.” It is amazing that in the last few years it has been resurrected and ballooned into conventional wisdom! Professional ecologists love it, for it is really their stock-in-trade, and so do many anthropologists, particularly social anthropologists. But this doesn’t tell us how it has got such a hold on the non-academic public. I wonder sometimes whether it doesn’t satisfy some deep-laid yearning that is common to most people. Perhaps it is simply that most people will not take personal responsibility for their lives if they can possibly avoid it, which they do by passing it on to “society,” or the weather, or to whatever environmental influence comes to hand.

Raup has told us of the influence of the thinking of geographers on his own work. Not unexpectedly he first wrote about environmental determinism in a paper published in the Annals of the Association of American Geographers. The year is 1942.

We have seen the problems that classification tends to generate. The same problem exists here. The following excerpt is being classified as environmental determinism, but the reader will also find reference to community and succession.

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Ecological plant geographers usually go back to Humboldt, Schouw and Grisebach for the classic foundation of their view. This seems to be due to the fact that these students broke away from the purely floristic idea of plant geography and set up descriptive units based upon pure form and community structure, thus releasing themselves at least in part from the problems of speciation that were becoming increasingly difficult in floristics. We have already seen, however, that in spite of these changes, the processes of logic had, for the older men, remained identical with those of the floristic geographers. Humboldt and his followers set themselves to describe the world of plants empirically, dealing with the relationships of plants to environment only on a comparative basis. They purposely refrained from plunging into problems of actual cause and effect, apparently because they had arrived logically at a strong presentiment that they could not solve such problems then, and probably never would. Ecological geographers, on the other hand, starting with the assumption of a causal relation between plant and environment, have built the entire structure of their science upon efforts to prove its significance and to interpret the distribution of plants on the basis of it. The initial reasoning, therefore, has not been by simple induction from a body of empirically and naively determined facts, but from a system of working hypotheses based upon assumptions of actual cause and effect.

It has already been noted that Warming and Schimper very carefully stated these conditions at the outset, and the same procedure was followed by Livingston and Shreve in their studies of climatic relations to vegetation (1921). Cowles (1911) attempted to do the same in a brief discussion of adaptation at the close of his textbook of plant ecology. In his earlier work on research methods in plant ecology (1905), Clements stated clearly that his premises were in environmental determinism. In the latest textbook of Weaver and Clements (1938), however, the causal relation is obviously no longer an assumption but an established fact, and no apology for it is given.

PHYSIOLOGICAL PLANT GEOGRAPHY

American physiological plant geography has remained strongly environmentalist, as already stated, though a few voices have been raised in

From Hugh M. Raup 1942c. Trends in the development of geographic botany. *Ann. Assoc. Amer. Geogr.* 32:319-354.

protest. These protests appear not to have been directed so much at the environmentalist view, however, as at some of its interpretations. There have been two outstanding concepts in synecology which have had their highest development in America. The first is what may be called the "organismic" concept of the plant community. It is one of the foundation stones of the plant ecology and geography of Clements. The second is the idea of plant succession, or the "dynamic" view of plant communities. This has become the cornerstone of the whole study so far as most American students are concerned.

Ecological plant geographers set out with high hopes of solving all the real problems of distribution on a physiological basis. The starting points for most of this work have been either among plants under cultivation or tendance, or among those that live on what might be termed the "physiological fringes" of the world habitat. The discovery, in the management of crop plants, of soil deficiencies that could be defined and corrected with fair precision has lent a great deal of weight to the theory of limiting factors. The finding that even the rarer elements in the soil could be significant has complicated the problem, but at the same time has seemed to emphasize the necessity for further extension of the factorial approach. In the realm of natural vegetation, the obvious suitability, structural and physiological, of aquatic and desert plants for their habitats has given an abundance of *cases* wherein the assumption of physiological causation could not be readily disproved, and the environmental complex was apparently simplified by being one-sided. There are also the large and apparently safe generalizations regarding a causal relation between climates and some of the great vegetation types and barren areas of the world. It is difficult to think of any other reason for the absence of plants from central Greenland than the rigor of the climate there; and the excess of moisture and heat in tropical lowlands is sufficient to preclude the development of grasslands or deserts in those regions. Likewise, in the study of plant communities, the starting points have been in the more obviously ecotonal habitats such as on pond and lakeshores, prairie or forest margins, arctic and alpine timberlines. In all of these situations there has been thought to be a possibility of reducing the causes to one or two factors. The material basis for the study of dynamic ecology also rests in these ecotonal areas, or in areas of naturally or artificially disturbed soil.

It has been the hope of the physiological plant geographer that, armed with causal relations derived from experiment or from these fringes, he could slowly work back into the great masses of the world's mesophytic vegetation, solving his causal problems in parts, as they arose. The literature of the attempt to do this has become extremely voluminous; but since the technique has involved a deliberate partition of the problem, the results are also in parts, the integration of which is a discouraging task. One of the few exhaustive attempts at the correlation of plant distribution with a complex of factors was that of Livingston and Shreve on *The Distribution of Vegetation in the United States as Related to Climatic Conditions* (1921). While it was admittedly only a partial treatment of the total habitat complex, the results achieved will serve

to illustrate the nature of the problem.

The philosophical grounds for this study were clearly in environmental causation. The authors drew inspiration directly from Schimper, whose work, they say, "has done much to stimulate interest and activity in what we may designate as causational or etiological plant geography." Some other quotations will further bear this out: "We have approached our problems in plant geography with the mental conception that they are merely problems in physiology . . ."; "Our attitude toward plants has been that of the physiologist, and we have tried to bear constantly in mind the conception that vegetational characters are simply expressions of the activities of individual plants. We maintain that all discovery of true causal relations in ecology must depend finally upon this point of view"; "Plant geography can progress but little further by qualitative observational methods, and the physiological and quantitative point of view must, of necessity, finally prevail"; "In an etiological study of plant distribution, either natural or artificial, the conception of physiological limits must hold a very prominent place"; and finally, "The existence of a causal relation between climatic conditions and the vegetation of any given region is so well known as to have become practically axiomatic."

Livingston and Shreve's statement of the net results of their work may be summarized with two brief quotations. "A relation between climate and the distribution of the common species which dominate the principal vegetations is . . . well-established fact. But the relations between climate and the distribution of the generality of individual species is indirect and is obscured by many considerations." With regard to the prime requisite of the physiological approach—experiment, they have the following remarks: "The problem of the role of climatic conditions in determining plant distribution is essentially a physiological one, since it rests, in ultimate analysis, upon the influence exerted by environmental conditions on the activities of individual plants. The attack upon this problem must, however, be made by methods quite different from those employed in purely physiological investigations. The conditions must be measured rather than controlled, and the plant material must be examined through its range of occurrence. . . . The methods that must be employed hinge very largely upon the interpretation of a vast series of uncontrolled experiments under the varying conditions of natural environment. It is to the geographic aspects of the problem that we must ascribe many of its complexities and much of its difficult nature."

Thus, in spite of repeated statements of faith in the initial assumption of environmental control in the distribution of vegetation, the authors could present as evidence only a coincidence between climate and the distribution of a few common species. They were left with not even good coincidence for the "generality of individual species." Their conclusion with regard to the experimental method was even more striking. It should be remembered that the prosecution of research in this field was predicated upon an experimental knowledge of plant reactions to environmental factors, as Schimper stated at the beginning (1898, 1903). We can measure the factors after a fashion, but we

have no way of knowing whether they are in terms significant to the plant until we know the plant's reactions to their values. This, if we use ordinary physiological method, involves experiment, and experiment involves control; but when we control the life of a plant, no matter what the results of the experiment they become greatly limited in their value for the original purpose—that of solving the environmental relationship. Ecologists realized this long ago, and devised means of approximating conditions of naturalness in the laboratory or partial control in the field, but they could not eliminate control or their experiments would no longer be experiments. Even under rigidly controlled conditions the solution of one problem only leads to another fully as complex as the first if not more so. These students have been faced with the same problem of the complex causal system which was recognized and appreciated by Humboldt and de Candolle, whose incisive logic warned them that the problem was probably unsolvable by any means then conceivable. Ecologists have tried to simplify the problem with the theory of limiting factors, but the isolation of such factors for most plants is almost as complex as the original cosmos.

Livingston and Shreve's conclusion with regard to the use of experiment in attacking the complex environmental relation is strongly reflected in the following statement found in the preface to their work: "On the whole, then, our aim has not been to discover true causal relationships between the two categories of observations here considered, but rather, simply to describe some of the vegetational and climatic features of the country. . . . Our work is primarily descriptive, as most ecological work must be for a long time to come, and the discovery of simple concomitancy is our nearest approach toward the establishment of causal relations. We have been led to the view that ecological science can be most rapidly advanced through this general method of quantitative comparison and by the placing upon record of such cases of concomitancy (between plants and their surroundings) as this method is able to bring forth."

This is sound method—simple inductive reasoning from empirically gathered facts—identical with that of Humboldt and the outstanding floristic geographers. As stated it involves no assumption of a causal sequence from habitat to plant. It is hardly consistent with some of the authors' later statements noted above, which place some of these elusive causal relations in the category of axioms; nor is it consistent with one in their introduction: "We can, in brief, put it down as a law of plant geography that the existence, limits, and movements of plant communities are controlled by physical conditions."

If all this be true, it would seem to reorient the experimental method, in the commonly accepted sense of the term for physiological plant geography. The latter then becomes, as floristic geography always has been, a search for what Livingston and Shreve call "simple concomitancy," with no particular prospect of finding causal relations except by approximation. The chief advantage of the physiological approach becomes its promise of presenting new kinds of factual patterns for comparison. Who shall say whether they are better or worse patterns than those presented by the field of morphology,

especially in view of all the latter's ramifications in cytogenetics? Experimental physiological techniques, used with complete realization of their limitations, will make valuable contributions to these patterns; but they do not seem to show any greater promise of solving the complex plant-environment relation than do other techniques such as are in use by students of floristics or genetics.

A more or less stable community of plants living together in an area can hardly be an "organism" in the sense of an individual, but Clements has insisted that its analogy with an individual is so close that many of the characteristics of an individual (growth, maturity, death) may be attributed to it. Gleason's criticism of the concept has probably been the most effective (1926, 1927). He maintains that the idea is untenable because the plant community cannot actually be defined in space—that the community is made up of individuals whose presence there depends so much upon chance as to render a finite description impossible. Clements' use of the concept has of necessity been limited to analogy, and his reasoning has thereby repeatedly fallen into error, as pointed out by Cooper (1926) and others (see also Phillips 1935, for a review of this matter).

The organismic theory has had a wide acceptance in the field of geography as a whole. Hartshorne, in his recent survey of the whole field (1939), devotes a long chapter to a critical discussion of it, with arguments that are strongly reminiscent of those advanced by Gleason for geographic botany.

Although the organismic concept has had many critics, the theory of succession, or at least of vegetational change, is almost universally accepted, especially among American students. It is looked upon as essential to an understanding of the plant world, and most of the organization of our material is based upon it. This received a clear statement by Cooper, in 1926. "One fundamental premise must dominate the whole, almost axiomatic, and yet needing constant emphasis—the universality of change. It follows from this that to confine our field to the present, or to include only the easily accessible portions of the immediate past, will seriously damage the prospect of valuable results. Notwithstanding the fact that the present must always furnish the bulk of our knowledge, the only truly scientific viewpoint is that which opens up the whole vista of vegetational history." In brief, it is urged that the student of plant succession should attempt to integrate the geography and history of the plant life of any given area.

Gleason is one of the few who have been so bold as to question the proposition that the present distribution and nature of vegetation can only be studied properly with the aid of its successional history (1927). His argument is simple and proceeds directly from his attitude toward the plant community. If a community cannot be defined in *space*, neither can it be in *time*. Here again, as will be noted later, the general geographers have had to deal with similar problems.

It is of interest to note in this connection that Braun-Blanquet has made an effort to organize the study of plant sociology around the static community (1923), and to keep the developmental concept in a secondary position. In a

brief criticism of Clements' methods Braun-Blanquet says, "He worked out methods for investigating the dynamic processes and sought to place the classification of communities on a dynamogenetic foundation. He has been criticized . . . for neglecting the static features of vegetation. His dynamics are often hypothetical, and the static social units are indispensable as a foundation for the study of vegetation."

DEVELOPMENT OF GEOGRAPHY AS A WHOLE

Before attempting to summarize the recent trends in plant geography it will be well to look briefly at developments in the field of geography as a whole. Here we have the advantage of the recent and highly critical review by Richard Hartshorne (1939) called "The Nature of Geography." This paper recounts the history of modern geography, with a rigorous examination of the philosophical grounds upon which it rests. The close parallels that exist between its problems and vicissitudes and those of biogeography should make the book "required reading" for any biologist whose work takes him into the geographic field.

Modern geography is regarded as having its origin in the work of the German masters, Alexander von Humboldt and Carl Ritter. We have already discussed Humboldt's points of view in plant geography, and we have noted that they were only a reflection of his views on geography as a whole. Ritter was in substantial agreement. His first principle "was that geography must be an empirical science rather than one deduced from rational principles—from philosophy—or from *a priori* theories of general 'geography' " (Hartshorne 1939). In his own words "The fundamental rule which should assure truth to the whole work is to proceed from observation to observation, not from opinion or hypothesis to observation" (1822, 1: 23). With neither Humboldt nor Ritter, however, did this degenerate into mere fact-gathering. Both were deeply conscious of the close interdependence of phenomena in a given area. They sorted their facts areally, and sought, through comparative studies, to arrive at some approximation to causal relationships, and at characterizations of different areas by outstanding factual complexes. Like Humboldt, Ritter thought that laws of interrelationship existed, but he felt that they could better be worked out inductively than by starting with assumptions. He thought we should "ask the earth itself for its laws" (1822, 1: 4).

After Humboldt and Ritter the next outstanding geographer whose work has large significance for biogeography was Friedrich Ratzel. Ratzel's first volume, significantly entitled *Anthropogeographie*, was published in 1882. It contained something of a new departure in that it began with the "natural" conditions of the earth and then related them to human cultures by way of their influences on these cultures. By this turn geography became, for the time, environmentalist, with the assumption that human culture was principally the product of the "natural" conditions which surrounded it. In a second volume of his work, published in 1891, Ratzel largely reversed this view, but a strong

tendency to invoke environmental causation directly in human geography became deeply embedded in geographic thought. The implications of Ratzel's work were brought to America by Ellen C. Semple who published, in 1911, her book on the *Influences of Geographic Environment*. Guided by Semple's writings, and modified by the school of "physiography" centering in the work of W. M. Davis, American geography continued to reflect this environmental determinism for two decades. Semple, and especially Barrows (1923), who treated geography as "human ecology," did not look for all ultimate causation in the external environment, but rather in an "adjustment between man and the earth." They sought thus to eliminate some of the one-sidedness in the study of environmental relations, but they did not at the same time clarify a reasoning which began with the assumption of human adjustment to environment.

Only a small and relatively inarticulate minority knew of or cared for contemporary developments in nonenvironmentalist schools. Then in 1925 Carl Sauer, impressed with some works by the German students, published a short paper called "The Morphology of Landscape." Sauer advocated, on logical grounds, a return to the earlier reasoning of Humboldt and Ritter and to that of some later German geographers: namely, that assumptions of environmental determinism should be eliminated, that geography should endeavor to ground itself upon safer, inductive methods.

These views have made notable changes in American geographic thought. They have apparently achieved wide acceptance, and are greatly elaborated and clarified by the work of Hartshorne already mentioned.

The similarity between the general outline of the history of geographic thought, and that of its special part, plant geography, is obvious. In both, the initial impulses for modern development occurred in the time of Humboldt, with their reasoning based upon inductive logic. Certain phases of plant geography, notably in the fields of lifeform and physiological studies, became strongly environmentalist under the influence of the theory of adaptation which grew out of Darwinian thought. Although Hartshorne makes no mention of it, the equivalent movement in human geography reflected by Ratzel probably arose from the same inspiration. In both cases the followers of environmentalism became remarkably one-sided and confident in their reasoning, failing to use the results developed from other points of view; and in each case there has been either a contemporary persistence of the older, more conservative reasoning, as in floristic plant geography, or an early revival of it as in the German school of geographers. The movement centering in the works of Warming and Schimper, who attempted to eliminate some of the post-Darwinian teleology from studies of structural adaptation to environment, trying at the same time to fix the geography of plants upon a basis of physiological adjustment, probably had its counterpart in the later work of Ratzel and in that of Semple and Barrows.

Here the comparison stops except for a few recent developments in plant geography, some of which have already been noted. The outspoken reaction of some Scandinavian and English botanists against the current functional

interpretations in lifeform classification, and their advocacy of return to a purely physiognomic basis, form a close parallel to the revolutionary geographic movement started in America by Carl Sauer. There are some further parallels among recent trends that also deserve attention. Gleason's criticism of the organismic concept of the plant association has its counterpart among general geographers, as shown in the following statement by Hartshorne: "In organic growth, all the individual parts develop from a common origin . . . , are nourished from a common food supply, and are controlled in their growth by some common directive agency. External elements introduced into a single part of the organism are either converted into materials that are spread through the whole, or are expelled, or in the abnormal case, are immediately recognized as 'foreign bodies' and isolated, as in a cyst. What do we find comparable to this in the alteration of an area of the earth? The soil erosion of any single slope may be entirely independent of all conditions in other parts of the area; the growth of a single tree is dependent only on the immediately surrounding conditions; what takes place in all the rest of the area may be of no importance to it whatever. The rainfall conditions are largely the result of external forces quite independent of changes in the area itself. Finally the cultural landscape developed by man cannot be understood either as a growth within the area nor as a process of digestion of external materials by the area as an organism: cultivated plants are introduced not into the area as a whole, nor into any common digestive organ, but first into some particular field. Foreign capitalists and engineers may insert factories into a region of primitive subsistence economy, as though a surgeon were to put a backbone in a starfish." Hartshorne concludes that regions cannot be defined as units of reality, and cannot be considered as concrete individual objects. It is not difficult for us to apply this conclusion to our concepts of the plant association.

Related to the primary significance of succession in the organization of plant geography, also questioned by Gleason, Hartshorne has described a similar problem in geography as a whole: "The various forces that alter the landscape of an area, whether they are internal or external, recognize no common limits to the area. It follows therefore, that, in whatever manner we may consider a particular area as a definite unit, that unity can be established only as of a given time. . . . Any study of the development of the cultural landscape of an area . . . is legitimate only if we remember that the area considered through a sequence of periods is an arbitrary unit. Whatever interest there may be in studying the combination of processes of changes in an arbitrary unit of area, there can be no logical requirement that geography must make such studies." Hartshorne thinks that underlying the thesis of the essential significance of development in a geographic area is the assumption—"commonly unmentioned, and even denied"—that the unit area will remain unchanged during the process. He thinks that this concept is, "in principle, a survival of the idea of environmental control (Broek 1938, in Hartshorne 1939). Unit areas do not, of course, maintain themselves thus in reality.

Again, the charge is commonly made that a geography that does not

emphasize change would be *static* and unimportant—that *becoming* is more important than *being*. To this Hartshorne replies that “If . . . one examines the question of what ‘is important’ objectively, one must ask what importance *becoming* can have, if the state of *being* is unimportant.” In this view history as applied to geography becomes a systematic study of any particular feature of the area under consideration. Hartshorne also calls attention to the inherent complexity of any proposed integration of history and geography, which, he maintains, appears “beyond the limitations of human thought.”

Anyone who has tried to define a plant community and to solve the impenetrable maze of cause and effect relations that exist in it at a point in time must have wondered how he could ever hope to project it backward into history without either losing it completely or merely compounding his unsolved problems. Yet we find that the developmental view of vegetation is confidently pushed back even into remote geologic time, and both complex communities and successions are reconstructed on meager paleontological evidence.

We have seen an excerpt from this 1975 paper earlier. Here we have a subtle discussion of the effects of species' inherent characteristics and chance on assemblages of plants. At the end of this excerpt Professor Raup shows how we must work with species—and he has already impressed on us the genetic variation in species—if we are to understand plant/site relationships.

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This study deals with the shore vegetation of lakes and rivers in the Athabaska-Great Slave Lake region of northwestern Canada. It is based on about 130 transects that extended from open water to the shrub-tree borders. Ten habitat-vegetation complexes are defined to embrace the principal variations that were found. Definitions of the habitats are based mainly on differences in local topography, substrata, and moisture regimes. Vegetative components are defined physiognomically as grass-sedge meadows, treeless shrub muskogs, shrub-tree borders, etc. Within the habitats the vegetation is described in terms of assemblages of vascular plant species which are visibly different from one another owing to the abundance and/or prominence of one or more "primary" species. All other species in the assemblages are considered "secondary."

In the course of the field work 424 species of vascular plants were noted, seven of which were eliminated from the analyses because they were endemic or marginal and their behaviour was not sufficiently known. Assemblages described numbered 550. Of these, 251 were found to differ from one another in their primary species composition. Thus the average number of times a given assemblage was repeated was 2.2.

One hundred and forty-five of the shore species were noted as primary in one or more of the different assemblages in which they occurred. All but 11 of them (134 spp.) were found in varying combinations of two to four species each, and 60 of these were also found as single primary species in their assemblages. The 134 primary species formed 180 different combinations. Twenty of these species were found in 7 to 19 combinations each, involving 75 other primary species and accounting for 128 of the 180 combinations observed.

With so little repetition among the assemblages, the feasibility of generalizing or rationalizing the vegetation in terms of these assemblages becomes remote. The large number of different combinations among the primary species suggests that most of the latter have very wide latitude in their "choice" of associates. It suggests a greatly reduced probability that species compatibility, or some kind of obligate relationship among species, has much effect upon the primary composition of the assemblages.

Coefficients of species' group relations to habitat, or of "preferred" associations among species, could be derived statistically, but the scale of refinement thus achieved would be far from commensurate with the scale of our present or foreseeable knowledge of the habitats; nor would it be

From Hugh M. Raup 1975. Species versatility in shore habitats. *Jour. Arn. Arb.* 56:126-163.

commensurate with our limited understanding of differences in behaviour known to occur among the species.

About 60 percent (252) of all the shore species were found growing in more than one of the 10 habitats, some of them in as many as five to seven. The "most successful" species—those that were found to be primary in the assemblages—were drawn mainly from those species growing in more than one habitat. It is proposed that the number of different habitats used by a given species is a rough index of its inherent tolerance or versatility ("ecological amplitude") in adjusting to habitat variation. It is suggested that the primary species have attained this rank at least in part because they are inherently more versatile than the secondary species. Their versatility appears to apply to both physical and biological habitats, for the primary species growing in the greater number of different habitats also formed the greater number of combinations with other primary species.

Size of geographic range appears to be correlated with differing tolerances of habitat variation. In general, the larger the continuous range, the greater the incidence of wide tolerance among the species. This is suggested by analysis of the major geographic elements of the flora, but is shown more clearly by species that have more or less limited ranges within the Athabaska-Great Slave Lake region. A major floristic boundary shows much greater tolerance among the species that cross it even for short distances than among those that do not.

Wide versatility in habitat occupance is not evenly distributed among life-forms of the plants. In the shore flora as a whole the trees and shrubs are the most versatile, while the herbaceous plants form a second group that do not differ greatly among themselves. The primary species in this group, however, show notable differences. Perennials that have fibrous roots as underground organs show considerably more versatility than the much more numerous perennials with caudexes, stolons, runners, or rooting stems. They are nearly as versatile as the primary shrubs. Least versatile are the perennials with taproots, bulbs, corms, tubers, or turions. Primary annual and biennial species are also very low in the scale of tolerance.

The life forms of species in different geographic affinities show some notable variations from the above. Plants whose general ranges are arctic-alpine have appreciably greater versatility in their fibrous-rooted and tap-rooted perennials than is shown by these forms in the boreal forest or timberline affinities. This difference is shared in part by the Alaskan-Cordilleran affinity, which has in it an arctic-alpine element. It is probable that the wider tolerance in these forms reflects their predominance in the arctic tundra.

Variations in the incidence of wide versatility in the floras of the ten habitats is shown. An explanation of the variation can only be suggested. It may be assumed that the most highly specialized species in the flora, morphologically and physiologically, are the aquatics and the halophytes. If this is the case, they are the least likely to be found in other habitats and should show the least versatility. By the same reasoning, there should be some effects of

specialization for partial desiccation toward the drier end of the moisture gradient. This is suggested among the last three of the habitats on the right side of the figure, where percentages of widely tolerant species are appreciably lower than in the preceding five habitats.

In view of the findings in this paper, it appears that the shore species of the Athabaska-Great Slave Lake region are behaving not so much as members of "communities" in which there are necessary relationships to specific habitats or to other species, but as populations of individual species that have found, perhaps in part by chance, sites that are satisfactory to them. Their adaptation to site seems to have considerable flexibility, which varies from one species to another. The flexibility is most pronounced among the primary species—those that give form and colour to supposed "communities" and make the shore vegetation look the way it does. The present paper, therefore, has dealt primarily with the behaviour and distribution of species rather than of "communities." The term "community" is replaced by "assemblages," which carries fewer implications of relationships that are nonexistent or unknown.

Only the effects of differences in versatility among the species are apparent, in local or regional behaviour and distribution. It is presumed that the differences are due to biotypic or ecotypic variations within the populations which, in turn, have been conditioned historically. Such variations are known to occur in species that have been studied cytotaxonomically and experimentally (Turesson 1922, 1925; Anderson 1936; Clausen, Keck and Hiesey 1940; Mayr 1964; Johnson and Packer 1965). Their probable significance in the study of "dominance," and in the concept of "niche" in ecological systems, has been stated by McNaughton and Wolf (1970). The genetic differentiation of plant populations within small areas has been discussed by Bradshaw (1972), who concludes that "the ecological amplitude of most species . . . has a strong genetical component." Further understanding of the ecological and geographic behaviour of the vegetation discussed here will depend in large measure upon investigations of its history and the processes of its inheritance. The starting point for this is at the species level.

On the occasion of Hugh Raup's remarks to the Ecology Program Seminar at Rutgers in 1972, it is not surprising that environmental determinism was one of his subjects. Raup was, after all, working with a new generation of ecologists.

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At the very outset Darwin formulated the assumption of a cause and effect relation between the existing form and behaviour of a plant and its physical surroundings. The core of his argument was in the idea of *adjustment*, for if the theory of natural selection were to be effective in the evolution of a species, then it would be impossible to admit that a plant could continue to live if it were not adjusted structurally and physiologically to its environment. This was a new departure in methodology. Earlier students had carefully avoided committing themselves to direct attacks upon cause and effect relations. The Renaissance and 18th century thinkers seem to have sensed the awesome problems they would get into if they did. Even with the encouragement given them by Newtonian physics and mathematics they despaired of reaching any viable solutions.

Darwinism had its least effect upon purely floristic geography. This geography had been practiced mainly by taxonomists, and continued to be. The taxonomists were already conditioned, by the work of such students as Linnaeus, to the idea of a "natural" system of classification showing family and generic relationships among plants. Their explanations for the distribution of plants had always been largely historical and they quickly adjusted their thinking to the Darwinian ideas of development.

Plant geography in terms of the forms of plants immediately underwent revolutionary changes. The physiognomy of plants now had to be interpreted in terms of survival values, and as a direct or indirect product of the environment. Form characteristics of plants were evaluated according to their supposed importance in the process of natural selection or, for antiselectionists such as Lamarck, according to their assumed direct causal relation to the environment. Most students of vegetation quickly discarded their old systems based on pure form in favor of systems that would involve the biological or survival significance of plant structures. These systems involved many characters, such as leaf form, size, venation, degrees of hairiness, etc: or flower structures as related to pollination processes, or seed dispersal mechanisms. Arguments were rife over whether a given structure had a true "adjustment" value, or was merely "indifferent" and essentially useless. The amount of teleology that developed in these efforts to find functions for plant parts probably has never been surpassed.

Incidentally, it was during this period that the word "ecology" came into use. Originally it was spelled "oecology" and came from a Greek word meaning "home," or "estate." The first definition of it seems to have been made in 1886 by a German naturalist-philosopher named Ernst Haeckel. He said it was a science treating of the reciprocal relations of organisms and the external world.

Closely related to the origin of the biologically interpreted lifeform systems was another view of plant geography, based upon the physiological relations of the plant to its environment. Like the new lifeform system, it was rooted in the assumption of adjustment to environment. Von Humboldt and de Candolle had tried to draw up relationships between temperature regimes and the distribution of species, but they made no pretense that they had found actual causal relations, only coincidences which, if they could find enough of them, might lead to sound generalizations. The physiological plant geography which now developed *started* with the assumption of causal relations. It was in terms of the physiological reactions of plants to the various parts or factors of the physical environment such as water, light, heat and mineral nutrients. Thus, it dealt in parts that could be measured, and was strongly influenced by methods of research in physics and chemistry. From the basic assumption of adjustment there was a logical step to another assumption: that a plant could continue to live in a given place only so long as none of the environmental factors varied beyond certain limits which were set by the physiological requirements of the plant. Because these factors could be measured with some degree of accuracy, it was expected that with some experiment on the plants' requirements it would be possible to find what factor or factors were actually limiting distribution. This was expected to solve the problems of plant geography.

These ideas were clearly spelled out in two classic works: the *Oecology of plants* by Eugene Warming in Denmark (1895, 1909) and *Plant-Geography upon a Physiological Basis* by A. F. W. Schimper in Germany (1898, 1903).

It seems now that these men, and others that followed them, had no premonition of what would come out of their particular Pandora's Box.

The recommended experiments, if they are to satisfy modern requirements, involve elaborate systems of control and sampling. This means that they have to be brought into greenhouses and laboratories where whatever we learn about the plants' environmental relations applies only to the artificial habitat we create for them—not to the one we brought them from. We are still trying to do this, by simulations of natural habitats in our huge phytotrons. We are learning a lot about the physiology of plants from such experiments, but nothing that is earth-shaking for the field of plant geography.

From our standpoint one of the most notable products of Darwinian theory was the rise to prominence of what has been called "environmental determinism." It is surprising that it was so widely and quickly accepted. In effect, the conventional wisdom in much of plant geography radically changed its character almost overnight. The only exceptions were among taxonomists, for whom the assumptions of adjustment and natural selection were incidental to the taxonomic relationships and distributions with which the floristic geographers had to deal.

From this point on the environment of an organism began to dominate the research and thought of most plant geographers. The notion of environmental determinism rested on assumptions which gave the environment direct or indirect causal influences on the lives of all living things. All sorts of people

picked up this ball and ran with it. It produced the Social Darwinism of Spencer, and it is inherent in the philosophy of the major 19th century economists and sociologists. In a curious way it dominated soil science for nearly half a century. . . .

In all of this development of ecology people seemed to forget or somehow managed to avoid thinking about a crucial point in Darwin's suggestions. If natural selection were to work, there had to be something to select. There had to be differences among and within organisms from which the environment could select the most suitable. The French naturalist Lamarck thought the variations were caused directly by the environment or by use in response to environment. This was his theory of the "inheritance of acquired characters," for which students of heredity could find no clear evidence. Modern geneticists and cytologists have now given us some sources for natural variation in organisms—mutations, hybridization and polyploidy. But the answers seem to be disturbing to most ecologists.

When a group of plant species arrives in a new habitat, whether by seed or by some other means of dispersal, each brings with it inherited requirements and limitations—in structure and physiological behaviour. What they can and cannot do in coping with the environment in their new place are fixed by this inheritance. Their immediate environment appears unable to change it—it can only sort the plants into those able to flourish and spread, those partially able to do so, and those incapable of it. Most species of plants are based on what we can see when we look at them. After a taxonomist has looked at a large number of individual plants in the flora of an area he sorts them into groups, within each of which the individuals look so much alike in all essential details that they can easily be separated from all the other groups. These groups are the species, and have names. The geographic ranges of the species may be small or they may be continent-wide and consist of millions of individuals. For example, one can pick up a common dwarf dogwood plant from Alaska and lay it beside one from New England, and be unable to tell them apart. We know, however, that they are genuinely different, for we cannot carry the New England plant to Alaska and expect it to thrive there. Horticulturists have known about this sort of thing for a long time, and have maps showing zones of hardiness for different species. So have foresters, particularly in western Europe where plantation forestry has been practiced for centuries. We now have cytogenetic evidence that a species is not merely a lot of individuals that look alike, but rather an interbreeding population of individuals that can pass its heritable materials around. What a plant can do in a given local environment depends upon the amount and kind of material it happens to have. Some of the species in a given locality, for example, have a wide tolerance for differences in water supply. They grow and flourish in the wettest places and also in the driest. Other species in the same locality are restricted to only one segment of the moisture gradient, the same two groups of species growing in another locality are likely to show reverse positions with respect to moisture, the one with wide tolerance may be more restricted, while the other has the wider latitude.

When ecologists renounced the species as a unit of study they cut themselves off from this great stream of ideas that has come out of cytogenetics, most of it since the rediscovery, about 1900, of Mendel's pioneer work. For most ecologists species are not much more than names that they get out of floristic manuals. There is very little in modern textbooks of ecology about the contributions that modern genetics has made, and in some of them nothing. I suspect that a basic reason for this is devotion to the idea of the immediate environment as an all-controlling influence. If it loses a part of this influence, as it seems to be doing, ecologists and ecological plant geographers will have to go back to studying the forms and behaviour of species, and they will have to rethink their whole position in the search for ultimate causes. They may find themselves only a little further ahead than were deCandolle, or von Humboldt, or even Theophrastos.

Chapter V

REFLECTIONS ON AMERICAN FORESTRY

When the history of American forestry is written, the influence of the ideas on silviculture and forest management that were imported from Europe will loom large. Sharing equal billing with that influence will be the effects of the environmental movement that began in the 1960s. Both influences have imbedded in them the questions of Ideas, Man and Nature. Professor Raup has commented on these and on the influence they have had on American Forestry.

LETTER FROM HUGH M. RAUP 1979

One meaning I can see in this chapter is the “significance” of Ideas. As I’ve said elsewhere in these pages, I think ideas can only come out of individual brains when separate observations of facts suddenly jibe and suggest relationships. What we can do with the ideas depends on how good the relationships really are, and on how they relate to other ideas. I’ve never written much about this, but I think it is the “mechanism” for starting everything the human race has ever done—good or bad. The process is full of slippage. Man not only has ideas—he knows he does and is proud of them, which can be a blessing or a curse. He is apt to hold on to them long after they are superseded or proved entirely wrong. But in spite of all the slippage his batting average is pretty high, certainly over 50 percent, or he wouldn’t be here.

Society makes only modest payment (in money or otherwise) to those who do only the work it asks or tells them to do. It pays much more to those who take the responsibility for getting the work done. But it pays rather handsomely those who come up with ideas that turn out to be genuine innovations.

I’m afraid I have never been an “appreciator” of Nature in the aesthetic sense. I’ve been associated with any number of people whose whole attitude toward the world around them has been primarily aesthetic, but somehow it has never rubbed off. I do not know why this is so! Maybe some psychologist could tell me, but I doubt that I would believe him if he did. I guess I’m too much of a pragmatist.

I cannot separate man from Nature. All living things, including ourselves, have evolved in different ways and at different rates. But as far as we know we came from the same primordial ancestor, and we all have the same basic urge—to stay alive as long as possible and to perpetuate our various races. We don't know whether our particular race will be more or less successful than some others that have disappeared. Nothing like us has ever appeared, so we have no precedents to judge by. Our big brain and our memory, with the capacity to use it, give us control of most of the Earth. We have only begun to find out how we can best use our domain in our own interest, and I don't see any sense in stifling our own basic urges to "save" all the other races of beings. We are all "natural" so far as the world is concerned. And the world is neutral; ours is the only race that has any ethics, and we have made them ourselves out of the necessity for protection. We can embroider all this to our heart's content, with aesthetics, the fine arts, technology, religion, or what have you, but we are not likely to change our urge to survive and keep our race going.

Some professional foresters were distraught when a non-forester was appointed director of the Harvard Forest. Nevertheless, Hugh Raup brought to forestry a fresh perspective. This paper in the Journal of Forestry, in 1967, questions several of the ideas and facts/assumptions considered basic tenets of forestry practice.

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American forestry has derived most of the biological base for its operations from the experience of botanists, zoologists and soil scientists: The first borrowings were from the Old World. Americans had nowhere else to turn if they were to get their young profession off the ground. Very little was known about the commonest American trees, and still less about the hazards connected with their use and culture. Not only did American forestry borrow facts from contemporary experts but, more important for its future, it borrowed most of its theory from the same sources.

Accepted facts commonly turn out to be merely assumptions, or if they are sound they prove useless when transported to new contexts. Ideas, on the other hand, are amazingly persistent and influential. They can be transported. When related ones are pinned together to form general theories, or conceptual frames of reference, they can last a long time and make or break the lives of many people. A common characteristic of such conceptual structures is that they outlive their usefulness, and become dams against the progress of human ingenuity. American forestry has had considerable experience with its general frame of reference, and I choose to hang this discussion on it rather than upon a simple recital of biological problems. It will be useful to look first at the origins of the theory. Then I shall try to interpret later developments that will have grown from it.

American forestry came to consciousness around the beginning of the present century with several influential ideas in its conceptual frame. At the risk of some over-simplification these can be grouped into four elements. First, American foresters had convinced themselves that usable wood in America was getting scarce and was bound to get more so in the foreseeable future. Second, they had a vision of a "forest primeval" which they believed their forefathers had found here at the time of early settlement. It was a sort of biological datum plane for much of their thought. Third, they believed that this old productive forest had been devastated by destructive exploitation. And fourth, they conceived that their mission in life was to stop the devastation, protect what was left, and rehabilitate as much as possible in order to alleviate the incipient famine.

Wood had been scarce in many parts of western Europe for a long time. Forest economies in those regions had been adjusted to the scarcity by carefully nurtured production, and by various subsidies that were socially justifiable in the total internal economies of the nations. When early American foresters were bringing European techniques to this country—

From Hugh M. Raup 1967a. American forest biology. *Jour. For.* 65(11):800-803.

techniques that had been developed over a century or more to deal with an economy of scarcity, it was inevitable that the idea itself should come with the methods of coping with it. Common observation in our eastern landscapes, together with other elements in the conceptual scheme, made it easy for Americans to accept the whole European program, including the idea of scarcity.

The impending shortage of wood led to the assumption that land, labor, and capital could be used intensively to produce wood profitably. This assumption was used to justify the heavy emphasis laid upon silviculture and management in the training of foresters. It also justified much of the weight given to forest protection in American institutions. All of these are fields in which the study of forest biology had promise of development.

Time has always been the forester's problem child. The growth of trees being a slow process, he has had to make long-term biological predictions based on the assumption that a planned and orderly production of trees would continue for many decades or even hundreds of years. He rationalized his predictions by borrowing a conceptual apparatus invented by the ecologists, notably by the American plant ecologists. This was the conception of vegetational development, *in situ*, over time periods long enough to cover the life spans of several to many generations of plants. For foresters, because trees are long-lived, the time periods could run to several centuries or even millenia. An integral part of the conception was that the developmental process was an orderly one which for any given region was predictable. It would eventually result in a kind of balance or equilibrium between vegetation and site which would then perpetuate itself. This biologically balanced forest was believed to have achieved great richness and productivity in pre-settlement time. It was the "forest primeval." This whole ecological conception was indeed an elegant one. It lent an aura of scientific precision to definitions of the forester's aims and methods.

A more important prediction the forester had to make in his conflict with time was that people would want his trees after the long period it took to produce them—want them badly enough to pay the price needed for their production. He justified this in part by recourse to the threatened scarcity, and in part by what seems to have been a simple article of faith. Because wood was going to be very scarce, and people would always want it and have to have it, they would, perforce, have to gear their demands to the supply and pay the price.

The Puritan settlers of eastern America in the 17th and 18th centuries were land-hungry. Their idea of what to do with their new land was to *use* it—to the hilt. The vegetation they found on it, including the forests, was a nuisance, to be got out of the way as quickly as possible to make room for the production of needed housing, crops, livestock, and profits. Although their notions of personal sin and depravity were extraordinarily acute, they seemed not to apply them to what they did to the landscape. In short, their exploitation of the land and all its resources gave them, in itself, no sense of sin. This characteristic was deep-laid in Puritan philosophy, and gave an honorable

precedent to much that has happened since in Americans' exploitive use of their natural resources.

The Puritans did consider it morally wrong, on the other hand, to be personally unsuccessful in the use of resources. We still have a good deal of this idea, too, in our makeup. A curious reversal of the first of these attitudes began to appear in the latter half of the 19th century. In that period it gradually became wrong to exploit the land and forests. From small and isolated beginnings this notion grew into the conservation movement of our time. It is not impossible that some of the roots of the movement, much of which was in the eastern states, were in efforts to rationalize the old stigma attached to personal failure. Large numbers of people were experiencing such failure in the eastern states during this period, with the decline of agriculture and trade in New England and disaster to the South in the aftermath of the Civil War. It is possible that they looked for scapegoats wherever they could find them, and a large number found them in the so-called devastators of the land.

By the turn of the century there were very few of our forests that had not been modified by the hand of the invading white man. The conventional wisdom of the time emphasized the destructive nature of man, and portrayed him as a ruthless vandal in his treatment of the woods. The ecologists were on hand with their picture of the ancient stable forest, to show what a priceless heritage he had destroyed—a heritage that could not be replaced until many centuries had elapsed, if then. Most of the existing forests were regarded as pale reflections of what the land had produced in the past and might produce in the future with careful management and protection.

In light of the foregoing concepts the mission of the American forester became clear. He had methods which he believed would work or could be made to work. He believed he had economic, social, and scientific justification. But he had something more than this. Like nearly everybody else, he was against sin, and he found a ready target in the newly defined but widely recognized sin against the land and the forests. From this conflict he got the sense of moral rectitude that pervaded American forestry and supplied its missionary zeal.

American forestry during the past 60 years has experienced a series of traumatic shocks to its whole conceptual apparatus. First, it has gradually begun to know that the threatened scarcity upon which much of its theory was based was not realistic. Our foresters have always been oriented almost exclusively toward their resource—the forest itself. This has had some tragic consequences because no forest has value until human beings feel a need for it. Therefore people have been as much a part of the equation as the trees. In spite of greatly increased numbers, with a vastly enlarged range not only of wants and desires but also of the means to get them, people are using very little more wood than they did 60 years ago. During this period they have been extraordinarily inventive, producing not only a technological explosion but also far-reaching innovations in social and economic institutions. Our foresters, prepossessed as they were with the physical resource—the woods,

made their long-term prognostications within a frame of reference that virtually excluded the largest single biological factor in the forest system—the cunning brain and contriving hand of man. The scarcity they thought they saw approaching was mainly in lumber of qualities that were then demanded by the trade. They seemed unaware of the simple fact that those demands were governed by peoples' value judgements, and that people changed their values at will. People had been doing it for centuries, reaching a crescendo of change in the industrial revolution of the 18th and 19th centuries.

Another shock has come with the collapse of the basic assumptions that shored up the American forester's ecological theory. The concept of the age-old stable primeval forest has all but disappeared. Accumulating evidence points in one direction, and indicates that most of the forests seen by the first settlers in America were in their first generation after one or another kind of major disturbance—fire, insect pests and diseases, or windthrow. It is becoming apparent that the old forests were scarcely different from the present ones, and that the latter form a far better datum plane for planning than the assumed balanced forest of the theory.

Because western Europeans could not be blamed for the catastrophic events, most of the validity dropped away from another element of the forester's conceptual structure—that man (European man, at least) was the arch enemy of forest productivity. It seems that the way was opening for erasure of much of our sense of sin against the land, and for reinstating the old Puritan ethic that enabled full use of the land for whatever purpose seemed most profitable.

Still another shock has risen from the appearance, on a large scale, of amenity values in forests and forest land. This might have been predicted if foresters had been paying more heed to the social and economic forces that were in play around their woods. The amenity values had been appearing in many parts of the country during the latter half of the 19th century. It is probable that our early foresters, if they considered them at all, wrote them off as passing fancies that made no contribution to the serious business of their war against famine.

Our forestry, early in its development, found itself severely limited in what it could do with its talents. This was felt particularly in the areas in which the biology of the forests played a large role. The foresters found that they had to devote themselves almost entirely to measurement, protection, logging, and sales. Although the terms of their mission included regeneration by silvicultural means, and management practices to upgrade the quality of the forests, the hard facts of life soon threw doubt on the capacity of these enterprises to attract investment capital. They were possible only where some form of subsidy was available. The social justification of this subsidy began to fade when scarcity was disappearing over the planning horizon. The failure of capital to move, without subsidy, into silviculture, management, and their handmaiden—silvics, left the primarily biological aspects of American forestry without much material support. The only biological areas that could draw such support were in forest pathology and entomology, which were

protective of immediately valuable growing stock.

Prevention and control of fire could also be supported. But the biological implications of fire got short shrift for many years. Fire had no real place in the ecological frame of reference that the foresters had adopted, for in the grand design of long-term forest development all such disturbances were either disregarded entirely or admitted as infrequent aberrant happenings. Within this frame it was easy to label fire as an unmitigated evil, and to give its elimination high priority.

What, then, are the present status and probable future of American forest biology? I cannot divorce this question from a similar one regarding American forestry in general. I do not consider the wreckage of initial aims and concepts merely as irreparable damage. Rather it is a release. The forester is no longer so limited in his choice of fields for the application of his talents.

Perhaps the most important element in this release is, paradoxically for many, the admission of the immediate wants and desires of people into forest calculations. It represents a vast opportunity that American foresters have never had. To utilize this opportunity, however, requires that our forestry construct a new frame of reference, in which the focal point is not the physical resource but the human mind, from which all forest values come. Because the human mind is inventive, fickle, and essentially unpredictable, any frame of reference built around it must have a large element of flexibility. The flexibility must apply not only to the physical resource, but also to the time it takes to produce it.

What kinds of demands can we expect people to make? Crooked trees can be just as valuable as straight ones. Clear openings in forested lands may have higher values than if they were covered with trees. Continued technological innovation can make little trees as valuable as big ones. Species that have never had value can turn into the most valuable of all. And if we make paper out of annual crops grown on good agricultural land of which we seem to have a plethora, huge acreages of forest will have none of the traditional values except those of wilderness. Serious famine has never forced us to produce wood culturally on a large scale in America. It is possible that we never will have to, and that over large areas the forest will become a nuisance as it was to the early settlers on the eastern seaboard. It is already acquiring this character in some parts of New England.

Our forests are, like the demands made on them, atomized. They are a hodgepodge of types, age classes, and form classes. Our studies of their history show that they have always been so. The only order we can see in them, in any given landscape, comes from their relations to site. When we come down to cases the individual species appear to be reacting far more to physical site factors than to each other in supposedly necessary community relationships. The fact that the species are as productive and persistent as they are and have been is mute evidence that they have immense built-in adjustability not only to local site variation but also to violent disturbance by external forces including man.

Thus both the demand for forests and forest products by people, and the

supply in the forests, are extremely variable in kind, quality, and quantity. Both have massive elements of uncertainty, which is part of their very fabric. The forests have a flexibility which matches that of human demand provided we can learn how to control and use it. What the demands for biological knowledge will be as we attack these complex problems is difficult and probably impossible to predict. I shall venture a proposal, which carries with it the proviso that it is more likely to be wrong than right.

I think that the variability and fragmentation in human demands and in the forest suggest that the forester's knowledge and treatment of the woods will likewise have to be much more varied and fragmented than they have been in the past. This leads me to our more neglected field—silvics and its allied problems in site relations. It deals directly with the fundamental units—the individual species—that will be most useful in coping with the uncertainties of a constantly changing man-forest system. Modern agriculture, horticulture, and animal husbandry are living examples of what can be done when people study species intensively. European foresters began doing this long ago, and have never neglected it. The present status of our silvics, like everything else in the field, has been conditioned by the old conceptual structure.

In accepting the ecological theory of the early 1900s our foresters failed to see a fundamental flaw in its structure. Ecology as we know it was first developed in western Europe, primarily in the field of plant geography which had a maze of unsolved problems. It was thought that physiological experiments with species of plants would produce a working knowledge of their requirements and limitations. This knowledge could then be correlated with measurements of site factors, and a means of explaining distribution would be at hand. But the proponents of the idea seemed not to have sensed the magnitude of the research that would be necessary before it could be productive. Ecologists at the turn of the century began, rightly, to despair of accomplishing enough of it to be effective in the foreseeable future.

The theory set up by American ecologists attempted to avoid a large part of the burdensome research proposed by the physiologists. The latter had insisted that the basic unit of study was the individual plant species. Our ecologists thought they could make more progress by using larger units composed of many species. They called these units by various names: communities, associations, or formations. Foresters called them forest types. They were worked into the general theory of vegetational development and became stages in natural successions. Beating their drum for this proposal the ecologists now proceeded to beat the head in. They ruled that the species was defunct as a unit of study, and that only the community was acceptable. This idea has had a dire effect upon the American forest biology of the past 60 years. It led both the botanists and the foresters to by-pass most of the field of silvics. Just at the time when they would otherwise have been making intensive studies of the native, untried forest trees, they found no place for them in their frame of reference.

Every kind of tree has built-in parameters of tolerance on gradients of moisture, light, nutrients, temperature, and factors of physical disturbance.

The individual tree in which the tolerances are expressed is only one unit in a large population, and in this population the parameters commonly change regionally. Thus species are apt to behave differently with respect to site from one region to another. Studies of structural variation and behaviour patterns among and within tree species can be approached through the disciplines of physiology, morphology, and genetics; but progress in all of these with respect to the common American trees is in its infancy. This is a field in which practical lumbermen, mill operators, and manufacturers of wood products commonly have more useful knowledge than technically trained foresters do. The collection and codification of this miscellaneous knowledge might well be a starting point for the definition of many research problems in silvics.

By way of summary, I think the largest single need in American forest biology is the study of man's relation to forest land. Our foresters need to understand much more than most of them do about purely human motives and aspirations with respect to the land. They ought to become genuinely knowledgeable and respectful of people's economic, social, and aesthetic institutions. Felt needs defined in these areas are the only ones in which foresters or anyone else can find sale for their goods and services. Secondly, I would place the study, in depth, of the behaviour of trees as species and individuals. Out of this study can come flexibility in technical knowledge and management practice. It would enable foresters to take up more efficiently the varied options that are now open to them in their new frame of reference.

In this 1979 article Professor Raup expands on the influence of the concepts of ideas, man and nature. The title, "Beware the Conventional Wisdom," suggests the stance he will take: look at the data.

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These days vast numbers of sincere people hold the point of view that the human race is headed toward inevitable disaster. The rate of our decline, they believe, is so rapid that there isn't much time left to us. John Maddox (1972) has called this view *The Doomsday Syndrome*. Melvin Grayson and Thomas Shepard (1973) call it *The Disaster Lobby*, and Sherry Olson (1971) called one phase of it *The Depletion Myth*.

Localized beliefs of this sort are merely fads or fashions, but when they involve larger areas and many more people they become movements, and if they affect whole nations or large segments of nations they become the conventional wisdom. History is full of them. Most of the smaller ones don't last much longer than a few months or years, but others, such as the romantic movement of the 18th century, are still with us. Some, though they affect a whole nation, shortly become so unpopular that they disappear almost overnight.

Such a one was the prohibition movement. I lived through that one, and even saw it start, for as a boy I lived not far from its point of origin and knew some of the people involved. I was in high school when the Volstead Act went through Congress. It is difficult now to picture the milieu in which all this could happen. Even radio was in its infancy, so that communication had to be personal or through the printed word. But the personal became enormously effective, with every militant prohibitionist (and there were thousands of them) becoming an expert on the deleterious effects of the "demon rum," whether he had ever drunk any of it or not. They displayed their expertise in the schools, theaters, churches and in any other place they could find congregations of people. They were honest and sincere in what they said, but I shudder now that I realize how much of it was sheer nonsense and how many people accepted it as gospel truth.

I don't think that any of us can ever become immune to these pressures. Their purveyors can be very persuasive indeed. But I hope we can retain enough skepticism to at least raise questions. If what I have to say here has a central theme it is to take issue with the doomsday experts when they deny that the human race is capable of dealing successfully with the predicament they believe it to be in.

We live in a world of "experts" and "expertise." I suspect that there have always been experts. They were the shamans and witch doctors among primitive peoples. They were the political, religious and military leaders in ancient and medieval times. Nowadays they clothe their expertise in a thing called science, and look upon those earlier experts as imprecise amateurs.

The old shamans weren't worth their salt if they couldn't predict the future.

From Hugh M. Raup 1979. Beware the Conventional Wisdom. *Wes. Wild.* 5(3):2-9.

I submit that they were pretty good. Their technical knowledge, in our terms, was extremely limited, but they knew a great deal about people. This was their real stock-in-trade.

We make the same prognostication requirements of our modern scientific seers as these earlier people made of their shamans. One of the most common questions asked about a research project nowadays is how much predictive value it has. The validity of this question got a great boost from our successes in the physical sciences. These successes required no knowledge of human reactions other than the reactions of those making or supporting the experiments. The predictions could be made successfully because the materials and variables involved were few in number, most of them well-known and calibrated with great precision.

In the last few decades natural resources and population seem to be favorite fields for prediction. In both of these fields our real knowledge is far from precise, and the variables we have to deal with are so many and so diverse that we have no mathematics or experimental methods to rationalize more than small isolated fragments of them. In spite of these deterrents, our resource and population experts go on making predictions as though they were working in the physical sciences. Much of their current prestige comes from their free use of numbers, which gives the impression of precision.

As a people we worship numbers. Madison Avenue found this out long ago. When I listen to radio or television shorts or commercials I can be sure that somewhere in nearly every one there will be numbers, always given in hushed tones which leave the impression that they are really the most important part of the story.

In describing our experts we could as well call them specialists. We live in an age of intense specialization. The day of the mechanic who could fix anything, or of the naturalist who was intelligent in many fields of natural history, is nearly gone. Our specialists may be very efficient in their chosen fields, but are woefully ignorant outside them. This failing becomes serious when they try their hands at prediction in fields that have multiple variables.

Our specialized population expertise says, essentially, that people are just mouths to feed and bodies to shelter. These bodies don't *think*. On the other hand our experts say that the resources are severely limited, and are sure to run out in the near or distant future, because people will continue to breed and enlarge the number that have to be fed and sheltered. The resource projectionists are so heavily oriented to their own fields (the resources themselves) that they join with the demographers in forgetting that people can and do *think*. No shaman in an Eskimo or African tribe would forget that. If he did, he would pay with his position, if not with his life.

Examples of this sort of resource prediction can be cited by the hundreds. I will try to illustrate it first by a brief review of a U.S. forest report published in 1919.

At the time of World War I, a committee of American experts in forestry and wood utilization was assigned by the Society of American Foresters to prepare a report on the existing state of U.S. forests and their prospects for the

future. The committee was chaired by Gifford Pinchot, who was regarded as the leader in his field. The report of the committee was entitled "Forest Devastation: A national danger and a plan to meet it." About 60 years have elapsed since this report was written, and it is useful to see how it looks in light of developments during this time.

The report was in two parts. The first was labeled, simply, "The Facts"; the second was a rather elaborate set of recommendations for legislation to accomplish the purposes set forth. Some members of the committee submitted minority opinions, but these were concerned primarily with the recommendations. There seems to have been no dissent from the published expression of what the facts were.

The report is based on a group of assumptions. They were the things called facts in the report. I have listed 10 of them.

1. A continuous supply of forest products is necessary for national defense and for general prosperity.
2. Shortage of timber was now, in 1919, beginning to appear in the United States.
3. We were consuming wood three times as fast as it was being produced.
4. Per capita consumption was declining, but the population was rising so fast that total consumption would increase.
5. Average production of wood by the trees was about two percent per year, and there was no way to increase it.
6. At present rates of consumption and production we would have a timber famine within 50 years.
7. There would always be a demand for good lumber.
8. Timber was essential to agriculture.
9. Forest devastation must be stopped.
10. We must invest in the culture of forests.

Throughout the report there is a tacit assumption that the primary products of the forests were and would continue to be saw timber of high quality, i.e., boards or planks with relatively few knots or none. This required large straight trees that would take 50 to 100 years to grow. This assumption tended to bias all of the figures given elsewhere in the report for standing crop, growth and yield in the United States. Barrett and Morse, in their study of the economics of natural resource availability (1963), had much trouble finding reliable data on the forest resource, and the results from the data they had were not consistent with those from other fields. I think this was due primarily to the old bias toward a saw-timber economy which was built into the available data.

I first became aware of this bias when I became director of the Harvard Forest in 1946. We were at that time heating the main buildings and some of the smaller ones with fuelwood cut on the forest. The professional foresters on our research staff came to me and said that this would have to be stopped because we would soon run out of fuelwood. One reason they gave was that the hurricane of 1938 had removed about 750 acres of trees which would yield nothing for perhaps 20 or 25 years. I found this story hard to believe, and asked the men to make a new inventory. They did so, and came up with an abundance of fuelwood, enough to carry us comfortably for at least 20 years,

construction material. No substitute will make building so easy and rapid, or fill so many of his needs." In another place they said: "Every peacetime industry is dependent in some degree upon a supply of forest products. Food, clothing and shelter of every kind require wood for their production. No wood, no agriculture, no commerce. Without the products of the forest, civilization as we know it would stop."

Members of the committee seemed to have no doubts about the economic feasibility of farm woodlot operations, as seen in the following sentence: "Today the farm forest plays a growing part in the profitable working of the eastern farm . . . [the woodlots] are soon to become of vast importance, both to their fortunate owners and to the nation."

The committee had no conception of the mechanization of the modern American farm, nor of the steady decline during the last 60 years of the need for wood on the farms. The great barns of the past, which answered for vast quantities of lumber, are built now in very small numbers. Even the most advanced dairy farmers do very well with a small milkhouse and a few poles to support a metal roof. When the report was written, a large part of the wood used on farms was for fuel. This practice has all but disappeared.

Studies of typical farms throughout New England have shown in recent years that most farmers cannot afford to operate their woodlots, even within the total budgetary structures of their enterprises (Barralough and Gould 1955). An exception might be in some long time period which would not be commensurate with a farmer's planning horizon. In fact the existing pattern of farmland tenure rules it out.

Much was said by the committee about the immediate practicality of cultural practices for the renovation of forest production on cutover lands and abandoned farms. This idea had been lifted bodily from the western European forest economy. Even there it had never been economically feasible without some form of direct or indirect subsidy. In America, where wood has always been abundant, there has never been much investment capital attracted to such programs. The committee rather carefully avoided this issue, but it is a crucial one. Even with the best of methods, and with a lot of good luck, investment in forest production probably would pay no more than about three percent. And this allows very little for risk and uncertainty, which are high in the culture of forests.

Perhaps an indication of the unattractive nature of forest production investment is the lack of innovation in the logging industry. I mean logging here in the broad sense of getting trees from the woods to the mills. Until very recently this process had been essentially unchanged for over a century, while nearly every other extractive process was developing by leaps and bounds. Wood has been so plentiful that the logging industry could afford to go on at the old stand. Innovations such as the chain saw and heavy harvesting machines have appeared, not in response to scarcity and a supposed need to culture trees, but in response to rising labor costs and competition for labor between woods operations and factories.

The following statement is found in the body of the Pinchot committee

report: "Well-managed forests add wood at an average rate of two percent, and there is no way to increase it." The improvement of production rates by selection or hybridization is about as old as agriculture, and the past 60 years have seen large developments in this field as it applies to forest trees. But the committee seemed oblivious of such research, which was going on even at the time they wrote. Great progress has been made in the ensuing years. In fact our progress probably has been considerably beyond what is economically feasible in America, even in the foreseeable future.

I have said little or nothing about the "forest devastation" which was the major element in the title of the committee's report. For this idea to have significance there had to be something to devastate. This was the "forest primeval," which was assumed to have been here when the first white settlers came to America. It has been the "biological datum plane" for American foresters throughout their whole development in the 20th century. It was visualized as a rich, productive forest that had developed *in situ*, essentially undisturbed for centuries, or even millenia. It was believed to have reached a kind of equilibrium in the balance of nature, delicately adjusted to its varied natural environments. It was thought that western Europeans had upset this balance by cutting and burning, and that this was forest devastation. Fire, especially, was looked upon as an evil to be avoided. The best-known symbol of this notion is Smokey the Bear.

This entire concept has all but collapsed. Accumulating evidence indicates that most of the forests seen by the first settlers were in their first generation following one or another kind of major disturbance by fire, insects, disease or windthrow. It is becoming apparent that the old forests were scarcely different from the present ones, and that the latter form a far better datum plane for planning than the assumed balanced forests of the theory. And it is probable that there were more and larger fires in presettlement time than subsequently.

Because western Europeans could not be blamed for these catastrophic events, most of the validity has dropped away from the idea that man has been the arch enemy of forest productivity. Most of our forests have not been devastated in the sense used by the committee.

Time has always been the forester's problem. The growth of trees is a slow process, and he has had to make long-term biological predictions. Also he has had to assume, essentially as an article of faith, that people would want his trees when the trees were ready for harvest 50 to 100 years in the future. The committee made its predictions in a closed, inflexible system. In the field of construction materials, for example, they failed to conceive of the phenomenal development of the plywood and chipboard industries, which turn out products that replace lumber for a host of uses and are much cheaper than lumber to process. They can be made of trees which are much lower in quality than those required for lumber, and can be grown in much shorter times. When the report was written, most of our paper was made from spruce. The committee did not visualize any change in this. It wasn't long thereafter that balsam fir was put to use for paper. Not many years later the hardwoods came into use, and at this point the supply of pulpwood became enormous,

because our hardwoods grow rapidly and reproduce profusely after cutting. Now we are hearing a good deal about the production of paper pulp from annual crops, and I haven't much doubt that this will come. If it does, it will alter every phase of our paper-making economy.

Dr. E. M. Gould (1967) has computed a possible effect of further innovation in the process of fabricating wood products from chips. If, he says, all the wood used in the United States each year were converted to these fabricated products, just the annual growth on forests now existing in the northeastern states would cover all needs. This would be the amount of wood represented by only the outermost annual growth ring on the trees.

The committee visualized rising costs for the harvesting and transportation of western timber to "centers of consumption" which they obviously saw as primarily eastern markets. They did not imagine the intricate transportation system that has actually developed in the last 60 years, nor did they consider the possibility of a vast urban-industrial market in the West itself.

The forest is an amazingly flexible, adjustable thing. It is far more amenable to short-term planning than our foresters have dreamed. It can be adjusted to the changing wants of people so long as we do not try to force it into some pattern that we form by projecting beyond the planning horizons of the people. What kinds of demands can we expect them to make? Crooked trees may be just as valuable as straight ones. Clear openings in forested lands may have higher values than they would if they were covered with trees. The committee did not dream of the recreational and aesthetic values that have arisen in the last 60 years. Continued technological innovation can make little trees as valuable as big ones. And if we make most of our lumber out of chips, and most of our paper out of annual crops, huge acreages of forest will cease to have any of the values assumed by the committee to be fixed.

Something of this sort is happening in western Europe where most of the basic ideas for American forestry originated. Svend Heiberg, a Danish forester who was for many years professor of silviculture at the New York State College of Forestry, gave some advice to western European foresters in 1963. He advised them to quit trying to grow commercially valuable wood in a vast strip of country extending from Spain through western France, much of West Germany, the low countries, and southern Sweden. He said that the recreational and aesthetic values in the woodlands of this region far exceeded any that could be gained by investment in the culture of commercial forests.

The Pinchot committee members left no room for people in their equation. They disregarded human adaptability, inventiveness and imagination. The behaviour of the human mind during the last 60 years has reduced nearly every prediction they made to absurdity.

Nowadays we are flooded with predictions. They come to us daily via the news media. The materials with which they deal have been expanded far beyond the forests. We are bombarded with words like "environment," "ecology" and "ecosystem," which connote emotional and aesthetic values that the foresters left out. These are blanket words, used collectively to express the idea that every process which goes on in the world, animate or inanimate,

is related in some highly variable cause-and-effect way to every other process. The old notion of the balance of nature raises its head again when we are told that these great systems of relationship are so delicately adjusted and fragile that if we disturb them we do so at our peril. The imminent doom predicted for our forests now extends to nearly everything, including ourselves. It is the "doomsday syndrome" (Maddox 1972), which is surely not new in the world. The seers of wisdom in every generation seem to have been certain that they were living at the peak of human knowledge, imagination and ingenuity. Having reached these heights, they seem to have been stricken with an occupational disease which caused them to view the future with alarm. There was no way to go but down.

To an amazing extent what we can call environmentalism has become the conventional wisdom of our time. We do not have 60 years of experience that might allow us to assess its predictions. But we can at least stand aside and try to see it in some kind of perspective.

Environmentalism resembles the romantic movement of the 18th century. Both movements began, not as groundswells among vast numbers of common people, but in the more learned and affluent fringes of society. The romantics were reacting negatively to the heady rationalism of the 18th century, and to the industrial revolution which was growing out of it. Our environmentalists show the same reaction to modern science and technology. Both glorify nature (the wilder the better) as a release from the tribulations of mankind, and have idealized primitive man, the noble savage, as the last of the human race to be truly in tune with nature.

Much turns on what people think of when they speak of nature. Is man a part of it, or does he occupy a special niche that separates him from it? The environmentalists are delightfully ambiguous about this, often in the same paragraph. In common thought, however, I suspect that most people see nature as something that is around them, in woods, fields, streams, mountains and plains. They go away from human things to observe and study nature. The recent environmental movement has done a great deal to further this dichotomy, though it surely goes far back in the history of our race.

Wild nature is believed to be good for man, and unless he learns to use it as a therapeutic he cannot avoid his own destruction. He is described as sick, heavily burdened with physical, mental and social ills (Nicholson 1970). His only hope is in some form of back-to-nature movement. The ideas of wilderness and natural areas play a large role in this conception, but with a heavy load of ambiguity attached to them. Though they are thought to be man's only hope they are to be used by selected people.

We are told that wild nature is harmonious, and that it is good, or at least neutral. Man is regarded as having contributed only disharmony to it. Some believe that he began his destructive progress through the world when he first scratched up some soil in which to plant crops (Darling 1960).

A sense of urgency runs through the movement. The end of civilization, or even of the world, is near at hand. There isn't much time left. Even if the common man were able to save himself, after a long period of individual and

social evolution, there is not time enough to allow him to try it. We are told that he must be “cajoled, led or driven” to it by an elite corps of experts (Nicholson 1970).

The environmental movement has many of the characteristics of a revealed religion. It has its major prophets of doom such as Thomas Malthus and George Perkins Marsh. Its later prophets have extended and embroidered those early jeremiads under such titles as *Our Plundered Planet*, *The Road to Survival*, *Deserts on the March* and *Silent Spring*. A space-age version carries the implication of doom in the limited resources of *Space-Ship Earth*. There is a self-appointed evangelical priesthood, like the shamans of old, which makes brilliant use of its own charisma and of the propaganda machine at hand in the communications media. Then there are the lesser clergy and the lay preacher/converts who carry the message to the pagan public. There are creeds galore, and there is heresy, for nearly every pronouncement that comes down from above is arguable.

A preoccupation with the idea of sin permeates this quasi-religious structure. The human race is pictured as having continuously sinned against nature and itself, getting into steadily worse messes, and never learning by experience. Man is regarded as a sort of willful pawn, living at the mercy of his environment and continually biting the hand that feeds him. I have found in the environmentalist literature descriptions of human relations with a natural environment in such terms as the following: humans are accused of thoughtlessness, cupidity, ulterior motives, carelessness, defective personalities and ignorance.

There is an implication that man is the only inherently vile and sinful living thing, and that whatever he does is more likely to be wrong than right. It sounds to me like the old doctrine of original sin, which is deeply embedded in the Judeo-Christian religion.

Sometime in the misty past a human-like being made the greatest discovery that our race ever made. He discovered himself. Herbert Muller (1952) has called it the beginning of consciousness. We can never know the sequence of impressions of which man first became conscious. An early one may have been fear, but I suspect that even earlier was a glimmer of what his remarkable brain could do for him. Along with fear and distress he also began to know the feelings of satisfaction and happiness and how to produce them. I think it is possible that the old Hebrews who wrote down the story of the Garden of Eden were basing it upon some ancient and hazy tribal memory of man's first consciousness of himself. We are told that Adam and Eve got their knowledge by eating the fruit of a certain tree, which they had been forbidden to do; and for doing it they were banished. Their sin was not against themselves, or against nature as represented by the Garden. Rather, it was against a God who was jealous of his own omniscience. But as we have all been taught, the idea of original sin goes far beyond the acquisition of knowledge. We have been told that all of us were “born in sin,” which implies that the process of human procreation is in itself a sin.

I am not enough of a biblical scholar to trace the origin of this notion but

the historian Herbert Muller (1952) could not find it in the Old Testament. He thought it began with St. Paul. Barbara Tuchman (1978), in her study of 14th century Europe, thinks that it was firmly installed in Christian dogma by St. Augustine. Whatever its origin, it is one of the strangest aberrations that the human mind has ever come up with. It makes a cardinal sin out of man's normal and pervasive impulse toward the perpetuation of his race—an impulse that he shares with every other living thing. It decries the animal heritage of man, separates him from the rest of nature, and gives rise to prevailing ambiguities in the environmental conventional wisdom of our time.

During most of my adult life I have been a student of wild vegetation and of the kinds of plants that make it up. I have never been able to find the harmony that is assumed to be there. I think it is merely another expression of the so-called balance of nature, which has been a millstone tied to ecology for over a century. All my experience of wild nature tells me that it is (and always has been) in a state of imbalance, disharmony and uncertainty. Civilized man has just added another kind of disturbance to the long list of cataclysms that the organic world has been living with since it came into existence. In this light the questions as to whether or not man is a part of nature, and whether or not he is the author of all the disharmony in nature, become rather pointless.

Adam and Eve leaving the garden are always pictured as bent and rather bedraggled figures, weeping and burdened with woe and fear. When they ate that fruit a whole new outlook on life appeared. They saw what they might be able to do if they could get out of that garden and exercise their new-found knowledge and curiosity. I don't think they were banished. I think they ran away. Of course they were frightened. Everything in their new world was risky and uncertain, as it still is. But I think they were far from depressed by it. They were exhilarated.

Anyone who finds himself on the outer fringes of knowledge with only the unknown ahead of him, understands the meaning of this allegory. He knows that if he goes on he will be alone, dependent upon his own judgment or upon the validity of his guesses. His fears are legion. He must learn to live amicably with uncertainties, not only in the field with which he is working, but also in his reputation among his peers. He knows that it may be a long time before anyone ventures to follow him and check his findings.

If at this crucial point he turns back to the safety of mapped knowledge he consigns himself to the crowded ranks of those who follow rather than lead. If he manages to sublimate his fears and goes on in spite of them, he has a chance to experience the exhilaration that comes with the subjection of some part of the wilderness of the unknown.

The foresters came to grief because they left out of account the most important single natural resource we have—one that affects our use of all others—"the contriving brain and the skillful hand of man" (Malin 1955). The environmentalists do not merely leave it out. They do not trust it, and they try to suppress it. Their major tool of suppression is fear, especially fear of the unknown and of making mistakes as we approach it. But people have always made mistakes. It is the way we learn; and we *do* learn by experience. We

wouldn't be here if we didn't.

Most of the trappings of environmentalism can, I think, be disposed of as intellectually groundless, or as fanatical aberrations. But we should look carefully and critically at the tendency of the movement as a whole to disregard, denigrate or even suppress our impulse to stifle our fears, to take chances and dangerous risks, and to go off the map if for no other purpose than the fun of seeing what we can see.

Conventional wisdom, valuable as it can be in achieving some kind of continuity and balance in our affairs, can in time become a dam holding back the flow of our development. Bernard DeVoto, in his study of the history of American geographical knowledge (1952), expressed this idea as follows: "In the infinitely difficult act of thinking, nothing is more difficult than to separate what is known from what is not known—unless it is to understand that the separation must be made. The pitfalls ready-made in the material with which the intelligence must work are not more formidable barriers to the achievement of knowledge than the traps intelligence sets for itself." He illustrated this point repeatedly from the history of the exploration and settlement of the North American continent. He demonstrated that the whole process was impeded throughout by projections from the knowledge of the day, made by the greatest geographers of the day.

The richest farm land in North America (and perhaps in the world) is in Iowa, southern Illinois, northern Missouri, eastern Kansas, southeastern Nebraska and southwestern Minnesota. When this region was first seen by Europeans it was covered with grasses. It was later known as the "humid" or "tall-grass" prairie. The first agricultural settlers carefully avoided the prairie land. They laboriously removed the forests from the river valleys, and planted their settlements there. James Malin, the great historian of the American grasslands, has demonstrated that settlement of the prairies was held up for at least a generation because the conventional agricultural wisdom of the time in western Europe and the Atlantic states held that any land that didn't have trees growing on it could not be fertile enough for crops (Malin 1956).

Chapter VI

OPTIMISM

We have seen in much of the foregoing that Raup does not mince words. In this last chapter we pull together some short segments which show that even though he has written about trends, problems, and blind alleys, there comes through an essence that is greater than the sum of the parts: Man can create solutions to problems that seem overwhelming.

LETTER FROM HUGH M. RAUP 1979

I was criticized for being pessimistic in the "Trends" paper! But I have never been able to see that I was. A good deal of that paper is about inductive vs. deductive methods of reasoning in plant geography. Perhaps I was called pessimistic because I expressed a preference for the first of these pursuits, which gave no expectation of final solutions for the problems of plant geography. It is a slow business, and involves endless trial and error which much of modern science seems to write off as old-fashioned. It is open-ended and its thought is "reticular" rather than "linear." It gives human minds the widest latitude for the use of their unique capacity to sense relationships among a welter of observed facts. Thus it is enormously productive of innovative ideas.

The ecologists started their career, not with mere facts, but with the assumptions that a cause and effect relationship existed, and that they knew what it was. It was the notion that the environment controlled all living things, which grew out of the great mass of later 19th century teleological interpretations of Darwin's theories of adjustment and natural selection. When they did this the ecologists' thought became "linear," in a "closed system." It has taken them down one blind alley after another. They have operated by piling up multiple assumptions, all of them stemming from the first one. Stanley Cain once called this mass of assumptions the "excess baggage" that ecologists lugged around with them.

I suppose my optimism is based in my "sense of history." In every era or period I have studied there have been people who viewed their fellow men and their future with alarm, and there always seemed to be good reason for their pessimism. Our race has rushed into innumerable blind alleys, and experienced serious setbacks galore. But when everything is

summed up I can see only steady improvement of our lot. I can see no reason why it shouldn't continue.

We have seen much of this paper earlier in the section on environmental determinism. In this selection, written in 1942, Raup's optimism first shines through.

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What are the prospects of formulating principles and generic concepts in plant geography as it is here conceived? In short, what prospect is there of reaching a resolution of the complex interplay of influences in a geographic area? We can expect such principles and concepts in some of the systematic elements which contribute to the complex. There are some generalizations with regard to climatic and edaphic factors, physiological requirements of plants, organizational and developmental characteristics of communities, and habits of variation among species—all of which supply materials and inspiration for study of the regional or areal unit. But it seems necessary to realize that in regional studies principles may be arrived at with great difficulty or not at all. Inductive logic gives us no expectation of anything beyond approximation.

Hartshorne has stated our limitations very clearly: "One major difficulty lies in the fact that the integration of phenomena which we must study in areas is an integration of a large number of independent, or semi-independent factors. Consequently we seldom have to do with simple relationships—e.g., rainfall to soil, temperature to crops, etc. Theoretically we might follow the logic of the systematic sciences, by assuming that all other conditions remain the same, but we have only the laboratory of reality in which to study these features, and in that laboratory the other elements do not remain the same, except perhaps in a very small number of cases, and we have no way of making them remain the same. Indeed, even if we knew the theoretical principles governing the relation of each individual factor to the total resultant, in the case of such complex resultants as cultural features, a principle which attempted to state the sum total of all the relationships, each in its proper proportion, would be far too complicated for us to be able to use. This is a general difficulty that applies not only to all the more complicated aspects of the social sciences, but also to many phenomena in the natural sciences. Even if one knew all the principles and had all the data, the solution would be involved in a mathematical equation so complicated that no finite mind could solve it" (1939).

It may be said that this is a defeatist view—that by denying so much of the expectation of final solution in the complex problems of causation we would eliminate much of the inspiration and incentive to further research. It would have to be admitted, however, that one of the most active, productive and persistent phases of plant geography has been thriving upon inductive methods for many generations. It has never hoped for more than an approximate solution to the problem of ultimate causation. The same would have to be said of other natural sciences such as geology and meteorology, and

From Hugh M. Raup 1942c. Trends in the development of geographic botany. *Ann. Assoc. Amer. Geogr.* 32:319-354.

of most of the broad field of plant and animal morphology. To hold that the logical methods of these sciences were “defeatist” would be denying the quality of logic that gave us the Renaissance and the development of nearly all of modern science.

Nearly a quarter century later, in 1964, Raup's optimism is still evident and one senses a feeling of impatience toward the "prophets of doom."



Ecological and conservation thought at the turn of the century was nearly all in what might be called closed systems of one kind or another. In all of them some kind of balance or near balance was to be achieved. The geologists had their peneplains; the ecologists visualized a self-perpetuating climax; the soil scientists proposed a thoroughly mature soil profile, which eventually would lose all trace of its geological origin and become a sort of balanced organism in itself. It seems to me that social Darwinism, and the entirely competitive models that were constructed for society by the economists of the 19th century, were all based upon a slow development towards some kind of social equilibrium. I believe there is evidence in all of these fields that the systems are open, not closed, and that probably there is no consistent trend towards balance. Rather, in the present state of our knowledge and ability to rationalize, we should think in terms of massive uncertainty, flexibility and adjustability.

Traditional emphasis in American conservation has been upon expected physical scarcity in our natural resources. We borrowed this from the Old World, forgetful that it had little meaning in the midst of our abundance. More important, we were caught in systems of thought that did not allow for uncertainty, and for the unpredictable effects of innovation throughout the whole society that would use the resources. Our experience with forests, for example, has made us acutely conscious of the preference for capital management over land and forest management. There is increasing evidence that this preference applies in other resource areas as well (Brinsler 1962). I can suggest only an outline of the way in which ecological theory, as I have tried to recast it, might relate to the resource problem.

When a resource is foreseeably in abundant supply, capital investment to increase the supply will not flow. On the other hand when the resource is scarce, decisions will be made to invest capital for its increase, or to produce substitutes for it. Technological innovation in the use of, and substitution for, natural resources now goes forward rapidly, and the society in which this process operates is evolving its institutions along with its technologies. Our experience of the last half century suggests that prediction of demand for the resources beyond one or two decades can have no precision. When I use the term "scarce" I propose that it will apply to all kinds of values, tangible or intangible.

There is a strong economic flavour in the views I have just expressed. It is necessary to recognize some fundamental weaknesses in them. They carry an assumption that we are dealing with measurable quantities, when this is only partially true. Further, they assume that production schedules for natural resources are all equally well known, which is far from the truth. We are

From Hugh M. Raup 1964a. Some problems in ecological theory and their relation to conservation. *Jour. Ecol.* 52 (Suppl.):19-28.

conditioned to think that the only measures of value which have much precision are those that come from the market place, but we find ourselves dealing with a vast array of resource values that do not go through the markets.

With our capacities to predict severely limited by inadequate measuring devices, by lack of knowledge of the resources themselves, and by the rapidity of innovation, it is probably reasonable to strive for efficiency in resource management only in the short run. Uncertainties in the long run call for the greatest possible flexibility in resource use. It is commonly assumed that these two objectives are incompatible, but I think we have reason to believe that they are not so in all cases.

Our natural vegetation in America, even before the coming of Europeans, seems to have lived in a continuing state of major readjustment. Its history of disaster had atomized it, and this I conceive to be one of the greatest blessings we received when we inherited it. In our material resource affluence, one of our largest problems is to spread the opportunity for gain and the risk of loss over many kinds and conditions of resources. This need is made essential by the constantly changing demands for the resources. The natural vegetation, as we found it, was ideally conditioned for manipulation and use in this pattern. Because of its abundance and atomization, both in kind and condition, it is adjustable to remarkably short-term planning so long as we do not attempt to achieve stability or uniformity in it.

I propose that we should plan ahead only so far as we can see with some degree of precision, and then readjust our plans at frequent intervals. We can be assured that there will never be enough facts available to give these plans any finality, and that we shall always be making judgments based upon probabilities. At every point of decision we will make use of whatever knowledge and measurement of value we can acquire, testing each for relevance to the point at issue as it relates to the frame of reference existing at the time. What we do with our capital or with our natural resources will rest upon these decisions.

Nicholson's book, The Environmental Revolution, was a burr under the saddle for Raup. In this review Raup takes issue with the author's views. Raup's optimism comes through loud and clear.

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People who have preserved some reverence for their ancestors will react negatively to this author's many pejorative statements and implications. He extrapolates backward in time with abandon, gratuitously assigning to human users of the land throughout the ages the same attitudes he believes to be responsible for the present sad state of affairs—carelessness, thoughtlessness, cupidity and ulterior motives. This view follows from the basic assumption that people in general, whether they know it or not, are and have been congenitally vile and sinful.

Closely related to these conceptions is the problem of time. The underlying motive in the lives of men, along with that of all other organisms probably is, as Schweitzer proposed, the "will to live." For most people this motive is limited in time by the life span of the individual. Most of the people in this work-a-day world, however, know in some measure that their survival and well-being depend upon their being adjustable to relatively short-term, unpredictable changes in their living conditions. It is probable that most conservationists' time scales have been more effective than anything else in making their opinions unacceptable. There is more than humor in the long-standing joke among foresters that they seldom live long enough to have to justify their mistakes. Their planning horizons usually are far beyond those of most people. It was predictable that Mr. Nicholson would show some preference for foresters among those who practice conservation.

Ecology plays a large role in the author's thoughts and proposals. His suggested elite corps of experts who are to advise on future environments seem to be some kind of ecologists. He appears to have infinite faith in the capacity of ecology to solve the complex problems of organism-habitat relations. Thus the field becomes in his mind the most promising handmaiden for conservation. On the other hand, immured in Chapter 10 is a critical review of the present status of ecology as a branch of science. He points out that in spite of its announced purpose of being "a means of dynamic and synoptic interpretation of the functions and relationships of living creatures within their natural environment," and in spite of half a century of growth and development, the expected results have not appeared. He compares the backwardness of ecology to the vigour and productivity of the physical sciences and molecular biology in the same period, and places most of the blame on the ecologists themselves. It is doubtful if this is entirely just, for the ecologist by definition is faced with a problem of interacting variables that is complex beyond anything that can be solved by presently known means. No experimental methods have yet been found that will deal realistically with more than a small fraction of it. In short, the human mind has not yet learned

From Hugh M. Raup 1971. *The environmental revolution*, by Max Nicholson. Review in *Jour. Ecol.* 59:312-316.

to cope with it except in terms of rather broad elements of probability. The author shores up his faith in ecology by repeated recourse to computerization and model-building, though he must know that no model or computer program can produce anything not put into it from the mind of its builder. Probably man has been facing this problem as long as he has been conscious of himself as man, for he has always had to make decisions. I am lost in wonder, not at the mistakes his forebears made and the damage they did by their decisions, but at the surprising number of times they were successful in view not merely of the scarcity of data available to them but also of the bewildering maze of conflicting data they had to evaluate and synthesize. Borrowing an expression from the author, and listening to the music in his book rather than the words, one gets the impression that man is regarded as a sort of wilful pawn, living at the mercy of his environment but persistently biting the hand that feeds him. This is reminiscent of the environmental determinism that pervaded many fields in the latter part of the 19th century and the early part of the 20th. It was the conventional wisdom in the period when ecology as we know it was founded, and ecologists have never completely rid themselves of it. True to this tradition, there is almost nothing in Mr. Nicholson's book about modern genetics, which has shown phenomenal growth in the last 70 years. It has demonstrated that every organism thus far studied cytogenetically brings into its relationship with environment a set of characteristics and capacities for adjustment that it inherits from its parents. These characteristics are not altered by the immediate environment, though by mutation, hybridization and selection they may change in the course of several to many generations. Thus an organism's survival in a given environment probably depends as much upon its ability to adjust as upon the impact of the environment itself.

We have no reason to exempt man from this generalization, but it must be said that he is probably the most flexible and adjustable organism the world has ever seen. He achieves this because he can remember, reason, and plan. The purveyors of wisdom, the experts, in every generation seem to have been virtually certain that they were at the peak of human knowledge and capacity, or would very soon reach the peak. It is inevitable that having achieved these heights they should succumb to their occupational disease of viewing the future with alarm. A glance backward shows clearly that they have been wrong far more times than they have been right, for they have had no way of knowing what the human mind, man's greatest resource, would come up with. Most people, through countless generations of experience, seem to sense their unique intellectual powers. They persist in exercising their human prerogative of experimenting with their human and non-human environment. In spite of all their obvious mistakes they remain confident that in the event of a real demonstrable crisis they have inherent capacity to deal with it, whether it involves their social and political institutions or their external environment. Who can say that their confidence is misplaced? We know of no limits in the innovative capacity of the human mind.

Young ecologists at Rutgers in 1972 heard Raup express optimism. As one who attended that lecture I vividly remember young graduate students saying in effect, "This is the first optimistic lecture I've ever heard." In this last excerpt Professor Raup captures the essence of the Newtonian admonition—we stand on the shoulders of our predecessors.

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My own ideas about these things must by now be evident. To state them more succinctly I can do no better than quote from the last sentences of two books by authors who have avowed their faith in humanity more cogently than I can. One is a journalist, Edmond Taylor (1969), who has said: "My confidence in the schemes for human betterment that I have seen my generation put forward tends with age to grow increasingly conditional and limited; my faith in man's potential for self-betterment grows steadily stronger and more absolute. That is why—paradoxical though it sounds—after 40 odd years as a watcher of men in an age of crises I believe more than ever that humanity and human civilization on this planet have the capacity to outgrow the crises that their own growth periodically generates, and will therefore keep on growing."

The other is by a historian, James Malin (1956), who said: "The potentiality of man to solve problems has not yet been exhausted, and the potentiality of the resources latent in the earth to be brought into the horizon of usefulness is still beyond the power of man to conceive. The key to the situation is not the earth, but the minds of men determined to realize their own potential. . . ."

From Hugh M. Raup 1972. An address to the Ecology Program, Rutgers University.

Afterword

Hugh Raup has rambled over Ohio, the Mackenzie Mountains, Massachusetts, Honduras, New York and other areas, using his eyes and collecting plants. He has read very deeply in many fields. He is familiar with the analytical methods of generations of natural scientists, and of many of those persons who philosophize on the condition of man. It is his habit to look at evidence himself, and to draw his own conclusions. His method of approaching the truth is careful, and is inductive. He is impatient with all fashionable determinisms, and distrusts from the start any explanation of a real situation that is based upon a pre-existing hypothesis.

The fashion of our times appears to be to seek certainty, and then to cry it from the housetops, on the principle that if others agree, one must be right. We see otherwise sane persons proclaiming a variety of holy grails, each simple and satisfying. To meet these criteria each holy grail must be easy to understand and capable of explaining a great deal of reality. There is something about "Nature" as a setting for certainty that is particularly appealing to members of our society.

Solemn and respected citizens in our culture have shifted their attachment from preservation of the gold standard and the delicate equilibrium of the price system (who remembers "the invisible hand?"), to preservation of endangered species and the delicate equilibrium of whatever natural system in which the citizen sees himself a participant. From a blind hostility to "government intervention" we find such individuals now seeking aid of governments at all levels. That foreign interference which used to be such a threat to the finely-tuned balance of the price system, is now the chosen protector of the delicate balances perceived to exist in swamps, river systems, oceans, "wilderness" areas, and neighborhoods.

Hugh Raup doubts the usefulness of "competition," "community," "succession," "climax," and "ecological niche" as things to look for on the ground. These for him are reified bits of someone's deductive theories.

Raup has found, rather, individual organisms, each trying to take root and to grow where its seed has fallen. Raup knows what can happen to a lonely seed, dropped by a parent who can do little more for it. Some fall on barren ground, others lack adequate light, air, warmth, moisture, nourishment, isolation from other plants seeking the same life-supporting resources, herbivores, the accidents of flood, fire, winds and feet.

Raup is a member of a small group at Harvard who called themselves the scholars of the here and now. All worked inductively. This takes courage.

Hugh Raup's career accomplishments, stated here in his own words, offer

the best kind of educational materials for those who are motivated to study "the environment." This for two reasons.

First, there is no environment without an organism at the center of it. There are as many environments as organisms. He who would study his own environment would be well advised to realize this—that his environment is his alone, exactly like the environment of no one else. Further, what his environment is, exactly, can be comprehended only by himself, for his own perceptions will govern the manner in which he reacts with it.

Second, one is well advised to begin with what one sees, and then proceed with the aid of the tools offered by the traditional academic disciplines, selecting from each just as much as appears useful in understanding the reality at hand. One need not be distracted by the shrill cries from peddlers of instant deductive explanations. These persons hadn't the time or perhaps the inclination to look the evidence in the face for themselves. Theirs are the instant solutions, particularly viable perhaps because they pluck strings within all of us of sympathy with "Nature." What these solutions do least of all is tell us what "Nature" is, or how we each as an individual can most happily find an accommodation with it.

—Calvin W. Stillman

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BIOGRAPHY

Hugh Miller Raup's first botanizing surely came on trips over the family farm near Springfield, Ohio. He was born there in 1901 and graduated from Wittenberg College in 1923. During his undergraduate years he spent a summer at Lake Laboratory, at Put-in-Bay, on Lake Erie. Graduate work at the University of Pittsburgh included field studies in western Pennsylvania and in British Guiana. He was awarded the Ph.D. by the University of Pittsburgh in 1928. Honorary degrees have been bestowed by Harvard (A.M., 1945) and Wittenberg (D.Sc., 1968).

A 1925 trip to Glacier National Park initiated a series of 17 summers studying arctic and boreal vegetation. The studies encompassed the flora and the distribution of vegetation assemblages. The sites were in the Mackenzie River drainage basin in northwest Canada, along the Alaska Highway from Dawson Creek to Fairbanks and in northeast Greenland. At intervals during the over half-century career there have been excursions into New England, New York, southern Utah, Cuba and Central America to study floristic and phytogeographic problems.

Wittenberg College appointed Raup as instructor upon his completion of the A.B. degree and later appointed him as assistant professor when he completed the A.M. at Pitt. He served at Wittenberg until 1932. Appointments as a research assistant and then associate at the Arnold Arboretum at Harvard preceded his appointment as an assistant professor in 1938. He was promoted to an associate professorship in 1945 and made full professor in 1949. From 1946 until his retirement in 1967 he served as director of the Harvard Forest. The last eight years of that tenure he was Bullard Professor of Forestry. From 1967 to 1970 he was Visiting Professor of Geography at the Johns Hopkins University.

Hugh and Lucy Raup live on the edge of the village common, Petersham, Massachusetts.



Photo Fabian Bachrach

Hugh Miller Raup